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Food niche of *Puma concolor* in central Mexico

Octavio Monroy-Vilchis, Yuriana Gómez, Mariusz Janczur & Vicente Urios

Optimal foraging theory predicts that predators choose the most energetically profitable prey. At the northern limit of its distribution the puma *Puma concolor* tends to prey on large mammals, whereas at the southern limit its prey comprises medium-sized and small mammals. We analysed the puma's food habits in Central Mexico, and concluded that the nine-banded armadillo *Dasypus novemcinctus* is the main prey, followed by the white-nosed coati *Nasua narica* and white-tailed deer *Odocoileus virginianus*. The puma's standardised niche breadth (B') was 0.21 and was in accordance with the expected in the exponential model. We compared this with niche breadths recorded in other studies carried out in the Americas. After a forest fire, puma changed their feeding habits and began to hunt prey >6.1 kg more frequently. Food preferences of puma in Central Mexico resemble those recorded for puma in South America rather than the preferences recorded for puma in other North American populations.

Key words: carnivore, diet, mountain lion, Sierra Nanchititla, State of Mexico

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Food habits are important niche parameters, since good nutrition implies a larger reproductive outcome and increased survival, and thus a higher net reproductive output (Krebs 1999). Prey availability and vulnerability affect carnivore prey selection (Sunkist & Sunkist 1989). The puma *Puma concolor* preys mainly on large mammals at the northern limit of its distribution and on medium-sized and small mammals at its southernmost distribution limit (Iriarte et al. 1990). Recent studies on the puma's food habits from the neoarctic region (Currier 1983, Sweitzer et al. 1997, Pierce et al. 2000, Logan & Sweanor 2001, Laundré & Hernández 2003) confirm that nearly all its prey are artiodactyls weighing

>6.1 kg. On the other hand, the average prey of neotropical puma weighs <6.1 kg (Wilson 1984, Yañez et al. 1986, Emmons 1987, Iriarte et al. 1990, Brach 1995, Romo 1995, Chinchilla 1997, Taber et al. 1997, Bank & Franklin 1998, Franklin et al. 1999, Novaro et al. 2000, Bank et al. 2002, Mazzolli et al. 2002, Polisar et al. 2003), and very rarely >6.1 kg (Moreno et al. 2006). A number of studies show that artiodactyls are also the principal prey of puma in the neoartic-neotropical transition region (Aranda & Sánchez-Cordero 1996, McClinton et al. 2000, Núñez et al. 2000, Rosas-Rosas et al. 2003).

Analysis of scat content (e. g. species frequency or percentage) of carnivores is not very accurate

(Weaver 1993, Monroy-Vilchis & Frieven 2006); therefore some authors suggest that complementary data such as relative biomass (Ackerman et al. 1984) and minimum number of individuals consumed (Monroy-Vilchis et al. submitted) should be gathered. Both of these methods involve correction factors that improve their precision.

In our study, we determined the puma's food habits in the Sierra Nanchititla, Central Mexico. The results of Iriarte et al. (1990) suggest that white-tailed deer *Odocoileus virginianus* would comprise the predominant prey of puma at the geographic latitude of our study area.

pine-oak forest in the highlands (47%) and tropical deciduous forest in the lowlands (18%). There are introduced grasslands (30%) and agricultural zones (4%) in both main vegetation types (Fig. 1). The closest large human population is Tejupilco with 84,897 inhabitants, situated 65 km away (INEGI 2000). Annual rainfall varies between 1,000 and 1,500 mm, and reaches its maximum during June - October (the rainy season). The climate in the pine-oak forest is temperate and semi-humid, with temperatures ranging from 12° to 16°C. In the deciduous forest the climate is hot and semi-humid (García 1988).

