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What are jaguars eating in a half-empty forest? Insights from diet in an overhunted Caatinga reserve

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Persistence of top predators in protected areas requires healthy populations of prey species. Jaguars (*Panthera onca*) are top predators in the Caatinga dry forest, a xeric domain in northeastern Brazil. Poaching is a threat to populations of jaguar prey in the Caatinga, but it is still widely popular among locals. Here, we investigated molecularly identified jaguar scats to assess prey composition in a protected area where large prey has been heavily depleted or driven extinct by poaching. We also make direct comparisons between trophic niche width and mean prey size through a literature review. We show that over 90% of the diet of jaguars was comprised of prey under 5 kg, mainly armadillos. Furthermore, we found that the values of trophic niche width (2.21) and mean prey size (5.23 kg) in our study area are among the lowest ever described for jaguars in the literature. Our results demonstrated that jaguars are able to shift their diet to small prey when larger quarry is scarce. However, subsisting in such a stressful trophic position may lead to decreased levels of recruitment and low emigration rate. Breeding females would have difficulty raising cubs without abundant large prey. If jaguars are to persist in the Caatinga, effective actions to reduce poaching inside protected areas and corridors must be implemented. One of the most important jaguar populations in this domain inhabits our study site, and prey conservation is paramount for long-term persistence of this top predator in the Caatinga.

A persistência de predadores de topo em unidades de conservação requer populações saudáveis de suas presas. A onça-pintada é um predador de topo nas florestas secas da Caatinga, um domínio xérico do nordeste do Brasil. Embora a onça-pintada seja localmente ameaçada, sua ecologia neste domínio ainda é pouco conhecida. A caça furtiva é uma ameaça às populações de presas da onça-pintada na Caatinga, mas ainda muito popular entre os habitantes locais. Nesse estudo, nós analisamos fezes geneticamente identificadas de onça-pintada para acessar a composição de presas de uma unidade de conservação onde as populações de presa foram seriamente diminuídas ou extintas pela caça furtiva. Nós também fizemos comparações diretas entre a amplitude do nicho trófico e do tamanho médio da presa através de uma revisão de literatura. Aqui, nós demonstramosque 90% da dieta da onça-pintada foi composta por animais de menos de 5 kg, principalmente tatus. Adicionalmente, nós notamos que os valores de amplitude do nicho trófico (2.21) e tamanho médio da presa (5.23 kg) estão entre os mais baixos descritos para a onça-pintada na literatura. Nossos resultados demonstram que a onça-pintada é capaz de mudar sua dieta para presas de pequeno porte quando animais maiores são escassos. Contudo, subsistir em uma posição trófica estressante pode diminuir os níveis de recrutamento e emigração. Fêmeas reprodutivas dificilmente seriam capazes de criar filhotes sem presas de grande porte em abundância. Se espera-se que as onças persistam na Caatinga, ações efetivas para a redução da caça furtiva dentro de unidades de conservação e corredores ecológicos precisam ser implementadas. Uma das mais importantes populações de onça-pintada nesse domínio habita nossa área de estudo, e a conservação de suas presas é fundamental para a persistência em longo prazo desse predador de topo na Caatinga.

Key words: armadillos, Caatinga, feeding habits, empty forest, hunting, *Panthera onca*, poaching, prey decline, reintroduction, Serra da Capivara

Conservation of top predators is paramount since their absence can trigger widespread community changes that lead to biodiversity loss (Newsome et al. 2017). Conflicts between predators and local human communities may make predator conservation difficult (Torres et al. 2018). Adequate prey availability is required for the persistence of predators (Sandom et al. 2017). However, many cultures still rely on wildlife as a source of food, entertainment, or income (Alves et al. 2009). In most tropical countries, wildlife use is poorly managed or not managed at all (Fa et al. 2002; Koster 2008; Fernandez et al. 2012), with negative consequences for animals and the livelihoods that depend on them (Wilkie et al. 2011). To understand which prey species predators rely on, prey composition must be known in detail (Uulu et al. 2014). Consequently, the study of feeding habits of top predators has the potential to improve conservation policies, particularly for threatened predator populations.

