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Source: Wildlife Biology, 19(2) : 179-187

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/12-092

Wildl. Biol. 19: 179-187 (2013)
DOI: 10.2981/12-092

Original article

Feeding ecology of puma *Puma concolor* in Mexican montane forests with comments about jaguar *Panthera onca*

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We analyse the diet and prey selection of puma *Puma concolor* and describe opportunistically the diet of jaguar *Panthera onca* in montane forest in the Sierra Nanchititla Natural Park, central Mexico. We analysed prey selection in relation to energy content and population abundance, inferred through camera trapping. Analysis of 209 puma scats showed that their main prey was nine-banded armadillo *Dasypus novemcinctus* followed by white-nosed coati *Nasua narica* and white-tailed deer *Odocoileus virginianus*. Pumas did not take prey in proportion to their relative abundance, but selected energetically profitable prey such as nine-banded armadillo, which formed the bulk of their diet. In 13 scats of jaguar, nine-banded armadillo was also the most important prey followed by domestic goat *Capra hircus*. We discuss the implications for management of predators and prey.

Key words: abundance, jaguar, Panthera onca, prey selection, profitable prey, puma, Puma concolor

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Received 27 August 2012, accepted 12 March 2013

Associate Editor: Al Glen

Prey selection is determined by a complex predator*prey interaction and by ecological parameters that vary with the distribution of the species (Sunquist & Sunquist 1989, Hayward & Kerley 2005, Gómez-Ortiz et al. 2011). Resource use overlap has been studied for several sympatric predator species (Neale & Sacks 2001, Breuer 2005, Andheria et al. 2007, Kortello et al. 2007, Hayward & Kerley 2008, Glen et al. 2011) and some studies report that the abundance and availability of prey and predators can modify the coexistence (Biswas & Sankar 2002, Breuer 2005, Hayward et al. 2006, Andheria et al. 2007, Azevedo 2008). For large felids, the most profitable prey are those with the largest body sizes and with the least risk in hunting and manipulating (Sunquist & Sunquist 1989), or the most abundantly occurring and vulnerable prey taken opportunistically (Ackerman et al. 1984, Power 2002, Wegge et al. 2009). Puma *Puma concolor* and jaguar *Panthera onca* prey on large and medium-sized prey with similar frequency where they are abundant (Iriarte et al. 1990, Taber et al. 1997, Núñez et al. 2000, Polisar et al. 2003). Overall, the niche breadth for both species in sympatry indicates that the jaguar is a more specialised predator than puma, which exhibits more generalist patterns (Emmons 1987, Taber et al. 1997, Scognamillo et al. 2003, Novack et al. 2005, Azevedo 2008). Only two studies in Mexico show an inverse foraging pattern (Núñez et al. 2000, Rosas-Rosas et al. 2008). Niche breadth can be associated with physical and biological factors, though they may be related to a diversity of unknown factors (Morse 1974). The puma's diet in our study area has been reported previously. In contrast to studies in northern areas, the most important prey species was nine-banded armadillo *Dasypus novemcinctus* (Iriarte et al. 1990, Monroy-Vilchis et al. 2009a, Gómez-Ortiz et al. 2011). In our study, we analysed the trophic niche of puma