Study area

Our study was carried out in the Sierra Nanchititla Natural Reserve (SNNR), State of Mexico, Central Mexico, located between 19°36'46" and 18°45'38"N and 100°15'54" and 100°36'28"W. Our study area covers more than 660 km² and the elevation varies from 420 to 2,080 m a.s.l. The main vegetation is

Material and methods

We collected scats along 22 km of trails every 15 days from August 2002 to July 2004, principally in temperate upland habitat. Each scat was identified by both its morphological characteristics (Aranda 2000) and by comparing it with the scats of captive pumas. Due the presence of other carnivores such

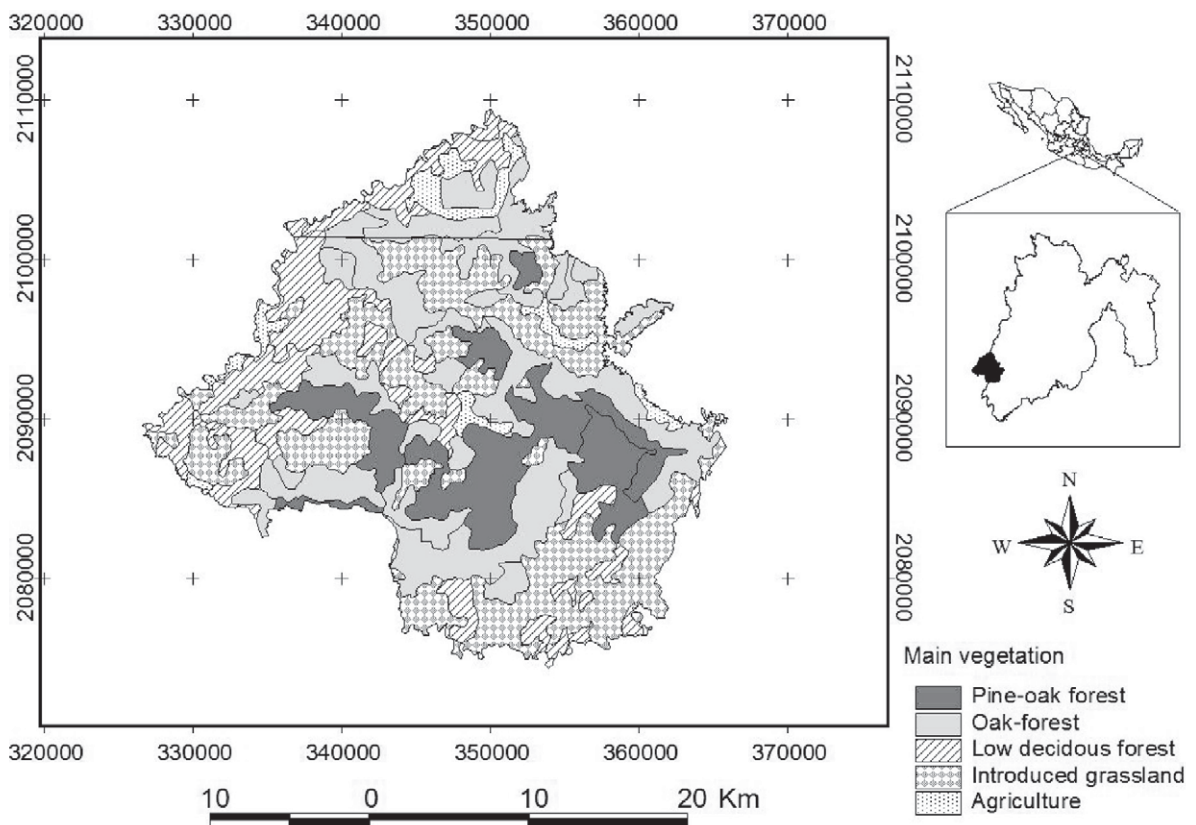


Figure 1. Main vegetation types at Sierra Nanchititla, México.

as the coyote *Canis latrans* and jaguar *Panthera onca* (Monroy-Vilchis et al. 2008), we placed camera traps on the trails to check the accuracy of our scat identification and, to avoid confusion with scats of smaller (ocelot *Leopardus pardalis*, margay *L. wiedii* and jaguarundi *Herpailurus yagouaroundi*) or larger (jaguar) carnivore species, we collected only scats which were >20 mm or <35 mm in width. We recorded date, geographic position, altitude (in m a.s.l.), weight, length and width of the scat as well as the vegetation cover. Furthermore, we washed the scats and separated their components (e.g. hair, bones, feathers and scales). Prey identification was carried out in two ways. The bones and teeth of mammals were compared with samples from the collection of Estación Biológica Sierra Nanchititla, Universidad Autónoma del Estado de México (EBSN-UAEM). Afterwards, hairs were identified according to the Monroy-Vilchis & Rubio-Rodríguez (2003) method which involves the estimation of both macroscopic (hair length and shape) and microscopic (hair width and medulla type) characteristics, as well as preparation of slides and comparison with those in the EBSN-UAEM collection. We identified birds and reptiles by comparing their claws, feathers and shells with samples from local species.