Poaching is a rampant problem in the Caatinga, a dry formation composed mainly of xeric vegetation, ranging from forests to exposed soil (Ab' Sáber 1990). The region remains one of the most undeveloped in Brazil, where 70% of the counties with the lowest Human Development Index are concentrated (Infante 2006). In this domain, poachers rely on wildlife as a source of income or animal protein (Barboza et al. 2016). As a consequence, wildlife in the Caatinga is disappearing. At Serra da Capivara National Park (hereafter, Serra da Capivara), poaching is characterized mainly as a leisure activity or as a commercial practice (Miranda and Alencar 2007). Between 2000 and 2003, patrols inside the park led to the confiscation of 167 mammals, of which 77% were armadillos (*Dasypus novemcinctus*, *D. septemcinctus*, *Euphractus sexcinctus*, and *Tolypeutes tricinctus*), 8% were lesser anteaters (*Tamandua tetradactyla*), and 4% were collared peccaries (*Pecari tajacu*). The poachers came predominantly from urban areas around the park (Miranda and Alencar 2007).

The jaguar (*Panthera onca*) is considered a focal species in conservation since its survival requires conditions that ensure high biodiversity levels, as occurs with other predators (Sérgio et al. 2006). For this reason and its high charisma, the species is the focus of several conservation and research initiatives, but its ecology remains poorly studied in several parts of its range. Jaguars currently occur only in a small fraction of the Caatinga domain (Morato et al. 2014). Jaguar densities in this domain are reported between 1.57 and 2.67 individuals/100 km^2, unexpectedly high considering the harshness of the Caatinga (Silveira et al. 2010; Sollmann et al. 2013a). This population has low levels of genetic diversity (Roques et al. 2014), and 23% of the individuals are melanistic (Astete, 2008; Fig. 1), the highest level of melanism known in a jaguar population to date. Habitat use by jaguars in the Caatinga is positively influenced by the presence of artificial waterholes (Astete et al. 2016). Long-term viability of jaguars in the region depends on the creation and maintenance of ecological corridors between current and future protected areas in the domain (Morato et al. 2014).

Jaguars are the only big cats that do not depend on large ungulates as primary prey (Miranda et al. 2016). Instead, they rely on capybaras (*Hydrochoerus hydrochaeris*), giant anteaters (*Myrmecophaga tridactyla*), armadillos, chelonians, and crocodilians, as well as on medium-sized ungulates such as peccaries. Their prey composition has been assessed by a number of studies, and reported preferences are for prey averaging 30 kg (Hayward et al. 2016). Jaguars have strong jaws that are adapted to prey on species that rely on armor or counter attack instead of flee (Miranda et al. 2016). In Serra da Capivara, prey species in the past included medium-sized vertebrates such as white-lipped peccaries (*Tayassu pecari*), collared peccaries, brocket deer (*Mazama guazoubira*), giant anteaters, and rheas (*Rhea americana americana*—Olmos 1992); all are considered game species in the Caatinga (Alves et al. 2016). However, poaching has eliminated rheas from the park, and while-white lipped peccaries were absent for decades (Wolff 2001; Astete 2008) before recolonizing the area during 2009–2010 (Astete 2012), occurring today in very low abundances. Reported as formerly abundant (Tega 2013), no live giant anteater had been observed in Serra da Capivara since 1994 (Wolff 2001); although extensive camera trapping revealed their existence in the park (Astete 2012), they are still considered functionally extinct.

We explored prey composition of jaguars in Serra da Capivara, a heavily poached park that still retains most jaguar prey species in low abundances. Our goals were 2-fold: 1) assess current prey composition, prey body size, and trophic niche width of jaguars in Serra da Capivara, and 2) compare such traits with jaguar diets reported in other studies. We predicted that depleted prey communities would lead to small prey sizes and narrow trophic niche width for this jaguar population.

Materials and Methods

Study area.—Serra da Capivara National Park is a 1,291-km^2 protected area located in the state of Piauí, northeastern Brazil, declared a World Heritage Site by UNESCO for its archeological legacy (Guidon 2003). There are 8 vegetation types recognized in Serra da Capivara (from open to dense arboreal Caatinga vegetation), the most common being tall, shrubby vegetation 6–10 m high (Emperaire 1984). Temperature varies from 2°C to 50°C. The rainy season is irregularly distributed from October to April. Annual mean precipitation is 689 mm (250–1,269 mm), below the 1,462 mm yearly evapotranspiration (Emperaire 1984). Elevation varies between 280 and 600 m a.s.l., and the park's topography consists of a main plateau bounded by 50–200 m high cliffs cut by canyons and valleys (Emperaire 1984). Serra da Capivara has no natural perennial rivers or lakes, and a series of permanent artificial waterholes have been installed since 1994 as part of the park's management actions (SMAPR 1994). To facilitate access and research, Serra da Capivara has an extensive network of dirt roads and trails.

