



Research Article

What should I eat: feeding behaviour of puma in a Brazilian protected semi-arid area

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Abstract

The feeding behaviour of the puma (*Puma concolor*) is a fundamental characteristic that guarantees its evolutionary success. It is one of the primary factors associated with its widespread distribution, including hostile regions like the Brazilian Caatinga, a semi-arid biome. We investigate the feeding ecology of the puma in a protected area located in the Caatinga by describing its diet and evaluating patterns of prey selection mediated by energetic trade-off and meeting probability. We found ten prey species consumed by pumas, with the collared peccary (*Pecari tajacu*) representing almost half of consumed prey items. Prey selection by puma was correlated with an overlap of activity patterns between predator and prey, suggesting that meeting probability is an important topic in its foraging ecology. Due to the predominance of a single prey species, the puma showed a narrow niche breadth (standardised Levins' index = 0.113), positing the collared peccary as a critical element in the persistence of puma in the area. The puma is commonly described as a generalist predator since it feeds on a broad range of species across its distribution area; however, our results and recent literature suggest a more specialised diet at a local scale. This apparent contradiction could indicate that the puma diet is subject to a hierarchical organisation on a spatial scale, in which different local specialisations and adaptive strategies would lead to a generalist feeding behaviour at the distributional scale. It is important to highlight that we did not find any evidence of livestock depredation, which is a significant result from a conservation perspective, which favours puma conservation in the study area.

Introduction

The puma (*Puma concolor*, Linnaeus, 1771) has a high adaptive potential to different ecological conditions (Zanin and Neves, 2019), which has enabled its long-term survival across a variety of environments throughout time (Johnson et al., 2006) and space (IUCN, 2017). Among the survival strategies of this species, the feeding behaviour has been a crucial factor in generating trade-offs leading to its evolutionary success (Iriarte et al., 1990). This was one of the factors responsible for its persistence through the Pleistocene mass extinction (DeSantis and Haupt, 2014) and its widespread distribution, which ranges from cold to semi-arid regions, like the Rocky Mountains (USA) and the Brazilian Caatinga, respectively (IUCN, 2017). In this context, understanding the feeding behaviour of pumas is fundamental to recognising their adaptive mechanisms and the ultimate ecological pattern derived from this behaviour (Iriarte et al., 1990). *Puma concolor* is considered a generalist predator because it can predate a large number of species, with mammals being the most common prey (Iriarte et al., 1990). However, the puma usually exhibits a specialist feeding behaviour at the local scale, with high consumption of few prey species and close to half of all consumed items belonging to a single species (e.g. Ávila-Nájera et al., 2018; Foster et al., 2010b; Lowrey et al., 2016; Soria-Díaz et al., 2018). Pumas' prey specialisation varies according to the studied population, ranging from large-bodied species, like peccaries and deer (Ávila-Nájera et al., 2018; Lowrey et al., 2016), to smaller ones, in-

cluding armadillos and agoutis (Foster et al., 2010b; Gómez-Ortiz et al., 2015; Soria-Díaz et al., 2018).

Despite its ecological plasticity, the puma has population declines due to habitat loss (Morrison et al., 2007; Zanin et al., 2015), prey depletion (Ripple et al., 2014; Wolf and Ripple, 2016), and retaliatory hunting motivated by depredation of domestic animals (Inskip and Zimmermann, 2009). Nevertheless, this species has expanded its distribution across agricultural lands and preyed on domestic animals (Buenavista and Palomares, 2017; Verdade et al., 2015). This distribution expansion, which could at first glance benefit the species, is probably increasing human-predator conflict and threats for puma populations.

