



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

Authors: Gómez-Ortiz, Yuriana, and Monroy-Vilchis, Octavio

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

Published By: Nordic Board for Wildlife Research

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

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

Yuriana Gómez-Ortiz & Octavio Monroy-Vilchis

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*

Yuriana Gómez-Ortiz & Octavio Monroy-Vilchis, Estación Biológica Sierra Nanchititla, Facultad de Ciencias, Universidad Autónoma del Estado de México, Instituto Literario 100, Colonia Centro, 50000 Toluca, México - e-mail addresses: ygo_19@yahoo.com.mx (Yuriana Gómez-Ortiz); omv@uaemex.mx (Octavio Monroy-Vilchis)

Corresponding author: Octavio Monroy-Vilchis

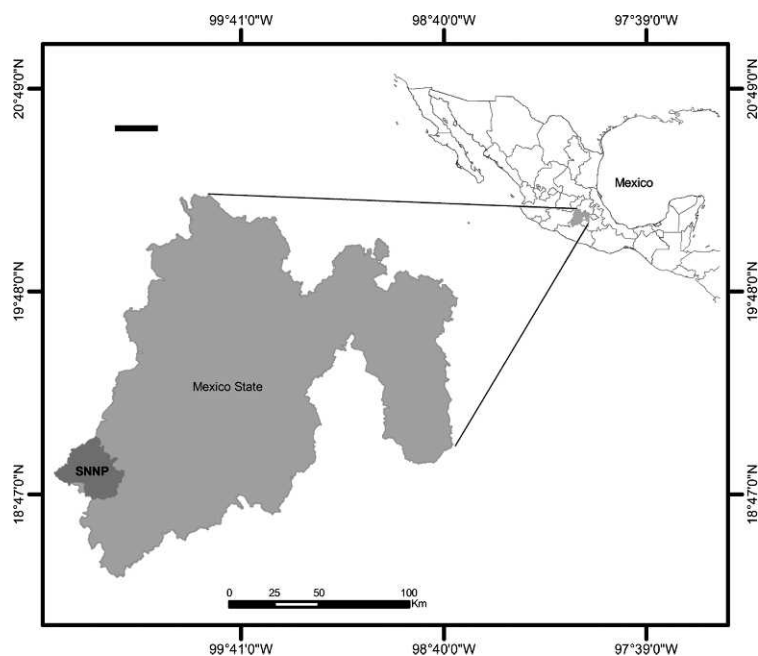
Received 27 August 2012, accepted 12 March 2013

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, Polis 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, Scognamiglio 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 km² 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						
<i>Bos taurus</i>	4.78	3.83	6.13	2.19	4.57	1.92
<i>Capra hircus</i>	5.74	4.60	6.13	2.19	5.48	2.31
<i>Ovis aries</i>	1.91	1.53	6.13	2.19	1.83	0.77
<i>Odocoileus virginianus</i>	7.66	6.13	6.13	2.19	7.31	3.08
Carnivora						
<i>Nasua narica</i>	16.67	13.41	4.88	2.15	15.59	8.25
<i>Procyon lotor</i>	1.91	1.53	5.50	2.17	1.81	0.85
<i>Bassariscus astutus</i>	3.35	2.68	0.92	0.92	1.34	3.76
<i>Conepatus leuconotus</i>	0.48	0.38	2.70	2.07	0.43	0.41
<i>Mephitis macroura</i>	0.48	0.38	1.73	1.73	0.36	0.54
<i>Spilogale putorius</i>	0.96	0.77	0.57	0.57	0.24	1.07
<i>Mustela frenata</i>	0.48	0.38	0.21	0.21	0.04	0.54
<i>Urocyon cinereoargenteus</i>	0.48	0.38	4.00	2.12	0.44	0.28
<i>Canis familiaris</i>	0.48	0.38	6.13	2.19	0.46	0.19
Cingulata						
<i>Dasypus novemcinctus</i>	55.02	44.06	4.82	2.15	50.43	36.25
Didelphimorphia						
<i>Didelphis virginiana</i>	4.31	3.45	2.48	2.07	3.87	4.04
Lagomorpha						
<i>Sylvilagus cunicularius</i>	3.83	3.07	1.76	1.76	2.93	4.30
<i>Sylvilagus floridanus</i>	1.44	1.15	1.35	1.35	0.84	1.61
Rodentia						
<i>Sciurus aureogaster</i>	3.35	2.68	0.58	0.58	0.85	3.76
<i>Spermophilus variegatus</i>	0.48	0.38	0.87	0.87	0.18	0.54
<i>Liomys irroratus</i>	0.96	0.77	0.04	0.04	0.02	1.07
<i>Liomys</i> sp.	0.48	0.38	0.05	0.05	0.01	0.54
Unidentified mammal	1.44	1.15				
Aves						
Galliformes						
<i>Ortalis poliocephala</i>	6.70	5.36	0.58	0.58	1.68	7.52
Unidentified bird	0.48	0.38				
Reptilia						
Squamata						
<i>Ctenosaura pectinata</i>	0.48	0.38	1.05	1.05	0.22	0.54
Testudines						
<i>Kinosternon integrum</i>	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		
<i>Capra hircus</i>	23.08	17.65
<i>Odocoileus virginianus</i>	7.69	5.88
Carnivora		
<i>Nasua narica</i>	15.38	11.76
<i>Procyon lotor</i>	7.69	5.88
<i>Conepatus leuconotus</i>	7.69	5.88
Cingulata		
<i>Dasyurus novemcinctus</i>	38.46	29.41
Lagomorpha		
<i>Sylvilagus cunicularius</i>	7.69	5.88
<i>Sylvilagus floridanus</i>	15.38	11.76
Reptilia		
Squamata		
<i>Ctenosaura pectinata</i>	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):