Scat collection.—Between November and December of 2008, a team comprised of a hound trained to find jaguar scats and its handler patrolled the dirt roads inside the park. The dog-handler team hiked 180.94 km across 21 transects along the roads of Serra da Capivara, covering a total area of approximately 506 km^2. Each scat was frozen for analysis

Fig. 1.—Melanistic jaguar (*Panthera onca*) in Serra da Capivara National Park, Brazil.

of prey composition, and a small portion was removed and stored in 96% ethanol for subsequent genetic analysis (Roques et al. 2014). DNA was extracted using protocols based on the GuSCN/silica method (Frantz et al. 2003). Posterior predator identification was carried out using an optimized PCR-based protocol as described by Roques et al. (2011). Genetic fingerprinting was used to infer the number of individuals. For identification of sex, we used a method described by Pilgrim et al. (2005), based on the size difference of the Amelogenin gene between males and females.

Literature review.—We conducted an extensive search of the literature concerning interactions between jaguars and their prey using Google Scholar, Web of Science, Scopus, and Scielo search engines. We also consulted other researchers for unpublished data and literature unrevealed by online searches. In our search, we used the following keywords: "jaguar," "Panthera onca," and "onça-pintada," combined with "diet," "feeding habits," "food habits," "habitos alimentarios," and "dieta." This allowed us to find published and unpublished data in English, Portuguese, and Spanish. From each study, we recorded the percentage of occurrence (PO) of each taxon in the diet of jaguars. We calculated the PO of prey using the percentage of total feces in which a certain prey species was found, divided by the number of prey occurrences in the whole study (see Ackerman et al. 1984 for more details about the method). We only used studies with more than 16 samples (Miranda et al. 2016) to avoid biasing estimates of niche width by sample size.

Analysis.—We identified prey remains to the lowest possible taxonomic level using a reference collection of bones and fur. Trichology techniques were used to discriminate species according to cuticle and medullae patterns (de Miranda et al. 2014). We counted the frequency of occurrence (*f*) for each species *i* in the scats (*fi*). When a scat sample contained remains of more than 1 species, these were counted as fractional contributions to the frequency of the respective species (Link and Karanth 1994). We calculated relative scat frequency fr_i as:

$$fr_i = f_i \sum f$$

To estimate the contribution of biomass of each prey species, we applied an established regression formula to calculate biomass consumed per field collectable scat, *y*, as a function of the live weight of a given prey species, *x*, taking into account that this relationship is not linear (Wachter et al. 2012).

$$y = 2.358 \times (1 - \exp(-0.075x))$$

The regression consequently approaches an asymptote, which we consider to be biologically more meaningful and realistic than the linear regression of Ackerman et al. (1984).

As different-sized prey can make differential energetic contributions to the diet of jaguars, we calculated the relative biomass consumed, b_i, as:

$$b_i = fr_i\, y_i \div \sum fr \times x$$

We obtained body mass of prey species from the Encyclopedia of Life (eol.org), Redford and Wetzel (1985), Hellgren et al. (1995), Hayssen (2011), and Lange (1998). To estimate trophic niche width, we calculated Levin's index *B* (Krebs 1999), where *B* was standardized according to Hurlbert (1978) and *b* is the frequency of occurrence of each group of prey species:

$$B = 1 \div \sum b^2$$

Mean prey size was calculated using the geometric mean, because prey sizes do not fit normal distributions and are poorly described by mean values. Every individual of each prey species was assumed to be an adult. Most studies provided no data regarding age classes of consumed prey or the weight of subadult prey individuals. We performed all calculations in the R software version 3.3.1 (R Development Core Team 2017).

