



## Original Investigation

## Diets of three sympatric Neotropical small cats: Food niche overlap and interspecies differences in prey consumption

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## ARTICLE INFO

## Article history:

Received 8 March 2010

Accepted 5 September 2010

## Keywords:

*Leopardus tigrinus**Leopardus pardalis**Puma yagouaroundi*

Food choice

Coexistence

## ABSTRACT

Dietary investigations of sympatric felids are means for understanding how closely related species deal with food resources in a potentially competitive scenario. The diets of the oncilla *Leopardus tigrinus*, the jaguarundi *Puma yagouaroundi* and the ocelot *Leopardus pardalis* were studied through the analysis of scats in Araucaria Pine Forest with Natural Grasslands of southern Brazil. Small mammals comprised the bulk of the diets of the three felids, followed by birds and reptiles. The smallest food-niche overlap index was 0.84, indicating that these felids shared an important portion of their food resources. Inter-species differences were detected in the consumption of the most frequent rodent prey; *L. tigrinus* was the only species that consumed all the most frequent rodent prey differently from the rate expected from their abundances. Although these findings suggest competitive interactions, with the oncilla being the most subordinate species, further experimental investigations are necessary to elucidate more precisely how these syntopic felids coexist. The effects of sample size and its influences on the evaluation of the diets of the felids, especially of the ocelot, are discussed. We compare our data to a previous study in the same area, to account for the possible influences of biased sampling and uneven distribution of food resources on the diet of the ocelot. The opportunistic feeding behavior and the abundance of their primary prey (cricetid rodents) seem to allow these small cats to be resilient despite severe anthropogenic disturbance in the study area. We further suggest guidelines for future studies in the study region, in order to understand the dynamics of mammalian carnivores demography.

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## Introduction

All felid species share specializations for capturing and killing live prey (Sunquist and Sunquist 2002). Where felids live in sympatry, such as in most of the Neotropical domain, the species differ among themselves especially in their body size and size-related traits (Kiltie 1984). As ecologists have often acknowledged, this body-size differentiation among sympatric felids enables differential food exploitation, and hence potentially reduces intra-guild competition (Rosenzweig 1966; Davies et al. 2007).

The oncilla *Leopardus tigrinus* (Schreber, 1775), the jaguarundi *Puma yagouaroundi* (Geoffroy, 1803) and the ocelot *Leopardus pardalis* (Linnaeus, 1758) are small Neotropical cats with a wide range of geographic overlap in the South American continent (Sunquist and Sunquist 2002). These species have discrete body weight distribution: oncilla 1.8–3.4 kg; jaguarundi 3.8–6.5 kg and ocelot 8–16 kg (Sunquist and Sunquist 2002).

Empirically, the discrete distribution of the body sizes of these species will hardly imply diet segregation, because for instance, small mammals comprise the bulk of the diets of most small Neotropical cats (Emmons 1987; Konecny 1989; Ludlow and Sunquist 1989; Facure and Giarretta 1996; Wang 2002; Bianchi and Mendes 2007; Abreu et al. 2008). Because small mammals are also the most abundant mammalian prey in tropical forests (Solari and Rodrigues 1997), one can presume that these predators hunt opportunistically (Jaksic 1989). However, beyond the random influence of encounter rates on food acquisition, different felid species living in sympatry can capture their prey selectively, as for instance, to minimize the negative effects of intra-guild competition (Durant 1998; Pierce et al. 2000; Ray and Sunquist 2001; Novack et al. 2005; Hayward and Kerley 2008).

To our knowledge, there are no previous studies concerning the food-niche characteristics of these felids in a syntopic context. The objectives of this study were to (1) describe comparatively the diets of the oncilla, the jaguarundi and the ocelot and to (2) compare the frequency of some small mammal species in the diet of the three felids with their relative abundance in the habitat. Further, we contrast our data with a previous study that described the diet of ocelots in the same area (see Abreu et al. 2008), and dis-

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cuss possible mechanisms that allow the coexistence of these three species.

## Material and methods

This study was carried out in the Devonian Scarp of the state of Paraná, Southern Brazil (25°20'–25°29' S and 49°39'–49°42' W). The local climate is subtropical, mesothermic, and constantly humid with mild summers. The mean annual temperature varies from 14°C in the winter to 21°C in the summer, and the mean annual rainfall averages 1600 mm with no marked seasonal incidence throughout the year (SEMA 2004). The terrain in the Paraná Devonian Scarp is rugged, and altitudes range from around 900 m to 1142 m above the sea level (Maack 1981).

The Paraná Devonian Scarp contains interfaces of two distinct landscapes: natural grasslands (Campos Gerais) and Araucaria Pine Forest (Mixed Ombrophilous Forest). The forested regions are associated with streams, hillsides and valleys, with the Paraná Pine *Araucaria angustifolia* as a characteristic element (Maack 1981). Many locally important species of trees have been intensively logged and are currently rare (Maack 1981). Natural Grasslands are dominated by Gramineae species, herbs, scattered shrubs, and sparsely distributed trees. These natural grasslands have been extensively converted to grazing fields and alternating crops, and are currently restricted to small fragments and undergoing alteration with the expansion of dispersing exotic *Pinus* species.