Recognising the main prey base of an apex predator and measuring the frequency of domestic animals in its diet are essential to design conservation strategies. We conducted a study of the puma diet in a protected area located in the Caatinga biome. This is a Brazilian semi-arid ecosystem considered a hostile environment due to the length of the dry season and low primary productivity. For this reason, *P. concolor* may come into conflict with the surrounding agricultural areas due to its use of their herds as a complementary food source. Furthermore, we investigated the ecological processes that modulate prey selection. We hypothesised that puma's prey selection could reflect an energetic trade-off, such that large-bodied prey should be consumed at a higher rate than small ones. However, prey consumption could also be related to meeting probabilities (Azevedo et al., 2018; Weckel et al., 2006), which result from a proximate or ultimate ecological or evolutionary process, making the proportion of consumed items contingent on the relative

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abundance of prey or overlapping activity patterns between predator and prey.

Materials and methods

Study area and faecal survey

The study was conducted in the Serra das Almas Nature Reserve (SANR), a private protected area with an area of 61.37 km² located in Ceará State Brazil, in the Caatinga biome (5°8'29.15"–40°54'58.60" W, Fig. 1). The Caatinga has dry vegetation and is characterised by two seasons: a short rainy period, usually between December and February, and a long dry period. Although it occupies a small area, SANR is environmentally heterogeneous due to its location between the Ibiapaba plateau and Crateús peripheral depression, with elevations reaching 700 m and 300 m, respectively. The SANR is comprised of three main habitats: (i) seasonal and dense shrub vegetation (*Carrasco*), in which the canopy of emergent and sparse trees is intertwined with lianas (Araújo and Martins, 1999); (ii) seasonal deciduous thorn forest (arboreal Caatinga), characterised by an arboreal stratification of approximately 8 m and the presence of cactuses and bromeliads (Araújo and Martins, 1999); and (iii) montane seasonal deciduous forest (dry forest), with vegetal stratification varying between 8–12 m, consisting of trees and shrubs (Lima et al., 2009).

We carried out faecal sampling during the dry season in 2015 and 2016, through active searches along dirt roads and trails by experienced people, for a total of 115 km of sampling (Fig. 1). Samples were stored in 100 ml plastic containers with silica gel, and the locations were georeferenced using GPS. The faecal samples were packed and sent for molecular identification and diet analysis.

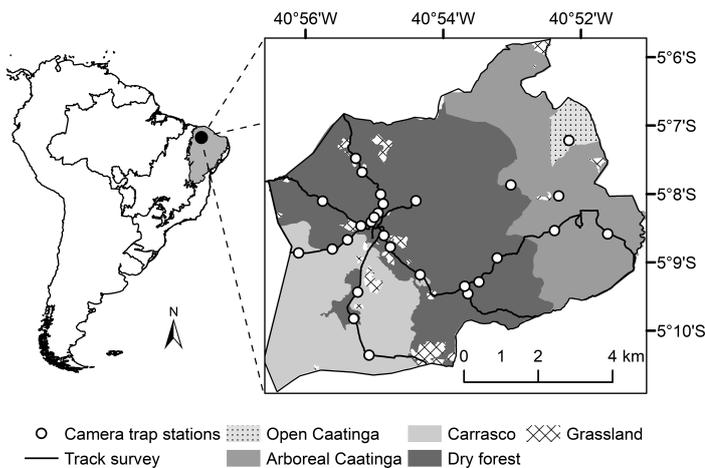


Figure 1 – Study area. Habitats, surveyed areas by track, and location of camera traps in the Serra das Almas Nature Reserve. The Caatinga biome is shown in grey, on the left map.

Identification of consumed prey

In the laboratory, faecal samples were washed in running water over two fine-mesh screens and dried (Gheler-Costa et al., 2018). Prey identification was carried out macro- and microscopically (Bianchi et al., 2014; de la Torre and de la Riva, 2009). The screened material consisting of teeth, scales, bone plates, feathers, nails, and claws were identified to the lowest possible taxonomic level by comparison with photographs and reference collections (Garla et al., 2001). Prey were identified microscopically by analysis of medullar patterns (Quadros and Monteiro-Filho, 2006), for which guard hairs were prepared as described by Quadros and Monteiro-Filho (2006) and the identification was carried out following Dias et al. (2012); Miranda et al. (2014); Quadros (2002).