Results

From 93 scat samples collected in Serra da Capivara, 52 could be molecularly attributed to 16 jaguars (9 males, 7 females). Prey composition based on 50 scat samples that had food content was dominated by yellow armadillos (*E. sexcinctus*), which represented 64% of eaten prey and 52% of biomass consumed. With a frequency of 22%, lesser anteater was the second most important prey in frequency. Although collared peccaries appeared in 10% of the scats, they represented the same amount of biomass as lesser anteaters (22% for both species). Other smaller-sized prey comprised the rest of the diet (Table 1); 91.3% of this amount was comprised of species under 5 kg.

Our literature review resulted in 27 studies with sufficient scat sample size. Food niche width of jaguars in Serra da Capivara was 2.21, which represents the second narrowest niche ever recorded for the species (range: 1.74–9.31; Fig. 2). Mean prey size was 5.23 kg, the second lowest value ever recorded for jaguars (range: 3.56–45.63 kg; Fig. 3). This is the lowest value ever recorded for mean prey size in a study with molecular confirmation (Table 2). Spearman correlation analysis revealed no relationship between sample size (number of scats) and niche width for reviewed studies ($P > 0.05$, $S = 4{,}380.2$).

Discussion

The feeding habits of jaguars in Serra da Capivara are characterized by a low diversity of small prey species. Despite limited direct evidence, poaching seems a likely cause of this pattern. As large prey is extirpated, jaguars turn to small-sized prey, mainly armadillos, as their main food source. The "large-sized" collared peccary assumes an important role as prey given its higher energetic contribution to the diet of jaguars, followed by the lesser anteater, which contributed the third highest amount of biomass but was the second highest in frequency and percent occurrence. The small number of prey species and their small size results in one of the lowest niche widths ever reported for jaguars, with important implications for its persistence in Serra da Capivara.

While subjected to some theoretical and practical improvements (Campos-Silva and Peres 2016; Renoux and Thoisy 2016), harvest of bushmeat is still widely unsustainable in Neotropical forests (Terborgh and Peres 2017). Bushmeat consumption is a problem in Brazil, a country with incipient legislation regarding wildlife management and hunting (Fernandez et al. 2012). Additionally, poaching is performed over most of its territory (Bizri et al. 2015), targeting random individuals year-round, producing greater damage than managed hunting would. The majority of Brazilian environmental stakeholders remain strongly opposed to the establishment of sustainable management of wildlife, complicating the path to its creation. Meanwhile, poaching has eliminated populations of important jaguar prey, such as white-lipped peccaries, from protected areas such as Iguaçu and Turvo (de Azevedo and Conforti 2008; Keuroghlian et al. 2012). Although living in conditions of poverty, the preference of poachers in the Caatinga for bushmeat over livestock is a matter of predilection rather than a real need of protein supplementation from wildlife (Barboza et al. 2016). However, the taking of wildlife for subsistence, as a leisure activity, and by commercial poaching also occurs at other sites in the Caatinga (Alves et al. 2009; Melo et al. 2014), threatening wildlife populations that are naturally scant due to the harshness of dry regions.

Poaching functionally eliminated giant anteater, white-lipped peccary, and rhea populations from Serra da Capivara (Olmos 1992; Astete 2012). The remaining medium-sized vertebrates are brocket deer and collared peccaries (Astete et al. 2016), and whereas collared peccaries are among the preferred prey of jaguars, brocket deer are avoided (Hayward et al. 2016). Jaguars have been shown to rely on armadillos as primary prey in areas where vertebrate communities are affected by poaching (Novack et al. 2005; Foster et al. 2009). Nevertheless, a simple analysis of energetic demands of pregnant jaguar females shows that they would have difficulty fulfilling their energetic demands based solely on small prey: 34 g of meat per kg of cat are required per day (Altman and Dittmer 1973). Assuming small sizes for jaguars in the Caatinga—40 kg for females and 55 kg for males—there is a demand of 1.36–1.87 kg of meat per day. Therefore, an armadillo or lesser anteater may provide enough meat to fill these energetic requirements for 2 days assuming that 75% of the carcass is edible. When providing for dependent cubs, females may have their energetic needs rise by a factor of 1.5 during pregnancy, and a factor of 2.5 during cub-raising (Loveridge 1986). This increases the demand to 2 kg of meat per day during pregnancy and 3.4 kg of meat per day during lactation. Consequently, a breeding female with 70% of their diet comprised of armadillos would need to kill 247 armadillos per year when raising cubs, an unlikely feat. As thoughtfully pointed out by Novack et al. (2005), the presence

Table 1.—Prey composition of jaguars (*Panthera onca*) in Serra da Capivara, Brazil. Prey body mass (kg) was obtained from: [a]Redford and Wetzel (1985), [b]Hellgren et al. (1995), [c]Hayssen (2011), and [d]Lange (1998). CF is the correction factor applied following Wachter et al. (2012). PO = percentage of occurrence, FO = frequency of occurrence, and BPS = biomass per consumed scat.