Scats were collected from three different localities within the Paraná Devonian Scarp: Bugre District, São Luís do Purunã District, and Santa Rita Ranch. We considered all these localities as a single sampling area, because their close proximity precluded assumption of sample independence (5–10 km between sites). We walked an average of 12 km per locality every month from April 2006 through March 2007, in order to search for carnivores' fecal samples in forest fragments, natural grasslands, and pasture fields. Fecal samples were collected, stored, and taken to the laboratory for identification and analysis.

Scats were identified exclusively by microscopic analysis of the cuticle patterns of the guard hairs (Quadros and Monteiro-Filho 2006). We compared guard-hair cuticle patterns of specimens in reference collection (MHNCI) with those found in the scats. A total of 363 scats was collected during the study, but only 108 (30%) could be identified unambiguously to one of the three felid species investigated, resulting in 36 oncilla scats, 51 jaguarundi scats, and 21 ocelot scats. Most of these scats were collected during drier periods (86% collected between March and November), because the steady rains during the summer removed or degraded a high proportion of the dropped scats.

The scats collected were washed and dehydrated, and food items were separated in the following categories: hair, bones, teeth, nails, feathers, and scales. Food items were identified to the lowest possible taxonomic level through comparison with voucher specimens in local collections (Coleção Mastozoológica do Departamento de Zoologia da Universidade Federal do Paraná, CCMZ-DZUP; Coleção de Mamíferos do Museu de História Natural do Capão da Imbuia, MHNCI; and Museu de Zoologia da Pontifícia Universidade Católica do Paraná, MZ.PUC.PR). Mammal species were identified to family, genus, or species levels, depending on the quality of the diagnostic structures. Feathers of birds were frequently unidentifiable even at ordinal level, and therefore all the specimens were identified as Birds. Reptiles were identified by comparing scales and jaw fragments.

To investigate the cumulative behavior of each individual prey item as a function of sample size, we randomly selected five scats, analyzed the FO (see below) of the food items, selected five more and analyzed the food items, and so on until all the scats had been

analyzed (Azevedo 2008). This iterative process allows the identification of a minimum number of items necessary to represent the most frequent prey taxa.

We estimated the minimum number of individuals consumed (MNI) by counting the teeth of mammals. We assumed birds and reptiles to have MNI equal to 1, because the feathers and scales encountered in scats were scarce and indistinguishable (see Ray and Sunquist 2001). Food items were represented as frequency of occurrence (FO) (the percentage of scats in which one food item was found) and percentage of occurrence (PO) (the percentage of one item in relation to the total MNI). Levin's standardized niche breadth and Pianka's food overlap indexes were calculated for the three species using the software Ecological Methodology (Krebs 1999).

Abreu et al. (2008) described the diet of ocelots within the same sampling area as the present study. Therefore we performed G-tests for goodness-of-fit to investigate if differences in the use of prey-size categories would appear by including the data from Abreu et al. (2008). Prey categories were arranged in size classes according to prey mean body mass ( $\leq 100$  g; 101–1000 g;  $> 1000$  g), as described in species accounts in the current literature (Reis et al. 2006; Bonvicino et al. 2008).

In order to estimate the relative abundances of some small mammal species in the habitat, we applied trapping efforts systematically from September 2006 through August 2007 (seven months concurrently with the collection of fecal samples). We used 100 Sherman live traps (50 traps with dimensions of 12 cm  $\times$  14 cm  $\times$  30 cm and 50 traps with 8 cm  $\times$  9 cm  $\times$  18 cm) per night. Each month, one locality was sampled during four nights of trapping, for a total of 400 trap-nights per month and 4800 trap-nights after 12 months of sampling. In each locality, we distributed the traps in two ways: (1) five parallel rows spaced every 10 meters, each row containing 10 traps spaced every five meters; and (2) one linear trail containing 50 traps spaced every ten meters. All traps were baited with banana and bacon. We checked all the traps each subsequent morning, to replace the bait and carry out the post-capture procedures. Individuals captured were weighed, sexed, identified to species level, and released. Chi-square tests were applied to detect differences between the relative abundance of small mammals in the diet of the felids and their relative abundance in the traps. We only included the small mammal species with a frequency in the traps  $\geq 5$ , to generate adequate numbers for calculating the expected frequency. We further calculated a simultaneous Bonferroni confidence interval to detect which prey taxa accounted for the statistical differences (Byers et al. 1984). All tests were considered significant if  $p < 0.05$ .

## Results

We found 19 prey items altogether in the diet of the three felids, which were represented by a minimum number of 276 prey individuals (MNI) (Table 1). Rodents of the family Cricetidae were both the most frequent and most abundant items for the oncilla (FO = 86.1%; PO = 82.3%), the jaguarundi (FO = 96%; PO = 77.6%), and the ocelot (FO = 100%; PO = 92.4%). Birds were also frequent, except in the diet of the ocelot (Table 1). Plant material was sporadically ingested by all three felids, but was excluded from the analysis because there were only small amounts of grass leaves, and we assumed that this material was accidentally ingested despite the possibility of its digestive usefulness. The evaluation of the cumulative frequency of occurrence of the most important (PO  $\geq 5\%$ ) prey items revealed that the relative contribution of these prey types was represented in 30 scats for the oncilla, 35 scats for the jaguarundi and 15 scats for the ocelot (but see Discussion).

The oncilla had the widest Levin's standardized niche, followed by the jaguarundi and the ocelot (Table 2). The food-niche over-

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