Jaguar (Panthera onca) and puma (Puma concolor) diets in Quintana Roo, Mexico

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Abstract

*Jaguar (*Panthera onca*) and puma (*Puma concolor*) diets in Quintana Roo, Mexico*. A study was carried out for two years in Northwest Quintana Roo, México, using scat analysis to determine the diet and prey preferences of pumas and jaguars. Cat species and gender were determined using molecular techniques (rapid classificatory protocol: polymerise chain reaction, RCP–PCR), and prey abundance was estimated from camera trapping. The scats contained remains from 16 wild mammal species, but there was no evidence of livestock or other taxa. The diet breadths of jaguar (0.32) and puma (0.29) indicated a high degree of prey specialization, which combined with their dietary overlap (Pianka index 0.77) suggested competition between them. However, both felids showed a preference for red brocket deer *Mazama temama*, and frequently consumed collared peccaries *Pecari tajacu*. The importance of such large ungulates in the felids' diets is similar to the expected patterns of wild meat consumption in rural areas of the Northern Yucatan Peninsula. Therefore, future conservation management plan initiatives should involve local rural communities in the management of sustainable hunting, considering these ungulates are also the felid prey species.

Key words: Diet breadth, Diet overlap, Felines, Human–felid conflict, Subsistence hunting, Wild meat

Resumen

*La dieta del jaguar (*Panthera onca*) y del puma (*Puma concolor*) en Quintana Roo, en México.* El estudio se realizó durante dos años en el noroeste de Quintana Roo, en México y se utilizó el análisis de excrementos para determinar la dieta y las preferencias de presas del puma y del jaguar. Se utilizaron técnicas moleculares para identificar la especie de félido y el sexo (protocolo de clasificación rápida: reacción en cadena de la polimerasa, RCP–PCR), y se estimó la abundancia de presas mediante el método de trampeo fotográfico. Los excrementos contenían restos de 16 especies de mamíferos salvajes, pero no se encontraron restos de ganado ni de otros taxones. La amplitud de la dieta del jaguar (0,32) y del puma (0,29) indica que son especies con un alto grado de especialización, lo cual, junto con el traslape de las dietas (índice de Pianka = 0,77) sugiere que ambos félidos compiten entre sí. Asimismo, ambos mostraron preferencia por el venado temazate, *Mazama temama*, y frecuentemente consumieron pecarí de collar, *Pecari tajacu*. La importancia de la presencia de este tipo de ungulados en la dieta de los félidos se corresponde con la pauta esperada de consumo de carne de caza en las zonas rurales del norte de la península de Yucatán. Por lo tanto, las futuras iniciativas encaminadas a planificar la conservación de ambos félidos deberían hacer partícipes a las comunidades rurales en la gestión de la cacería sustentable, considerando que estos ungulados también son presas de los félidos.

Palabras clave: Amplitud de dieta, Traslape de dieta, Félidos, Conflicto humano–félido, Caza de subsistencia, Carne de caza

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Introduction

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are two large felids that occur sympatrically across much of the Americas. The distribution of jaguar populations ranges from northern Mexico to Argentina, but has declined in recent years and they are currently thought to occupy only about 46 % of their historic range (Sanderson et al., 2002). The IUCN considers the jaguar to be a Near Threatened species and it is listed in Appendix I of CITES (Caso et al., 2008). In contrast, pumas have a much wider geographical distribution and tolerate a wider range of climate types than jaguars, and occur from Canada throughout parts of the USA, Central and South America, including the southern tip of Chile (Sunquist and Sunquist, 2002). Pumas are listed as being species of Least Concern by the IUCN (Nielsen et al., 2015) and are included in Appendix II of CITES, although they no longer occur in some regions where they were previously common (Nowell and Jackson, 1996). However, the rarer Eastern and Central American subspecies of puma (*P. c. coryi*, *P. c. costaricensis* and *P. c. cougar*) are listed separately in Appendix I of CITES (Nowell and Jackson, 1996). In general, global populations of large felids continue to decline due to habitat loss and fragmentation, frequently exacerbated by the impact of increased human activity and the risk of conflict and persecution by hunters and livestock farmers (Loveridge et al., 2010; Foster et al., 2014). In the Yucatan Peninsula, socioeconomic development has caused large scale land–use changes including deforestation and habitat fragmentation (Cespedes–Flores and Moreno–Sánchez, 2010) which have been accompanied by increased hunting of wild game species (Naranjo et al., 2010). In tropical Mexico, up to 70 % of the meat consumed by rural communities originates from hunting, mainly large species of ungulate such as tapirs *Tapirus bairdii*, white–tailed deer, *Odocoileus virginianus*, and collared and white–lipped peccaries (*Pecari tajacu* and *Tayassu pecari*) (Marmolejo, 2000), which are also consumed by large predators.