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

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): $E_i = (r_i - n_i)/(r_i + n_i)$ where r_i is the percentage of species i in the diet and n_i 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
<i>D. novemcinctus</i>	2398.7 ^a	4.82	Males	3143.7	60
			Females with/cubs	2705.4	52
			Females without/cubs	2420.0	46
<i>N. narica</i>	2225.3 ^a	4.88	Males	3143.7	19
			Females with/cubs	2705.4	17
			Females without/cubs	2420.0	15
<i>O. virginianus</i>	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
<i>Bassariscus astutus</i>	5	0.07	6
<i>Conepatus leuconotus</i>	13	0.19	13
<i>Dasyurus novemcinctus</i>	8	0.12	8
<i>Didelphis virginiana</i>	30	0.44	31
<i>Mephitis macroura</i>	6	0.09	6
<i>Nasua narica</i>	233	3.38	483
<i>Odocoileus virginianus</i>	86	1.25	120
<i>Procyon lotor</i>	15	0.22	30
<i>Sciurus aureogaster</i>	24	0.35	28
<i>Spilogale putorius</i>	2	0.03	2
<i>Sylvilagus cunicularius</i>	36	0.52	44
<i>Sylvilagus floridanus</i>	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

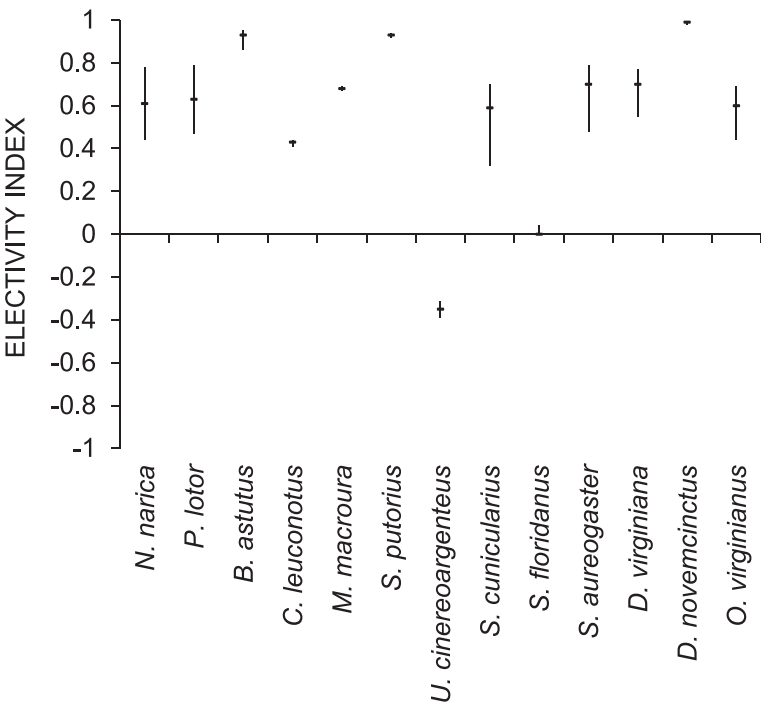


Figure 2. Values of electivity index with confidence interval (95% CI) of diet of pumas in the SNNP, Mexico.