We used the following method to estimate the minimum number of scats needed to describe the puma's diet in the further studies. We selected a random sample of 10 scats out of the scats collected and compared the frequency of prey species in the samples with their frequency in all the scats collected by using χ^2 test. If this frequency differed, we selected another random sample of five scats and compared the frequency of prey species in the 15 scats with their respective frequency in the whole set of scats collected (N=104). We repeated the sampling and incremented the sample size until the frequency in the sample was not significantly different from its frequency in the total scat set. Additionally, we carried out an analogous estimation of scat sample size by plotting a prey accumulation curve.

We used frequency of occurrence to compare our results with results obtained in other studies, even though this method is not very accurate (Floyd et al. 1978, Ackerman et al. 1984, Monroy-Vilchis & Frieven 2006). Additionally, we looked at other data such as relative biomass consumed (Ackerman et al. 1984) and minimum number of prey consumed (Monroy-Vilchis et al. submitted). We obtained niche breadth using Levin's index and niche over-

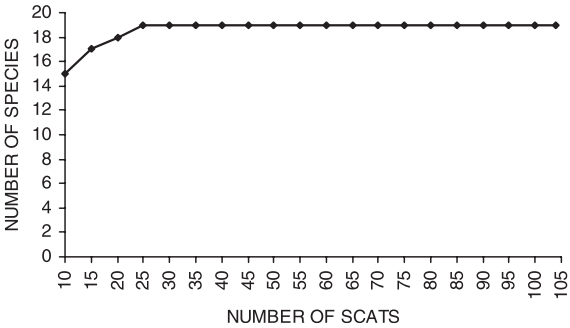


Figure 2. Relationship between number of scats and number of prey species in the diet of pumas at Sierra Nanchititla.

lap between humid and dry seasons using the MacArthur and Levin's measure (Krebs 1999). Finally, we estimated the relationship between standardised niche breadths and geographic latitude based on several studies of puma, using the highest indicator

Table 1. Frequency of occurrence of prey in 104 puma scats at Sierra Nanchititla.

Prey items	Season		Total
	Wet	Dry	
MAMMALIA			
Artiodactyla			
<i>Bos taurus</i>	1	4	5
<i>Odocoileus virginianus</i>	6	9	15
<i>Capra hircus</i>	5	2	7
Carnivora			
<i>Urocyon cinereoargenteus</i>	0	1	1
<i>Nasua narica</i>	5	18	23
<i>Procyon lotor</i>	1	1	2
<i>Bassariscus astutus</i>	1	4	5
<i>Canis latrans</i>	0	1	1
<i>Mustela frenata</i>	0	1	1
<i>Spilogale putorius</i>	0	1	1
Xenarthra			
<i>Dasypus novemcinctus</i>	14	47	61
Lagomorpha			
<i>Sylvilagus floridanus</i>	1	3	4
<i>Sylvilagus cunicularius</i>	1	2	3
Rodentia			
<i>Sciurus aureogaster</i>	1	5	6
<i>Lyomys</i> sp.	1	0	1
Didelphimorphia			
<i>Didelphis virginiana</i>	0	3	3
Unidentified mammals	0	3	3
AVES			
Galliformes			
<i>Ortalis poliocephala</i>	0	8	8
REPTILIA			
Testudines			
<i>Kinosternon integrum</i>	0	1	1
TOTAL	37	114	151
Number of scats	25	79	104

Table 2. Frequency of occurrence of relative biomass consumed and minimum number of consumed organism in 104 puma scats at Sierra Nanchititla. The daily maximum biomass of large prey a captive puma can ingest is 6,130 g (O. Monroy-Vilchis, unpubl. data).