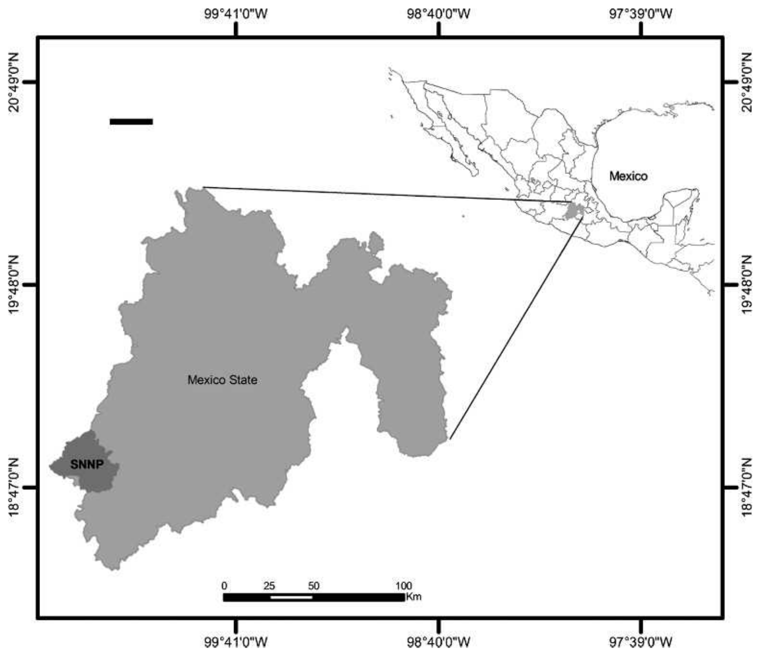

Figure 1. Location of the Sierra Nanchititla Natural Park (SNNP), Mexico.

and describe some opportunistic observations of the jaguar's diet in a montane forest, where pumas are more abundant than jaguar; occurring approximately 3:1 (Soria-Díaz et al. 2010). In addition, we analysed prey selection in relation to energy content and relative abundance.

Material and methods

Study area

Our study area is located in the central region of Mexico in the Sierra Nanchititla Natural Park (SNNP) located between the coordinates 19°04'13''-18°45'38'' N and 100°15'59''-100°36'34'' W (Fig. 1). It covers 663.93 km^2 and has an altitude range between 410 and 2,080 m a.s.l. The vegetation types are: pine-oak forest (17%), oak forest (30%), deciduous tropical forest (18%), induced grasslands (30%) and cultivations (4%; Monroy-Vilchis et al. 2008b, Zepeda et al. 2008). In the area, 53 species of mammals have been recorded of which white-tailed deer *Odocoileus virginianus*, white-nosed coati *Nasua narica* and eastern cottontail *Sylvilagus floridanus* are the most abundantly occurring, whereas nine-banded armadillo is one of the most scarcely occurring (Monroy-Vilchis et al. 2011a,b). In this area, five of the six species of Mexican wild felids occur (Sánchez et al. 2002, Monroy-Vilchis et al. 2008a).

Diet

During August 2002-May 2009, we monthly collected puma and jaguar scats that were identified using the following four methods: a) on the basis of their morphologic characteristics and presence of associated sign (i.e. scrapes, trace and hair of predator; Aranda 2000), b) using camera traps located in the study area, c) comparisons with samples from captive animals and d) analysing bile acids.

We used the methodology proposed by Salame-Méndez et al. (2012) to analyse bile acid profiles, which were standardised according to zoo samples. Both species present cholesterol, dehydrocholic, lithocholic, quenodeoxicholic, deoxicholic and cholic, but we could differentiate the two species by the presence of glycocholic and a spot between cholic and chenodeoxycholic in the bile acid profile of puma.

Furthermore, we washed the scats and separated their components (e.g. hair, bones, feathers and scales). Prey identification was carried out in the two following ways: the hairs were identified according to the method described by Monroy-Vilchis & Rubio-Rodríguez (2003). Bones and teeth of mammals were compared with specimens from the collection of the Sierra Nanchititla Biological Station, the Autonomous University of the State of Mexico. The diets were analysed according to Monroy-Vilchis et al. (2009a) and Gómez-Ortiz et al. (2011) by means of their frequency of occurrence (FO), percentage of occurrence (PO), relative biomass consumed (RBC) and relative number of individuals consumed (RNIC). The trophic niche breadth for puma was estimated using standardised Levins' index (Krebs 1999). The small sample size of jaguar scats precluded rigorous dietary analysis. However, we report some descriptive observations.

Energy content

The energy content of the three prey species showing the highest frequency of occurrence in the diet of puma (i.e. nine-banded armadillo, white-nosed coati and white-tailed deer) was obtained based on values reported by Gómez-Ortiz et al. (2011). We calculated the number of individuals necessary to satisfy the energy requirements of pumas considering the energy

Table 1. Diet analysis of puma at Sierra Nanchititla Natural Park, Mexico, during August 2002 - May 2009.