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 de-

termine 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.

References

Ackerman, B.B., Lindzey, F.G. & Hemker, T.P. 1984: Cougar food habits in Southern Utah. - *Journal of Wildlife Management* 48: 147-155.

- Andheria, A.P., Karanth, K.U. & Kumar, N.S. 2007: Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. - *Journal of Zoology* (London) 273: 169-175.
- Aranda, M. 2000: Huellas y otros rastros de los mamíferos grandes y medianos de México. - Instituto de Ecología A.C, Xalapa, México, 212 pp. (In Spanish).
- Aranda, M. & Sánchez-Cordero, V. 1996: Prey spectra of jaguar (*Panthera onca*) and puma (*Puma concolor*) in tropical forest of Mexico. - *Studies of Neotropical Fauna and Environment* 31: 65-67.
- Azevedo, F.C. 2008: Food habits and livestock depredation of sympatric jaguars and pumas in the Iguazu National Park Area, South Brazil. - *Biotropica* 40: 494-500.
- Biswas, S. & Sankar, K. 2002: Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. - *Journal of Zoology* (London) 256: 411-420.
- Breuer, T. 2005: Diet choice of large carnivores in northern Cameroon. - *African Journal of Ecology* 43: 97-106.
- Cunningham, S.C., Haynes, L.A., Gustavson, C. & Haywood, D.D. 1995: Evaluation of the interaction between mountain lions and cattle in the Aravaipa-Klondyke area of southeast Arizona. - Arizona Game and Fish Department, Phoenix, Arizona, USA, technical report 17, 64 pp.
- Emmons, L.H. 1987: Comparative feeding ecology of felids in a tropical rainforest. - *Behavioral Ecology and Sociobiology* 20: 271-283.
- Fox, L.R. & Morrow, P.A. 1981: Specialization: species property or local phenomenon? - *Science* 211: 887-893.
- Garla, R.C., Setz, E.Z.F. & Gobbi, N. 2001: Jaguar (*Panthera onca*) food habits in Atlantic rain forest of southeastern Brazil. - *Biotropica* 33: 691-696.
- Glen, A.S., Byrom, A.E., Pech, R.P., Cruz, J., Schwab, A., Sweetapple, J., Yockney, I., Nugent, G., Coleman, M. & Whitford, J. 2012: Ecology of brushtail possums in a New Zealand dryland ecosystem. - *New Zealand Journal of Ecology* 36: 29-37.
- Glen, A.S., Pennay, M., Dickman, C.R., Wintle, B.A. & Firestone, K.B. 2011: Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. - *Austral Ecology* 36: 290-296.
- Gómez-Ortiz, Y., Monroy-Vilchis, O., Fajardo, V., Mendoza, G.D. & Urios, V. 2011: Is food quality important for carnivores? The case of *Puma concolor*. - *Animal Biology* 61: 277-288.
- Griffiths, D. 1975: Prey availability and the food of predators. - *Ecology* 56: 1209-1214.
- Hackenburger, M.K. & Atkinson, J.L. 1983: The apparent digestibilities of captive tigers (*Panthera tigris* spp.). - In: Meehan, T.P. & Allen, M.E. (Eds.); *Proceeding of the third annual Dr. Scholl Conference on the nutrition of captive wild animals*. Park District and Lincoln Park Zoological Society, Chicago, USA, pp. 70-83.
- Hass, C.C. & Valenzuela, D. 2002: Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). - *Behavioral Ecology and Sociobiology* 51: 570-578.

- Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley G.I.H. 2006: Prey preferences of the leopard (*Panthera pardus*). - Journal of Zoology (London) 270: 298-213.
- Hayward, M.W. & Kerley, G.I.H. 2005: Prey preferences of the lion (*Panthera leo*). - Journal of Zoology (London) 267: 309-22.
- Hayward, M.W. & Kerley, G.I.H. 2008: Prey preferences and dietary overlap amongst Africa's large predators. - South African Journal of Wildlife Research 38: 93-108.
- Iriarte, J., Franklin, A., Johnson, W. & Redford, H. 1990: Biogeographic variation of food habits and body size of the American puma. - Oecologia 85: 185-190.
- Ivlev, V.S. 1961: Experimental ecology of the feeding of fishes. - Yale University Press, New Haven, Connecticut, USA, 302 pp.
- Kortello, A.D., Hurd, T.E. & Murray, D.L. 2007: Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff national park, Alberta. - Ecoscience 14: 214-222.
- Krebs, C.J. 1999: Ecological methodology. - Benjamin Cummings, California, USA, 620 pp.
- Kunkel, K.E., Ruth, T.K., Pletscher, D.H. & Hornocker, M.G. 1999: Winter prey selection by wolves and cougars in and near glacier national park Montana. - Journal Wildlife Management 63: 901-910.
- Laundré, J.W. 2005: Puma energetics: a recalculation. - Journal of Wildlife Management 69: 723-732.
- Logan, K.A. & Sweanor, L.L. 2001: Desert Puma. - Island press, Washington D.C., USA, 463 pp.
- Monroy-Vilchis, O., Gómez, Y., Janczur, M. & Urios, V. 2009a: Food niche of *Puma concolor* in Central Mexico. - Wildlife Biology 15(1): 97-105.
- Monroy-Vilchis, O., Rodríguez-Soto, C., Zarco-González, M. & Urios, V. 2009b: Cougar and jaguar habitat use and activity patterns in central Mexico. - Animal Biology 59: 145-157.
- Monroy-Vilchis, O. & Rubio-Rodríguez, R. 2003: Guía de identificación de mamíferos terrestres del Estado de México, a través del pelo de guardia. - Universidad Autónoma del Estado de México, Toluca, México, 115 pp. (In Spanish).
- Monroy-Vilchis, O., Sánchez, O., Aguilera-Reyes, U., Suárez, P. & Urios, V. 2008a: Jaguar (*Panthera onca*) in the State of Mexico. - Southwestern Naturalist 53: 533-537.
- Monroy-Vilchis, O., Zarco-González, M.M., Ramírez-Pulido, J. & Aguilera-Reyes, U. 2011a: Diversidad de mamíferos de la Reserva Natural Sierra Nanchititla, México. - Revista Mexicana de Biodiversidad 82: 237-248. (In Spanish).
- Monroy-Vilchis, O., Zarco-González, M., Rodríguez-Soto, C., Soria-Díaz, L. & Urios, V. 2011b: Fototrampeo de mamíferos en la Sierra Nanchititla, México: Abundancia relativa y patrón de actividad. - Revista de Biología Tropical 59: 373-383. (In Spanish).
- Monroy-Vilchis, O., Zarco-González, M., Rodríguez-Soto, C., Suárez, P. & Urios, V. 2008b: Uso tradicional de vertebrados silvestres en la Sierra Nanchititla, México. - Interciencia 33: 308-313. (In Spanish).
- Moreno, R.S., Kays, R.W. & Samudio, R. 2006: Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. - Journal of Mammalogy 87: 808-816.
- Morse, D.H. 1974: Niche breadth as a function of social dominance. - American Naturalist 108: 818-830.
- Neale, J. & Sacks, B. 2001: Resource utilization and interspecific relations of sympatric bobcats and coyotes. - Oikos. 94: 236-249.
- Novack, A.J., Main, M.B., Sunquist, M.E. & Labisky, R.F. 2005: Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. - Journal of Zoology (London) 267: 167-178.
- Núñez, R., Miller, B. & Lindzey, F. 2000: Food habits of jaguars and pumas in Jalisco, Mexico. - Journal of Zoology (London) 252: 373-379.
- Núñez, R., Miller, B. & Lindzey, F. 2002: Ecología del jaguar en la reserva de la biosfera Chamela-Cuixmala, Jalisco, México. - In: Medellín, R.A., Equihua, C., Chetkiewicz, C., Crawshaw, P.G., Rabinowitz, A., Redford, K.H., Robinson J.G., Sanderson, E.W. & Taber, A.B. (Eds.); El jaguar en el nuevo milenio. Una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de jaguares en América. - Fondo de cultura económica, Distrito Federal, México, pp. 107-126. (In Spanish).
- O'Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. 2003: Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. - Animal Conservation 6: 131-139.
- Pianka, E.R. 1974: Niche overlap and diffuse competition. - Proceedings of the National Academy of Sciences of the United States of America 71: 2141-2145.
- Polisar, J., Maxit, I., Scognamiglio, D., Farrell, L., Sunquist, M.E. & Eisenberg, J.F. 2003: Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. - Biological Conservation 109: 297-310.
- Power, R.J. 2002: Prey selection of lions *Panthera leo* in a small, enclosed reserve. - Koedoe 45: 67-75.
- Rabinowitz, A.R. 1989: The density and behavior of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. - Natural History Bulletin of the Siam Society 37: 235-251.
- Rodríguez-Soto, C., Monroy-Vilchis, O., Maiorano, L., Boitani, L., Faller, J.C., Briones, M.A., Núñez, R., Rosas-Rosas, O., Ceballos, G. & Falcucci, A. 2011: Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: identification of priority areas for conservation. - Diversity and Distributions 17: 350-361.
- Rosas-Rosas, O.C., Bender, L.C. & Valdez, R. 2008: Jaguar and puma predation on cattle calves in Northeastern