Prey species	Body mass (kg)	*n*	PO (*n* = 57)	FO (*n* = 50)	CF	BPS (%)
Yellow armadillo (*Euphractus sexcinctus*)	4.68[a]	32	56.14	64	0.70	52.94
Collared peccary (*Pecari tajacu*)	22.8[b]	5	8.77	10	1.93	22.89
Lesser anteater (*Tamandua tetradactyla*)	4.83[c]	13	22.81	26	0.72	22.08
Azara's agouti (*Dasyprocta azarae*)	2.76[d]	2	3.51	4	0.44	2.09
Unidentified armadillos		3	5.26	6		
Unidentified bird		1	1.75	2		
Unidentified opossum		1	1.75	2		

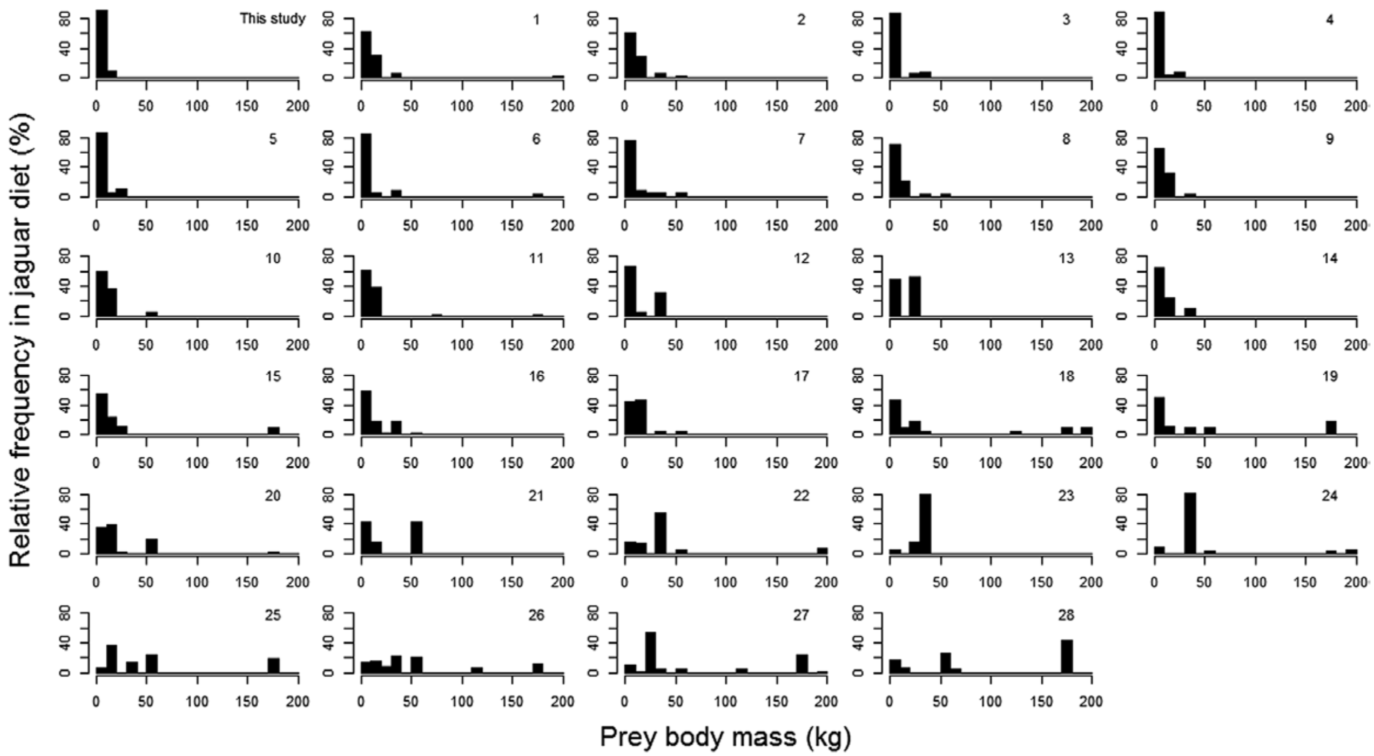

Fig. 2.—Jaguar (*Panthera onca*) prey size frequency over all surveyed studies. Notice the concentration of small prey at Serra da Capivara (first histogram). Other studies are represented by: 1 Taber et al. (1997), 2 Emmons (1987), 3 Rabinowitz and Nottingham (1986), 4 Oliveira et al. (2010), 5 Prado (2010), 6 Foster et al. (2009), 7 Novack et al. (2005) (unhunted), 8 Novack et al. (2005) (hunted), 9 Hernández (2008), 10 Rueda et al. (2013), 11 Ramalho (2010), 12 Chinchilla (1997), 13 Crawshaw et al. (2004), 14 Weckel et al. (2006), 15 Azevedo (2008), 16 Garla et al. (2001), 17 Aranda and Sánchez-Cordero (1996), 18 Nuno (2007), 19 Porfírio (2009), 20 SaintMartín et al. (2015), 21 Nuñez et al. (2000), 22 McBride et al. (2010), 23 Silveira (2004), 24 Sollmann et al. (2013b), 25 Scognamillo et al. (2003), 26 Azevedo and Murray (2007), 27 Perilli et al. (2016), and 28 Rueda et al. (2013).

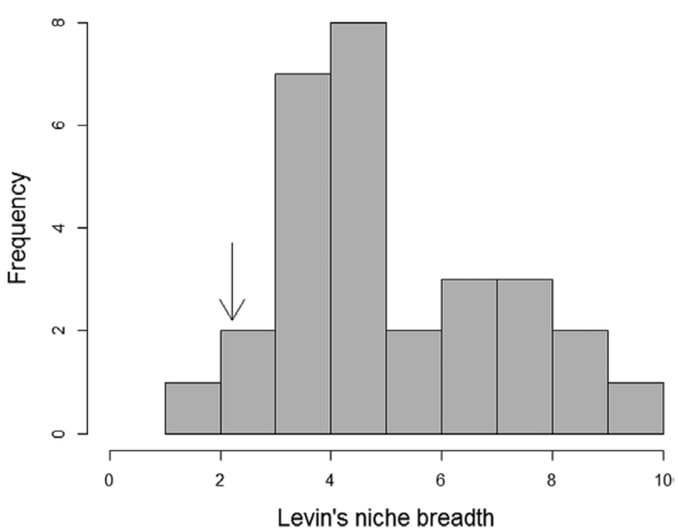

Fig. 3.—Levin's niche breadth across studies of jaguar (*Panthera onca*) diets ($n = 27$) performed to date (see list of studies in legend for Fig. 3). The arrow indicates the niche breadth of the present study, at Serra da Capivara.

of large-sized prey is critical to the recruitment of new jaguars to a breeding population.