Prey species	FO (%)	PO (%)	Biomass (kg)	Correction factor[a]	RBC (%)	RNIC (%)
Mammalia						
Artiodactyla						
Bos taurus	4.78	3.83	6.13	2.19	4.57	1.92
Capra hircus	5.74	4.60	6.13	2.19	5.48	2.31
Ovis aries	1.91	1.53	6.13	2.19	1.83	0.77
Odocoileus virginianus	7.66	6.13	6.13	2.19	7.31	3.08
Carnivora						
Nasua narica	16.67	13.41	4.88	2.15	15.59	8.25
Procyon lotor	1.91	1.53	5.50	2.17	1.81	0.85
Bassariscus astutus	3.35	2.68	0.92	0.92	1.34	3.76
Conepatus leuconotus	0.48	0.38	2.70	2.07	0.43	0.41
Mephitis macroura	0.48	0.38	1.73	1.73	0.36	0.54
Spilogale putorius	0.96	0.77	0.57	0.57	0.24	1.07
Mustela frenata	0.48	0.38	0.21	0.21	0.04	0.54
Urocyon cinereoargenteus	0.48	0.38	4.00	2.12	0.44	0.28
Canis familiaris	0.48	0.38	6.13	2.19	0.46	0.19
Cingulata						
Dasypus novemcinctus	55.02	44.06	4.82	2.15	50.43	36.25
Didelphimorphia						
Didelphis virginiana	4.31	3.45	2.48	2.07	3.87	4.04
Lagomorpha						
Sylvilagus cunicularius	3.83	3.07	1.76	1.76	2.93	4.30
Sylvilagus floridanus	1.44	1.15	1.35	1.35	0.84	1.61
Rodentia						
Sciurus aureogaster	3.35	2.68	0.58	0.58	0.85	3.76
Spermophilus variegatus	0.48	0.38	0.87	0.87	0.18	0.54
Liomys irroratus	0.96	0.77	0.04	0.04	0.02	1.07
Liomys sp.	0.48	0.38	0.05	0.05	0.01	0.54
Unidentified mammal	1.44	1.15				
Aves						
Galliformes						
Ortalis poliocephala	6.70	5.36	0.58	0.58	1.68	7.52
Unidentified bird	0.48	0.38				
Reptilia						
Squamata						
Ctenosaura pectinata	0.48	0.38	1.05	1.05	0.22	0.54
Testudines						
Kinosternon integrum	0.48	0.38	0.30	0.30	0.06	0.54

[a] Correction factor reported by Ackerman et al. (1984).

Table 2. Opportunistic description of diet of jaguar at Sierra Nanchititla Natural Park, Mexico, during August 2002 - May 2009.

Prey species	FO (%)	PO (%)
Mammalia		
Artiodactyla		
Capra hircus	23.08	17.65
Odocoileus virginianus	7.69	5.88
Carnivora		
Nasua narica	15.38	11.76
Procyon lotor	7.69	5.88
Conepatus leuconotus	7.69	5.88
Cingulata		
Dasypus novemcinctus	38.46	29.41
Lagomorpha		
Sylvilagus cunicularius	7.69	5.88
Sylvilagus floridanus	15.38	11.76
Reptilia		
Squamata		
Ctenosaura pectinata	7.69	5.88

demand for pumas reported by Laundré (2005), as well as the digestibility constant (0.91) suggested by Hackenburger & Atkinson (1983). We did the calculation based on the following formula (Gómez-Ortiz et al. 2011):

$$\text{Number of organisms/year} = \frac{\left(\frac{(ED*365)*P}{DE}\right)}{B},$$

where ED = energy demand of predator (kcal/day), P = proportion of prey's frequency of occurrence, DE = digestible energy (GEx(0.91), GE = Gross energy (in kcal/kg prey, fresh meat) and B = prey's mean biomass (in kg).

Abundance of prey species

During December 2003 - January 2008, we placed 17 camera traps with automatic detection systems (Wildlife Pro II Camera System). We calculated the relative abundance index (RAI = number of photographs acquired/100 trap days; O'Brien et al. 2003, Monroy-Vilchis et al. 2011b). Analysing them, we only considered independent photographs; consecutive photographs of different individuals of the same or different species, consecutive photographs of individuals of the same species with a separation of $>$ 1 minute (Yasuda 2004) and non-consecutive photographs of individuals of the same species.