Prey availability and predator-prey overlap of daily activity patterns

Data on prey availability and overlapping daily activity patterns between predator and prey species in the SANR were based on a study conducted between 2013–2015 by Matos Dias et al. (2018). These variables were estimated using photographs from camera traps at 30 sampling stations distributed across the same road and tracks surveyed for faecal samples (Fig. 1). The variables were calculated by independent photographic records of species, for which the criterion adopted was photos captured at least 1 h apart in a given sampling unit (camera trap station) (Ferreguetti et al., 2018). Daily activity pattern were measured by circular kernel density probabilities and temporal overlap between predator and prey were estimated by Dhat 1 coefficient, recommended for samples <50 records (Ridout and Linkie, 2009; Ferreguetti et al., 2018). Overlap coefficients range from zero to one, meaning no overlap up to complete overlap, respectively (Schmid and Schmidt, 2006). Prey availability was calculated by dividing the number of detections (photographic records) of each species by the sampling effort and multiplied by 100, providing an index of the species frequency in the SANR.

Statistical analysis

We performed a species accumulation curve to assess the adequacy of the sampling effort by evaluating if the total number of faecal samples (sampling units) were enough to characterise the puma diet. Species accumulation curve relates the observed prey richness with the accumulation of sampling units, demonstrating if prey richness stabilised or if needed more sampling units are needed to reach stabilisation, indicating that the sampling effort was not enough to describe puma diet. We also estimated the confidence interval around the species accumulation curve through bootstrap, using 1,000 random permutations of the data without replacement (Colwell et al., 2012; Gotelli and Colwell, 2001).

We characterised the puma diet by describing the prey consumed using the following estimators: (i) absolute frequency, represented by the observed proportion of each prey species in faecal samples; (ii) relative frequency, which is the rate between occurrence of prey species and all occurrences of prey animals; (iii) consumed biomass, calculated using the non-linear estimation proposed by Wachter et al. (2012); (iv) relative consumed biomass, which is the rate between the consumed biomass of prey species and total consumed biomass. Prey species with a relative frequency higher than 5% were considered to be a relatively important component of the puma diet (Foster et al., 2010a).

The dietary niche breadth of pumas was calculated using Levins' index B (Levins, 1968) and standardised following Hurlbert (1978). The standardised index varies between zero and one, corresponding to a 100% specialist to 100% generalist, respectively.

Finally, we correlated the estimators of prey consumed with prey body mass (following Jones et al., 2009), relative abundance, and overlap of daily activity patterns between pumas and prey species, following Matos Dias et al. (2018). For prey animals identified to a taxonomic level higher than species, we used the average body mass of species that belong to the taxon identified which can be found in the SANR, based on the species list of the SANR Management Plan (Associação Caatinga, 2012). Statistical analyses were conducted in the R software (R Core Team, 2016), using the *stats* and *vegan* packages (Oksanen, 2012).

Results

We found 63 faecal samples of pumas, of which 59 contained identifiable prey remains. We found remains of ten different prey animals, including five identified at the species level, while the rest could only be identified at the genus (n=1), family (n=1), order (n=1) or class (n=2) levels (Table 1). A few samples contained traces of two (n=7) or three prey species (n=1), while most samples contained traces of only one prey species (n=51). The species accumulation curve stabilised around 50 samples, so the sampling effort was sufficient to describe the puma diet in SANR (Fig. 2).

Table 1 – Puma diet in the Serra das Almas Nature Reserve, described through different estimators of prey consumption.