The jaguar and puma are obligate carnivores and where their distributions overlap in Central and Latin America (Sunquist and Sunquist, 2002) they both prey opportunistically on mammals (Oliveira, 2002; Scognamillo et al., 2003; Novack et al., 2005; Weckel et al., 2006). In the Southern Yucatan Peninsula, Mexico, both these felids mainly consume large prey like collared and white–lipped peccaries, red brocket deer (*Mazama temama*) and white–tailed deer (Chávez et al., 2007). Despite the potential for interspecific competition for food, these similarly–sized felids are able to coexist in many parts of their range through differences in their prey–use, including specialization according to the size, species, age and total biomass of prey consumed, combined with differences in their spatial and temporal habitat–use (Taber et al., 1997; Chávez, 2010). Therefore, the prey preferences and diet breadths of the two cats can vary according to the local availability and abundance of prey (Núñez et al., 2000; Hernández–Saint Martín et al., 2015).

The Yucatan Peninsula has the largest jaguar population in Mexico (Chávez et al., 2007) and is one of six proposed priority areas for its conservation (Rodríguez–Soto et al., 2011). However, little is known about the diet or likely competition for prey between these two felids and humans in the Northern Yucatan Peninsula (Ávila–Gómez, 2003). Therefore, the objectives of the present study were: (1) to determine the diet and prey consumption patterns of both cat species; (2) to estimate their trophic niche widths and the degree of prey specialization; and (3) to measure the amount of dietary overlap between them. The results were compared with published data on local hunting practices to explore the potential competition between the cats and local rural communities, and are considered in terms their implications for the sustainable management of large felids and their prey species in a region where socio–economic development continues to make profound changes to rural lifestyles (Santos–Fita et al., 2012).

Material and methods

Study site

The study took place in the Eden Ecological Reserve (Eden) and surrounding Lazaro Cardenas municipality, Quintana Roo, Mexico (21° 36' 00'' – 20° 34' 00'' N and 87° 06' 00'' – 87° 45' 00'' W). This 3077 ha private reserve is part of the Yalahau biological conservation region (Gómez–Pompa et al., 2011). The vegetation is dominated by medium–stature tropical forest and secondary forest (Schultz, 2003), and the reserve is surrounded by a landscape mosaic of secondary forest and managed habitats, including indigenous milpa cultivation (slash and burn) and rural villages.

Methods

Faecal pellet collection and camera trapping occurred during May to July 2011 and August to September 2012. The camera trap locations were selected using the CENJAGUAR (Chávez et al., 2007), which requires at least nine adjacent 9 km^2 study plots each containing two or three camera stations, with at least one station per plot having two cameras directly facing each other. Cameras were placed 1.5–3 km apart along a series of forest trails, firebreaks and dirt roads of differing lengths (8–16 km) and their locations are shown in figure 1 and described in Ávila–Nájera et al. (2015). In 2011, there were 22 camera stations operating continuously for 82 days, with 24 cameras operating over 72 days in 2012.

Scats were collected daily by systematically searching along each dirt road, firebreak and forest trail where the cameras were located. Scats were stored in plastic bags and divided into two. One half underwent a rapid classificatory protocol–PCR (RCP–PCR) to assign a species (jaguar or puma) and gender to the scat (Roques et al., 2011). This method consisted of a single–tube multiplex RCP–PCR yielding species–specific banding patterns on an agarose gel, which