Prey selection

Using the relative abundance of prey in the environment (RAI) and the percentage frequency of occurrence of prey categories in the predator's diet, we calculated Ivlev's prey selectivity index (Ivlev 1961): Ei = (ri - ni)/(ri + ni) where ri is the percentage of species i in the diet and ni is the percentage of species i in the environment (Krebs 1999). Dietary selectivity index values range from -1 to +1. Index values near +1 indicate that the prey category is selected by the predator in much greater proportion than it is available in the habitat. Conversely, index values near -1 indicate that the prey category is selected much less than its abundance in the study area. We used bootstrap resampling (10,000 samples, with replacement) in R software (version 2.15.2) to estimate 95% confidence intervals (CI) for each electivity index. We inferred selection for or against a

Table 3. Number of individuals needed by year to satisfy the energy demand for puma at Sierra Nanchititla Natural Park, Mexico, during August 2000 - May 2009.

Prey species	Gross energy (kcal/kg)	Prey biomass (kg)	Predator category	Energy demand Kcal/day[c]	Number of organisms/year
D. novemcinctus	2398.7[a]	4.82	Males	3143.7	60
			Females with/cubs	2705.4	52
			Females without/cubs	2420.0	46
N. narica	2225.3[a]	4.88	Males	3143.7	19
			Females with/cubs	2705.4	17
			Females without/cubs	2420.0	15
O. virginianus	2165.5[a]	6.13[b]	Males	3143.7	7
			Females with/cubs	2705.4	6
			Females without/cubs	2420.0	6

[a] Data reported by Gómez-Ortiz et al. (2011).
[b] Maximum suggested biomass consumption by Monroy-Vilchis et al. (2009a).
[c] Energy demand reported by Laundré (2005).

Table 4. Relative abundance index (RAI) of prey species of the diet of puma at Sierra Nanchititla Natural Park, Mexico.

Prey	Independent photographs	RAI	Total photographs
Bassariscus astutus	5	0.07	6
Conepatus leuconotus	13	0.19	13
Dasypus novemcinctus	8	0.12	8
Didelphis virginiana	30	0.44	31
Mephitis macroura	6	0.09	6
Nasua narica	233	3.38	483
Odocoileus virginianus	86	1.25	120
Procyon lotor	15	0.22	30
Sciurus aureogaster	24	0.35	28
Spilogale putorius	2	0.03	2
Sylvilagus cunicularius	36	0.52	44
Sylvilagus floridanus	103	1.50	125

particular food category if the 95% CI did not overlap zero (Glen et al. 2012).

Results

Diet

From 209 puma scats, we determined 24 prey species at species level and two could not be identified (one mammal and one bird). The main prey was nine-banded armadillo followed by white-nosed coati and white-tailed deer, which represented all together 64% of the total occurrence frequency. The main prey in relation to the percentage of RNIC was, in order of importance, nine-banded armadillo followed by white-nosed coati and finally the west Mexican chachalaca *Ortalis poliocephala*, which provide 68% of RBC (Table 1). The niche breadth for puma's diet was specialised (B' = 0.13).

We collected 13 scats of jaguar and identified nine prey species. The main preys were nine-banded armadillo and domestic goat, which represented 62% of the total frequency of occurrence (Table 2).

Energy content

Nine-banded armadillo had the highest energy content/kg, followed by white-nosed coati and white-tailed deer. Nine-banded armadillo had a high percentage of fat (19%), whereas white-tailed deer contain a high percentage of proteins (29%; Gómez-Ortiz et al. 2011). The hypothetical number of animals required according to the energy needs of pumas suggests an average annual consumption/puma of 53 nine-banded armadillo plus 17 white-nosed coati and seven white-tailed deer (Table 3).