Species	Absolute frequency	Average weight of prey (g)	Frequency of occurrence	Correction factors ^a	Relative biomass consumed	Relative biomass consumed (%)	Correction factors ^b	Minimum number of organisms consumed	Proportion consumed by organism
Mammals >6,130 g									
<i>Bos taurus</i>	5	6130	4.80	2.19	0.034	3.4	8.69	0.57	0.026
<i>Odocoileus virginianus</i>	15	6130	14.42	2.19	0.103	10.3	8.69	1.72	0.081
<i>Capra hircus</i>	7	6130	6.73	2.19	0.048	4.8	8.69	0.8	0.037
Mammals <6,130 g									
<i>Urocyon cinereoargenteus</i>	1	5000	0.96	2.15	0.006	0.6	8.17	0.12	0.005
<i>Nasua narica</i>	23	4800	22.12	2.14	0.155	15.5	8.06	2.85	0.134
<i>Procyon lotor</i>	2	5500	1.92	2.17	0.013	1.3	8.41	0.23	0.01
<i>Bassariscus astutus</i>	5	1250	4.80	2.02	0.031	3.1	5.34	0.93	0.043
<i>Conepatus mesoleucus</i>	1	2700	0.96	2.07	0.006	0.6	6.76	0.14	0.006
<i>Mustela frenata</i>	1	279	0.96	1.98	0.006	0.6	3.38	0.29	0.013
<i>Spilogale putorius</i>	1	386	0.96	1.99	0.006	0.6	3.73	0.26	0.012
<i>Dasypus novemcinctus</i>	61	4800	58.65	2.15	0.413	41.3	8.06	7.56	0.356
<i>Sylvilagus floridanus</i>	5	1500	4.80	2.03	0.031	3.1	5.65	0.88	0.041
<i>Sylvilagus cunicularius</i>	3	1500	2.88	2.03	0.019	1.9	5.65	0.53	0.025
<i>Sciurus aureogaster</i>	6	555	5.76	1.99	0.037	3.7	4.17	1.43	0.067
<i>Liomys</i> sp.	1	50	0.96	1.98	0.006	0.6	0.98	1.02	0.048
<i>Didelphis virginiana</i>	3	2700	2.88	2.07	0.019	1.9	6.76	0.44	0.02
<i>Ortalis poliocephala</i>	8	2940	7.69	2.08	0.052	5.2	6.94	1.15	0.054
<i>Kinosternon integrum</i>	1	300	0.96	1.99	0.006	0.6	3.45	0.28	0.013

^a These correction factors are from Ackerman et al. 1984, and

^b unpubl. data from this study.

(r) of several relationship analyses (using Statgraphics Plus 5.0 1994-2000). A natural forest fire occurred in the study area in May 2003. This event coincided with the mid point of the scat collection period and involved approximately 10 km². To evaluate the response of puma diet to disturbance, we grouped the prey into two categories, <6.1 kg and >6.1 kg.

Results

We covered approximately 1,440 km of different trails in the Reserve and collected 104 puma scats. Scat width ranged within 19.5-34.93 mm (28.94 ± 3.52 mm). These values were higher than those found from the other three felid species (margay, ocelot and jaguarundi) present in the study area (Sánchez et al. 2002). The minimum number of scats required to determine the puma's diet at Sierra Nanchititla was 15 using the analysis of frequencies ($\chi^2 = 12.72$, df=5, $P < 0.05$), and 25 using the prey accumulation analysis (Fig. 2).

We divided the remains of prey species into 21 groups: in some cases we were unable to determine the species accurately. We determined 17 species,

Table 3. Niche breadth of pumas as reported by different researchers from various parts of the American continent. References marked with ^a were not included in correlations because the exact location was not given.