If jaguars are to persist in the long term at Serra da Capivara, prey populations may benefit from population reinforcement (in the case of white-lipped peccaries and giant anteaters) and full reintroduction (for rheas) programs. All 3 large-sized prey species are common in Brazilian zoological collections and those populations could supply a reintroduction program. We emphasize that any reintroduction or reinforcement program must be accompanied by an increase of ranging services in the park and its surroundings to prevent poaching. The number of rangers in the park has varied during the last decades due to unstable resources provided by the Brazilian government. The quick recovery of tigers (*Panthera tigris*) in Nepal, resulting from prey protection (Lamichhane et al. 2018), may be replicable for jaguars. Furthermore, the protection of wildlife may have consequences that go beyond jaguar conservation, as the reduction of armadillo and anteater populations, who feed mainly on termites (Vaz et al. 2013), led to termite nests damaging rock paintings in the park (Tega 2013; Silva and Andrade 2016). Consequently, poaching may threaten the Serra da Capivara archeological legacy.

We stress that the population in our study site is of high importance for jaguar persistence in the Caatinga (Morato et al. 2014). Jaguars are only present in southern areas of the domain, and Serra da Capivara is the most isolated patch they inhabit. Genetic diversity of jaguars inside Serra da Capivara is already under impact (Roques et al. 2014); therefore, management actions that allow emigration and immigration from and to the park are required. The creation of multiple-use corridors between protected areas may benefit jaguar dispersal between

Table 2.—Levin's niche breadth value and mean weight of vertebrate prey (MWVP) in kilograms, for studies of jaguar (*Panthera onca*) diets. GenID stands for the molecular identification of jaguar scats, Y = confirmed and N = not confirmed by this technique.