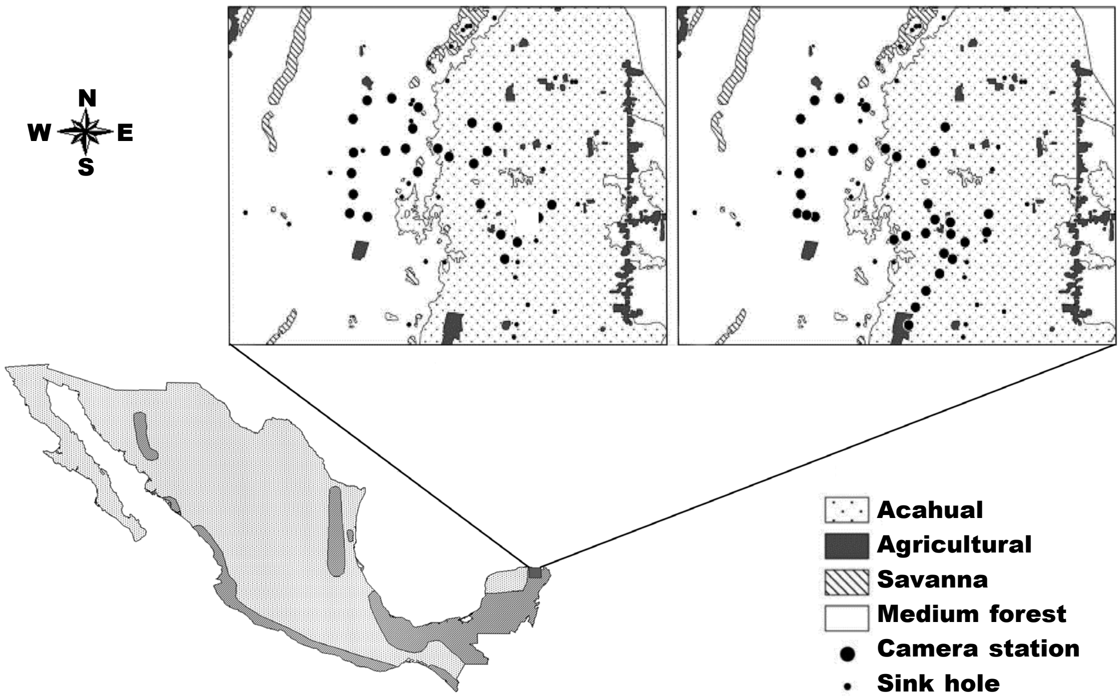

Fig. 1. Map of Mexico showing the current distribution of jaguars (*Panthera onca*) in grey dots and pumas (*Puma concolor*) in dark lines. The two boxes show the study site (the Eden Ecological Reserve, Quintana Roo) with vegetation types and camera site locations for 2011 (left) and 2012 (right).

*Fig. 1. Mapa de México en el que se muestra la distribución actual del jaguar (*Panthera onca*), en puntos grises, y la del puma (*Puma concolor*), en líneas oscuras. Los dos cuadros muestran el área de estudio (Reserva Ecológica El Edén, en Quintana Roo) con los tipos de vegetación y los sitios de muestreo fotográfico de 2011 (izquierda) y 2012 (derecha).*

ensures the unambiguous identification of jaguars and pumas from other felid species. For sex determination, we used Pilgrim et al.'s (2005) method based on the differences in size between the RCP–PCR products amplified from the male Y–chromosome copy (AMELY) and the X–chromosome gene (AMELX), and optimised for faecal samples from Neotropical felid species such as jaguar, puma, ocelot and margay, as described by Palomares et al. (2012). The other half of each scat was washed with water and oven dried at 45 °C; the remains of all traces of hair, bones and teeth were removed and identified by comparison with Mexican reference material, as described by Monroy–Vilchis and Rubio–Rodríguez (2003).

The relative consumption of each prey species was estimated from the frequency and percentage frequency of occurrence, and the percentage of times that remains of each species were recovered from scats. The relative amount of biomass consumption (RBC) of each prey species and the number of organisms consumed (NOC) were calculated for both felids using Ackerman et al.'s (1984) conversion for puma:

$$RBC = (AF*Y) / \sum / FA*Y$$

where AF is the absolute frequency of prey in the scats and Y is the weight of food consumed to generate a scat for each prey species and:

$$NOC = (RBC/p) \,/\, \sum (RBC/p)$$

where p is the mean live prey weight (kg) according to Ceballos and Oliva (2005), but excluding long–tailed weasels, *Mustela frenata*, which were the only species below the 2 kg threshold for this equation (Ackerman et al., 1984).

Dietary diversity (diet breadth) was calculated using Levins' index (Levins, 1968) and the overlap between the diet of jaguars and pumas was estimated using Pianka's index (Pianka, 1973). The overlap between the potential prey based on species identified in the camera traps, and actual prey species recovered in the scats was estimated using Sorensen's similarity coefficient (Ss) (Krebs, 1999). The significance of the overall niche overlap between the cats was tested by comparing our observed values with values obtained by randomizing the original matrices following 1,000 iterations with the ra3 algorithm, using the EcoSim–R package in R (Gotelli and Entsminger, 2001; Winemiller and Pianka, 1990).