Niche breadth	Location	Reference
0.08	Utah, USA	Ackerman et al. (1984)
0.06	Florida, USA	Darlympe & Bass (1996)
0.15	Florida, USA	Maehr et al. (1990)
0.41	USA-Mexico Border	Mcbride (1976) ^a
0.25	Sonora, Mexico	Rosas-Rosas et al. (2003)
0.38	Jalisco, Mexico	Núñez et al. (2000)
0.21	Central Mexico	Our study
0.37	Campeche, Mexico	Aranda & Sánchez-Cordero (1996)
0.27	México-Guatemala Border	Novack (2003)
0.79	Costa Rica	Chinchilla (1997)
0.34	Venezuela	Polisar et al. (2003)
0.29	Peru	Emmons (1987)
0.65	Peru	Romo (1995)
0.30	Brazil	Crawshaw (1995) ^a
0.33	Brazil	Brito et al. (1998) ^a
0.94	Brazil	Bachega (2004)
0.43	Brazil	Crawshaw & Quigley (2002)
0.40	Brazil	Leite & Galvão (2002)
0.68	Paraguay	Taber et al. (1997)
0.24	Chile	Courtin et al. (1980) ^a
0.13	Chile	Yáñez et al. (1986)
0.28	Chile	Rau et al. (1991) ^a
0.34	Southern Chile	Iriarte et al. (1990) ^a
0.24	Argentina	Branch (1994)

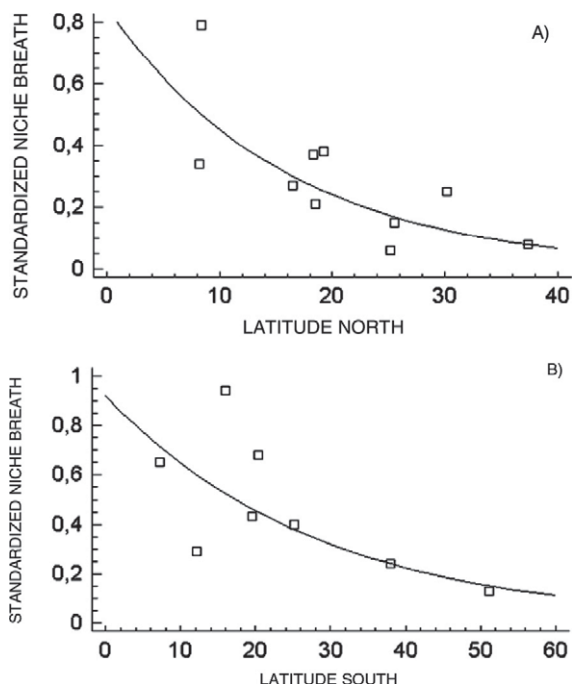


Figure 3. Relationship between latitude and niche breadth for puma in the North (A) and the South (B).

one genus and three unidentified species. Of the 104 scats, 50 contained grass, 90% mammals, 5% birds and 5% reptiles. The frequency of the nine-banded armadillo was the highest and was followed by the white-nosed coati and white-tailed deer (Table 1). We found puma hair in 12 scats, probably due to grooming activity.

Also, the relative biomass of the nine-banded armadillo was the highest (41.35%), followed by the white-nosed coati (15.54%) and white-tailed deer (10.35%). We recorded only one bird species, the West Mexican chachalaca *Ortalis poliocephala*, and one turtle species, the Mexican mud turtle *Kinosternon integrum* comprising 5.24 and 0.62% of relative biomass consumed, respectively (Table 2).

The puma's standardised niche breadth (B') over both seasons was 0.21, ranging from $B' = 0.21$ during the wet season, to $B' = 0.203$ during the dry season. The niche overlap between seasons was high ($O = 0.87$), suggesting a similarity of diet in both seasons. The rather low value of the standardised niche breadth suggests specialist habits of the puma at Sierra Nanchititla and resembles the pattern found at both its northern and southern distribution limits (Table 3). Data from our study and those of other authors (see Table 3) revealed a non-linear relationship between niche breadth and geographic latitude.