Taxon	Absolute frequency	Relative frequency	Consumed biomass	Relative consumed biomass
<i>Pecari tajacu</i>	50	46.154	1.875	0.723
<i>Mazama</i> sp.	13.333	12.308	1.773	0.182
Didelphidae	8.333	7.692	0.067	0.004
Rodentia	8.333	7.692	0.056	0.004
<i>Dasypus novemcinctus</i>	6.667	6.154	0.604	0.031
Birds	6.667	6.154	-	-
<i>Tamandua tetradactyla</i>	5	4.615	0.713	0.027
<i>Sapajus libidinosus</i>	5	4.615	0.261	0.01
<i>Euphractus sexcinctus</i>	3.333	3.077	0.704	0.018
Reptile	1.667	1.538	-	-

In our samples, the most frequent prey was the collared peccary (*Pecari tajacu*, Linnaeus, 1758), which represented 46% of consumed animals and the highest relative consumed biomass (Table 1). Five other taxa had a relative frequency higher than 5%, suggesting that they are also important prey for puma. These are the brocket deer (*Mazama* sp.), rodents (Rodentia), opossums (Didelphidae), the nine-banded armadillo (*Dasypus novemcinctus*, Linnaeus, 1758), and birds (Aves) (Table 1). The standardised Levins' index was 0.113, suggesting a narrow niche breadth and a specialised diet.

We evaluated the prey selection pattern using a Spearman correlation. Due to the hierarchisation of values generated by non-parametric analysis, all variables used to describe prey consumption had the same variation. Therefore, we selected relative frequency of consumed prey to represent prey consumption, which showed a positive correlation with the overlap of daily activity patterns between predator and prey ($n=8$, $r=1$, $p=0.017$), but no evidence of correlation with body mass ($n=9$, $r=0.265$, $p=0.526$) and relative abundance of prey ($n=8$, $r=0.446$, $p=0.268$).

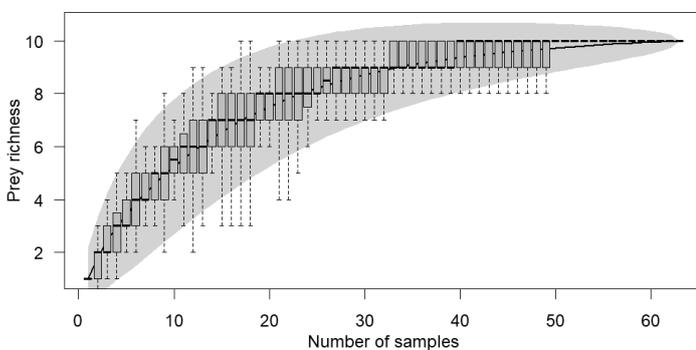


Figure 2 – Species accumulation curve showing prey richness and the number of puma faeces analysed in the Serra das Almas Nature Reserve. Boxplots represent the average and standard deviation of richness by sampling units, whereas the grey shadow represents the confidence interval measured by 1,000 random samples.

Discussion

Our study showed that at least 10 species comprise the prey base of *P. concolor* in SANR, in line with previous studies conducted in tropical rainforests (Ávila-Nájera et al., 2018; Foster et al., 2010b), where a higher species richness could be expected due to higher biodiversity, in comparison to the semi-arid environment of the Brazilian Caatinga. The assumption of a generalist feeding behaviour among pumas would imply that a higher richness of prey species would favour a higher diversity of consumed items (Redpath et al., 2010; Terraube and Arroyo, 2011), driven by random encounters. However, our results and those of recent studies call this assumption into question by reporting relative specialisation in the puma diet at the local scale (Ávila-Nájera et al., 2018; Bryce et al., 2017; Cassaigne et al., 2016; Foster et al., 2010b; Gómez-Ortiz et al., 2015).

The generalist feeding behaviour attributed to pumas is probably a result of two different interpretation biases. The first is a hierarchical property related to the scale of inference, in which distinct local specialisations and adaptive strategies would sum up to arise in a generalist feeding behaviour at the level of the species distribution. Therefore, the puma diet would be subject to a hierarchical organisation through the spatial scale, an important characteristic of ecological systems (Englund and Cooper., 2003). The other bias is related to predator identification, to the extent that more reliable methods of predator identification (e.g., genetic or chemical analyses of faeces and stomach or colon content) provide a more congruent description of diet than studies using identification methods that are not very reliable (e.g., appearance and/or morphology of faeces and associated tracks) since predator misidentification leads to erroneous inclusion of prey species in the diet description (Martínez-Gutiérrez et al., 2015). Therefore, although currently less common, these low-confidence methods tend to overestimate prey richness, which would lead diet studies to a conclusion of a generalist diet.