Reference	Niche breadth	MWVP (kg)	Sample size	GenID
Sollmann et al. (2013b)	1.74	30.60	35	Y
This study	2.21	5.26	50	Y
Rabinowitz and Nottingham (1986)	2.93	5.53	228	N
Silveira (2004)	3.31	29.20	18	N
SaintMartín et al. (2015)	3.45	45.63	27	N
Aranda and Sánchez-Cordero (1996)	3.50	10.22	37	N
Foster et al. (2009)	3.59	6.40	322	Y
Novack et al. (2005) (nonhunted)	3.68	6.52	53	Y
Nuñez et al. (2000)	3.74	14.04	50	N
Hernández (2008)	3.95	6.98	206	N
Weckel et al. (2006)	4.10	8.97	23	Y
Ramalho (2010)	4.28	7.78	29	N
SaintMartín et al. (2015)	4.30	12.92	43	Y
Crawshaw et al. (2004)	4.47	8.66	73	N
Taber et al. (1997)	4.76	3.56	106	N[a]
Rueda et al. (2013)	4.84	7.45	22	N
Novack et al. (2005) (hunted)	4.88	6.54	23	Y
Perilli et al. (2016)	4.95	42.78	125	N
McBride et al. (2010)	5.13	26.71	41	N
Prado (2010)	5.31	6.21	32	Y
Oliveira et al. (2010)	6.13	5.81	18	Y
Scognamillo et al. (2003)	6.35	32.99	42	N
Azevedo (2008)	6.54	9.23	51	N
Chinchilla (1997)	7.56	7.96	22	N
Porfírio (2009)	7.84	12.58	134	N
Azevedo and Murray (2007)	7.97	33.81	149	N
Nuno (2007)	8.07	12.23	25	N
Garla et al. (2001)	8.80	9.25	101	N
Emmons (1987)	9.31	5.45	25	N

[a]Identified by using bile acids profile.

fully protected parks, and help mitigate conflicts with locals. Those corridors may also benefit from the waterholes that are valuable to jaguars and many of their prey in this region (Astete et al. 2016).

As our data collection was limited to 2 months in the rainy season, we may have missed annual variation in prey availability. However, a seasonal increase in armadillo abundance during the rainy season is unlikely, since the < 700 mm of rainfall is sparsely distributed throughout a period of 7 months (Emperaire 1984). Furthermore, if this rainfall pattern was sufficient to trigger seasonal increases in breeding or activity, several prey species should respond similarly, not only armadillos. Additional data collection during the dry season, ideally in a multiyear sampling design, with parallel estimates of prey abundance may further increase our understanding of jaguar diet in Caatinga.

In this and several other studies relying on molecular identification of scats, no prey under 2 kg was found. This calls into question reports of jaguars preying on a variety of small mammals based on scats whose attribution hinges on tracks or fecal morphology. We suggest that relying on nonmolecular methods to identify scats may introduce errors into analyses of prey composition. Our comparisons to estimates of prey size from studies that did not use molecular confirmation are therefore conservative, and our findings of small average prey size for jaguars in the Caatinga may be even more striking.

In summary, we have shown that jaguar diet in Serra da Capivara is mainly composed of a few species of small prey. While the connection between prey poaching and this pattern is only correlational, comparisons with other study sites strongly suggest that poaching has a destructive effect on vertebrate communities inside Serra da Capivara. Managing wildlife in regions that suffer from poverty cannot be trivialized (Terborgh and Peres 2017). Even when not killing wildlife for subsistence, a great number of poor and uneducated people around the park's borders will be unlikely to prioritize jaguar conservation. Consequently, they will continue to rely on poaching as an economic complement or leisure activity. Regulatory laws that allow responsible, managed, and sustainable hunting outside national parks in Brazil may play a role in overcoming this problem. Like many big cats, jaguars have considerable dietary plasticity. However, stressful trophic positions will certainly limit recruitment and dispersal, impacting long-term persistence of the species in the Caatinga.

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