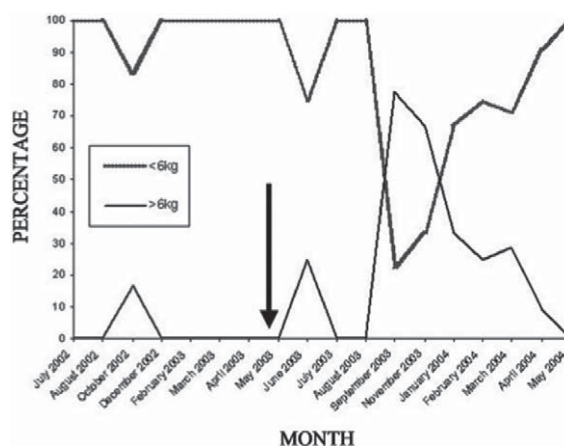


Figure 4. Percentage of prey larger and smaller than 6.1 kg biomass. The forest fire occurred in May 2003.

North of the equator line, it is described by the equation: North breadth niche = $\exp(-0.166 - 0.063 * \text{latitude North})$ ($r^2 = 56.53$, $P < 0.01$; Fig. 3A); and south of the equator line by the equation: South breadth niche = $\exp(-0.083 - 0.035 * \text{latitude South})$ ($r^2 = 62.32$, $P < 0.01$; Fig. 3B).

We observed a significant modification in the puma's diet after the forest fire, when the pumas began hunting larger prey (Fig. 4). Interestingly, more species were taken after the fire ($N = 19$) than before ($N = 5$).

Discussion

Our study contradicts the conclusions of several previous studies regarding the puma's diet in North America. For example, Iriarte et al. (1990), Rosas-Rosas et al. (2003) and Núñez et al. (2002) argued that the puma's main prey are ungulates. However, we did not find such a pattern: the predominant prey in our study area was the nine-banded armadillo. This is probably not because armadillos are more widely available in our area, since white-tailed deer are also quite common and are the third most important prey of the puma. We do not know the precise cause of this phenomenon. At least three hypotheses can be put forward: 1) the armadillo is easier to hunt, 2) the armadillo's energy content is higher, and 3) armadillos are more abundant in the area than deer. In a future study we intend to estimate the energy content of different puma prey and to perform a cost-benefit analysis.

Analysis of minimum scat number provided similar results. The χ^2 test showed that a sample of 15

scats is sufficient to describe the puma's diet, whereas the prey accumulation curve indicates that 25 scats should be sampled. The two methods differed by only one prey species (see Fig. 2), so we considered 15 as a minimum sample size to determine the puma's diet at Sierra Nanchititla. Based on a total of 65 scats, Núñez et al. (2000) estimated an optimal sample size of 35 using a χ^2 test and 50 using a prey accumulation curve. The discrepancy between the results obtained by Núñez et al. (2000) and our own study is difficult to explain, although we note that their work was conducted in a tropical environment where prey diversity is much higher. Furthermore, their identification method was less robust, since they identified 11 items, many of them only to genus and class level.

An interesting outcome of our study is the low frequency of large mammals, e.g. white-tailed deer, which is similar to the pattern found in studies carried out at the southern limit of the species' range (see Table 2). On the other hand, this frequency is different to that recorded in studies performed in the northern and southern parts of Mexico (Aranda & Sánchez-Cordero 1996, Núñez et al. 2000, Rosas-Rosas et al. 2003) and in North America (Ackerman et al. 1984, Maehr et al. 1990, Darlympe & Bass 1996, Logan & Sweanor 2001).

The frequency of the main prey in the puma's diet varies considerably in relation to geographic zone. The factors that determine prey size of large felids are availability and vulnerability (Sunquist & Sunquist 1989, Malo et al. 2004, Lozano et al. 2006). Rabinowitz & Nottingham (1986) stated that the armadillo is particularly vulnerable to attack by large felids such as jaguar and puma. The nine-banded armadillo is the principal prey of puma in Brazil (Leite & Galvão 2002). We believe that a puma would have to invest more energy in hunting a deer than in hunting an armadillo, as it is morphologically adapted to stalking and short runs rather than to long-distance runs (Sunquist & Sunquist 2002). Additionally, an armadillo better fulfils the caloric requirements of the puma (Monroy-Vilchis et al. submitted).