Overestimating the number of prey species can also affect the number of samples deemed necessary to stabilise their species accumulation curve, which is an important analytical aspect to describe species diet. For example, Foster et al. (2010a) suggested that 70–100 samples would be necessary to describe the puma diet in a tropical rainforest. Although performed in the Brazilian Caatinga, our study provided a consistent diet estimation with fewer samples ($n=59$) and showed a similar prey richness to studies conducted in rainforests (see Ávila-Nájera et al., 2018; Foster et al., 2010b,a). These findings were probably influenced by the bias in the studies included in their revision since they included both high and low-confidence methods to identify the predator. Therefore, *a posteriori* evaluation is probably a better approach to assure the sufficiency of study design.

Regarding prey selection by *P. concolor*, we observed that six taxa were the most common items in its diet, comprising the main prey base of this species in the SANR. The prey species identified here are consistent with previous studies that found peccaries, large rodents, deer and armadillos to be the main prey species (Ávila-Nájera et al., 2018; Foster et al., 2010b). Nevertheless, our results showed that puma has a strong preference for *P. tajacu* in the SANR, suggesting that *P. concolor* is specialist predator, as also observed in other areas such as the El Eden Ecological Reserve, Mexico (Ávila-Nájera et al., 2018). Furthermore, prey selection by pumas seems to have been, at least partially, driven by a daily activity pattern synchronism between predator and prey, suggesting that meeting probability is an essential aspect in the foraging ecology of pumas (Soria-Díaz et al., 2016, 2018).

It is important to highlight that we did not find any evidence of intra-guild and/or livestock depredation since no carnivores or domestic animals were detected in the faeces analysed. Intra-guild depredation is an essential aspect in competition among carnivores since it influences the hierarchical position of the species in the assemblage and, consequently, regulates population dynamics (Wachter et al., 2015). Therefore, it is a key factor to study carnivore ecology and has been target of several works (Elbroch and Kusler, 2018; Hunter and Caro., 2008; Oliveira and Pereira, 2014; Palomares and Caro, 1999;

Thompson and Gese, 2007; Vance-Chalcraft et al., 2007; Wachter et al., 2015).

Livestock depredation, in turn, is one of the main factors of conservation of large carnivores because it generates direct persecution of predators by humans (Inskip and Zimmermann, 2009). The human-felid conflict can generate population decrease in elevated levels, even within protected areas having an adequate amount of habitat, and prey availability (Aryal et al., 2014; Jiang et al., 2017; Malviya and Ramesh, 2015). Even if we did not complicitly monitored pumas killed by man, the lack of wildstock prey in our sample suggests that the conditions in the SANR are conducive to *P. concolor* conservation.

On the other hand, our results also suggest other potential conflicts of conservation generated by prey depletion, since the prey base of puma consisted of species commonly targeted in subsistence hunting, mainly in areas with low development income, like those surrounding the SANR. Fortunately, the hunting pressure in the surrounding areas of this natural reserve has decreased in the last fifteen years due to federal (such as *Bolsa Família*, an governmental project to enable income distribution; <http://www.caixa.gov.br/programas-sociais/bolsa-familia/Paginas/default.aspx>) and local social projects (such as *No Clima da Caatinga* project, developed by SANR and Associação Caatinga), which have provided some financial support to families, food safety, and positive perception of the SANR. Therefore, social policies are directly related to the persistence of the puma in the region, since they provide an appropriate refuge for this predator and ensure the availability of its prey base. ☞

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