Prey selection

We obtained 1,013 photographs of 13 prey species of puma in 6,884 trap days; white-nosed coati was the prey with the highest RAI followed by eastern

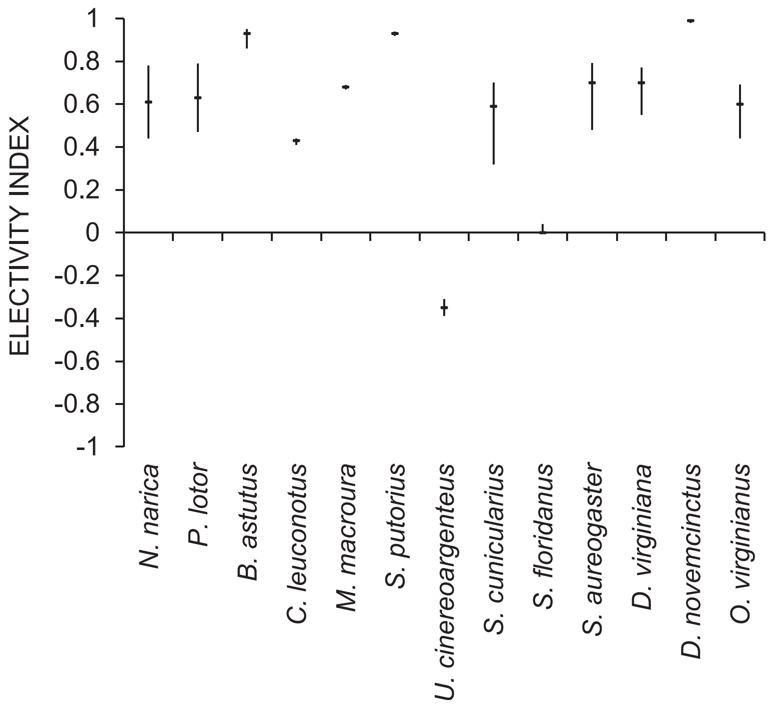

Figure 2. Values of electivity index with confidence interval (95% CI) of diet of pumas in the SNNP, Mexico.

cottontail and white-tailed deer, whereas nine-banded armadillo had a lower index (Table 4). Our estimates of the electivity index suggest that pumas preyed preferentially on several species including nine-banded armadillo. Only eastern cottontails were consumed according to their availability, whereas consumption of grey fox *Urocyon cinereoargenteus* was weakly avoided (Fig. 2).

Discussion

Niche breadth

In the SNNP, puma had a narrower niche breadth than has been recorded in areas from its central and southern distribution range (Emmons 1987, Taber et al. 1997, Scognamillo et al. 2003, Novack et al. 2005), reflecting the fact that puma uses a narrower portion of the resource spectrum. The theory predicts that if one species is socially dominant to another, the subordinate species usually narrows its niche when they occur together, or when two species are dominants in the same place, both narrow their niches (Morse 1974). The feeding specialisation that we observed can be explained in two ways. First, feeding partitioning is probably related to the high carnivore richness in SNNP (14 species; Monroy-Vilchis et al. 2011a). Second, an intrinsic specialisation tendency related to low richness of large prey compared to northern areas, and of medium-sized prey compared to southern areas. This situation supports the idea that in many cases dietary width may be a local phenomenon rather than a species characteristic (Fox & Morrow 1981). In western ($B' = 0.38$) and northwestern ($B' = 0.22$) Mexico, pumas are specialist foragers but focus on large prey such as white-tailed deer and bighorn sheep *Ovis canadensis*, respectively (Núñez et al. 2000, Rosas-Rosas et al. 2003).

Prey selectivity

Prey selection has been approached in relation to their costs and benefits as well as their vulnerability, abundance and availability factors (Emmons 1987, Sunquist & Sunquist 1989, Iriarte et al. 1990, Kunkel et al. 1999, Polisar et al. 2003). Our results support the theory of optimal foraging, considering that nine-banded armadillo presents the highest energy content in relation to other prey and that prey selection is influenced by their energy content and not by the abundance in the environment as had been suggested by Griffiths (1975). Despite white-nosed coati being one of the most abundant prey, it was not the main prey in the diets of this felid species. This may be explained by a predation strategy that considers decreasing the risk of being hurt by species that live in groups, i.e. capybara *Hydrochaeris hydrochaeris*, collared peccary *Tayassu tajacu* and white-nosed coati (Sunquist & Sunquist 1989, Hass & Valenzuela 2002). In addition, white-nosed coati presents a low energy contribution compared to nine-banded armadillo, suggesting that prey selection is based on energy gain (Sunquist & Sunquist 1989, Scognamillo et al. 2003, Gómez-Ortiz et al. 2011).