We did not identify species of the genus *Lyomis* because we found only teeth and damaged hairs, and were therefore unable to estimate hair-width, a necessary criterion for identification of *Lyomis* species (Monroy-Vilchis & Rubio-Rodríguez 2003). The only bird species we found in the puma's diet, the West Mexican chachalaca, was the fourth most common prey according to the three methods of

analysis used. In our study, the intake of birds was more frequent than found in other studies. This may be a result of the dietary flexibility of puma or/and disturbance of the environment. Ingestion of turtles (Testudines) was low (0.96% during the dry season only) and our results were similar to those reported by Núñez et al. (2000) and Logan & Sweanor (2001). The presence of grass is associated with its emetic function during hair expulsion, formation of the faecal matter and its antihelminthic property (Logan & Sweanor 2001).

In Sierra Nanchititla, small livestock e.g. domestic goat *Capra hircus* predation is more important than predation of large livestock e.g. domestic cow *Bos taurus*, primarily because goats are more abundant than cows. However, livestock predation in our study zone is less important (6.73 and 4.8% of domestic goats and cows, respectively) than has been found in other studies (Yañez et al. 1986, Cashman et al. 1992), and may be considered incidental. Traditionally, livestock predation is attributed to old, sick, wounded or young puma and/or livestock displaying the same condition (Sáenz & Carrillo 2002).

The results of our study do not match the geographic dietary pattern predicted by Iriarte et al. (1990) and confirmed by other studies from México (Aranda & Sánchez-Cordero 1996, Núñez et al. 2000, Rosas-Rosas et al. 2003) because artiodactyls are not the most important prey of the puma in Nanchititla. The nine-banded armadillo and the white-nosed coati are the main prey in Nanchititla (both weighing <6.1 kg), and our results are similar to those reported from South America (Taber et al. 1997, Leite & Galvão 2002, Polisar et al. 2003, Bachega 2004). Contrary to the suggestion put forward by Iriarte et al. (1990), we believe that dietary pattern cannot be explained by geographic latitude alone. Our results suggest that altitude, vegetation cover and prey availability modify the dietary pattern of the puma. Even in the highlands, where dietary patterns of puma should be similar to those of northern North American puma, small non-artiodactyls were more abundant in the diet. Iriarte's model may not be robust enough because it includes fewer studies, a large area and homogenises information from places as different as Chiapas (tropical forest), Chamela (tropical deciduous forest) and Sonora (desert). On the other hand, the puma's diet depends on the abundance, vulnerability and energy content of its prey. Furthermore, coexistence with the jaguar may modify the latitudinal dietary pattern of puma (Iriarte et al. 1990, Aranda & Sánchez-Cordero

1996, Novaro et al. 2000, Mazzolli et al. 2002, Moreno et al. 2006), although more studies would be required to confirm this.

Puma diet changed after a forest fire, switching back to the original diet in the second year after the fire. This was a result of an increase in the food-base of deer which mainly feed on shrubs and herbaceous plants (Galindo-Leal & Weber 1998). Puma probably hunted more species after the fire because they were forced to search for prey outside their previous hunting habitat. Indeed, Dess et al. (2001) observed an increase of the habitat use by puma during the first year after a fire, correlated with the appearance of new prey species. In our study, we registered an increase in the consumption of white-tailed deer and domestic cows and goats during this period which is concordant with the results reported by Woodroffe (2001), who stated that in disturbed habitats the puma tends to hunt larger prey. Michalski et al. (2006) also provided evidence of an increase in livestock predation by puma in fragmented areas of South America. This phenomenon has implications for conservation of the puma because increased predation on livestock leads to an increase in human-puma conflict, thus adding a new factor which may contribute to the extinction of the species (Woodroffe & Ginsberg 1998).

The niche breadth found in our study ($B' = 0.21$) suggests that the puma consumes large amounts of few prey species, which reveals a tendency for food specialisation. Our results do not confirm results obtained in other studies as we did not find evidence for selective consumption of large animals such as artiodactyls. In Sierra Nanchititla, we found puma specialise in small mammal prey such as the nine-banded armadillo. The availability of wild artiodactyls at some sites within the puma's distribution range is important in determining its diet. However, greater availability of small mammals, particularly of armadillos, modifies puma feeding behaviour, and the nine-banded armadillo is a key component of the puma's diet in some places.

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