- Sonora, Mexico. - *Rangeland Ecology and Management* 61: 554-560.
- Rosas-Rosas, O.C., Valdez, R., Bender, L.C. & Daniel, D. 2003: Food habits of puma in northwestern Sonora, Mexico. - *Wildlife Society Bulletin* 31: 528-535.
- Salame-Méndez, A., Andrade-Herrera, M., Zamora-Torres, H., Serrano, H., Soto-Mendoza, S., Castro-Campillo, A., Ramírez-Pulido, J. & Haro-Castellanos, J. 2012: Método optimizado para evaluar ácidos biliares de muestras fecales secas o preservadas en etanol como herramienta para identificar carnívoros silvestres. - *Acta Zoológica Mexicana* 28: 305-320. (In Spanish).
- Sánchez, O., Ramírez-Pulido, J., Aguilera-Reyes, U. & Monroy-Vilchis, O. 2002: Felid record from the state of México, México. - *Mammalia* 66: 228-294.
- Scognamillo, D., Maxit, I., Sunquist, M. & Polisar, J. 2003: Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. - *Journal of Zoology (London)* 259: 269-279.
- Seymour, K.L. 1989: *Panthera onca*. - *Mammalian Species* 340: 269-279.
- Soria-Díaz, L., Monroy-Vilchis, O., Rodríguez-Soto, C., Zarco-González, M.M. & Urios, V. 2010: Variation of abundance and density of *Puma concolor* in zones of high and low concentration of camera traps in central Mexico. - *Animal Biology* 60: 361-371.
- Sunquist, M. & Sunquist, F. 1989: Ecological constraints on predation by large felids. - In: Gittleman, J.L. (Ed.); *Carnivore behaviour, ecology and evolution*. University Press, Cornell, USA, pp. 283-301.
- Taber, A., Novaro, A., Neris, N. & Colman, F. 1997: The food habits of sympatric jaguar and puma in the Paraguayan Chaco. - *Biotropica* 29: 204-213.
- Wegge, P., Odden, M., Pokharel, C.P. & Storaas, T. 2009: Prey relationships and responses of ungulate predators to the establishment of protected areas: a case study of tigers, leopards and their prey in Bardia National Park, Nepal. - *Biological Conservation* 142: 189-202.
- Yasuda, M. 2004: Monitoring diversity and abundance of mammals with camera traps: a case study on mount Tsukuba, central Japan. - *Mammal Study* 29: 37-46.
- Zarco-González, M.M., Monroy-Vilchis, O. & Alaníz, J. 2013: Spatial model of livestock predation by jaguar and puma in Mexico: Conservation planning. - *Biological Conservation* 159: 80-87.
- Zarco-González, M.M., Monroy-Vilchis, O., Rodríguez-Soto, C. & Urios, V. 2012: Spatial factors and management associated with livestock predations by *Puma concolor* in Central Mexico. - *Human Ecology* 40: 631-638.
- Zepeda, C., Monroy-Vilchis, O., Velázquez-Montes, E. & Rodríguez-Soto, C. 2008: Primer registro de *Cyathea fulva* (Cyatheaceae, Polypodiopsida) en el Estado de México. - *Boletín de la Sociedad Botánica Mexicana*. 83: 93-96. (In Spanish).