Cannibalism and consumption of mesocarnivores (Canidae, Procyonidae and Felidae) has been suggested as occasional (Ackerman et al. 1984, Logan & Sweanor 2001, Rosas-Rosas et al. 2003). Consumption of grey fox was avoided. Occasional intraguild predation may be caused by unexpected encounters between foxes and puma.

In relation to the sizes of the prey consumed by puma and jaguar along their distribution, the consumption of large prey has been suggested for the felids distributed away from the equator, and a dependency on medium-sized prey for those distributed closer to the equator. This is related to a pattern in which pumas are smallest in equatorial regions and increase in body size with latitude (Iriarte et al. 1990, Monroy-Vilchis et al. 2009a). In several studies focussing on the diet of jaguar, a preference for large prey has been reported even if the jaguar is sympatric with the puma (Emmons 1987, Iriarte et al. 1990, Taber et al. 1997, Garla et al. 2001, Polisar et al. 2003, Scognamillo et al. 2003). By contrast, we observed the consumption of medium-sized prey by both predator species, despite the fact that sympatry with the larger-bodied jaguar may have imposed additional selective pressure on puma to use smaller prey (Scognamillo et al. 2003). Nonetheless, the case of jaguar must be interpreted with caution because of the small sample size. Several studies on the diet of both felid species in Mexico showed segregation in the size or species of consumed prey (Aranda & Sánchez-Cordero 1996, Núñez et al. 2002, Rosas-Rosas et al. 2008). Only one report shows that both felid species prey on medium-sized prey; however, it was associated with a decrease of large prey because of human hunting pressure (Novack et al. 2005). The results of our study can be explicated by the lowest abundance of jaguar, and maybe, by the fact that our study area represents an atypical habitat (montane forest) for the species (Rodríguez-Soto et al. 2011). As not only the predator size is important to determine the dominance between species, there are some ecological patterns such as the abundance of predators, which might invert the roles (Rabinowitz 1989, Moreno et al. 2006).

Livestock predation

Pumas occasionally prey on livestock, but livestock represents a small part of their diet. Predation on cattle has been associated with 'easy detection' linked with poor livestock management (Cunningham et al. 1995, Logan & Sweanor 2001). In our study, we found livestock infrequently in the diet of the puma. Three domestic species occurred in the diet (12% FO), suggesting that domestic species are eaten occasionally. Nonetheless, the local disapproval of cattle predation has caused the death of at least 40 pumas during the last 10 years in the study area (Monroy-Vilchis et al. 2009b, Zarco-González et al. 2012). This is of particular concern for conservation of the species, because hunting is one of the main threats for pumas in Mexico (Zarco-González et al. 2013).

Our study supplies a hypothetical number of prey individuals needed to satisfy the energy requirements of the puma. This might be the basis for evaluating important biological factors such as the carrying capacity, and advise the traditional use of wildlife by the inhabitants in the SNNP, which might help establish management strategies to decrease possible competition between the carnivores and people. The analysis of feeding ecology shows the importance of medium-sized mammals, mainly nine-banded armadillo, which is one of the most used species by people in the SNNP (Monroy-Vilchis et al. 2008b).

Acknowledgements - we are grateful to the Mexican people for the funding of our study through the Universidad Autónoma del Estado de México with the projects FE012/2006, FE09/2007, FE014/2007-2009, the Consejo Nacional de Ciencia y Tecnología (CONACYT) with project 105254 and scholarship (YG-O) 255868 and PROMEP with project 103.5/10/0942. We would like to thank the State Commission of Natural Parks and Fauna for granting us access to the SNNP and to the Zoo of Zacango, and the students of Sierra Nanchititla Biological Station, who helped us in the fieldwork. Two reviews strengthened the manuscript considerably.

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