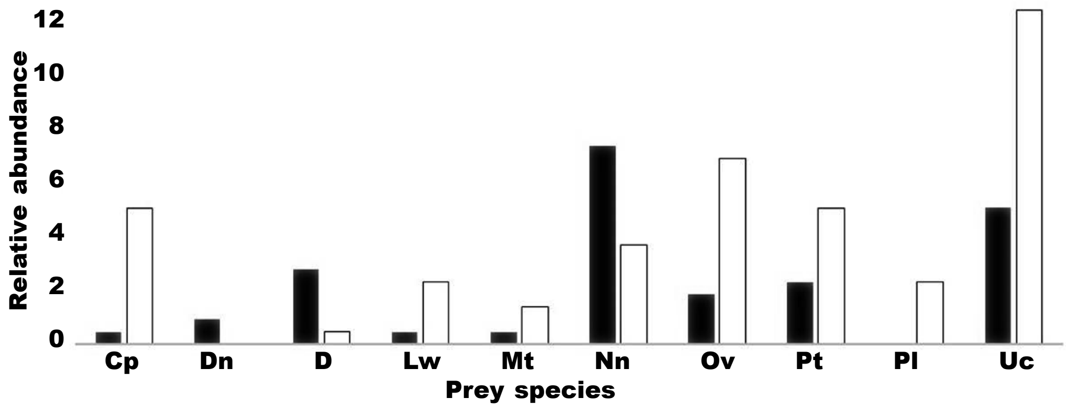

Fig. 2. Annual relative abundance of felid prey from camera trapping at the Eden Ecological Reserve, Mexico, for 10 species photographed (black bars show records for 2011 and white bars show records for 2012): Cp, *Cuniculus paca*; Dn, *Dasypus novemcinctus*; D, *Didelphys sp*; Lw, *Leopardus wiedii*; Mt, *Mazama temama*; Nn, *Nasua narica*; Ov, *Odocoileus virginianus;* Pt, *Pecari tajacu*; Pl, *Procyon lotor;* Uc, *Urocyon cinereoargenteus*.

Fig. 2. Abundancia relativa anual de presas de félidos por medio de trampeo fotográfico en la Reserva Ecológica El Edén, en México, para 10 especies fotografiadas (las barras negras y blancas muestran registros correspondientes a 2011 y 2012, respectivamente). (Para las abreviaturas de las especies presa, véase arriba).

The relative abundance of prey was derived from the number of independent records of each species photographed in camera–traps per sampling effort (Monroy–Vilchis et al., 2011). An independent record was considered to have occurred when (1) photographs of an individual animal were more than 30 min apart, (2) different individuals of the same species could be distinguished in consecutive photos, (3) several individuals could be identified in the same photo and (4) a new event was recorded after three hrs if it was not possible to identify different individuals of the same species in consecutive photos.

Each predator's preference for a prey species was calculated using Ivlev's electivity index (E) (Strauss, 1979) on a scale from –1 to +1, where –1 indicates rejected or inaccessible prey, +1 indicates actively selected prey, and zero indicates prey that were consumed according to their relative abundance. Finally, the biomass and estimated number of prey consumed by both felids were compared with published data on patterns of wild meat hunting from Quintana Roo to assess potential competition between felids and humans.

Results

We found a total of 49 scats, of which 23 were from jaguars and 26 were from pumas. Of the jaguar scats, 20 were from males and the other three could not be assigned a gender by RCP–PCR, whilst for pumas, 13 scats were assigned as males and nine as females, with four puma scats that could not be assigned. We found remains from 16 mammal species in the scats from both felids, with no evidence of bird, reptile or livestock remains. We detected diet breadths of 0.32 for jaguar and 0.29 for puma, and the dietary overlap between them was 0.77 with a mean similarity index of 0.50 and a variance of 0.02 at P (observed ≥ expected) < 0.04.

In the jaguar scats we found remains from 15 species, with up to five prey per scat. Their most frequently occurring prey were the large ungulates *M. temama* and *P. tajacu* (in > 18 % scats), followed by smaller mammals, kinkajous *Potos flavus* and nine–banded armadillos *Dasypus novemcinctus* (in > 8 % scats) (table 1). In the puma scats we found remains from 11 species, with up to three prey per scat. Their most frequently occurring prey were *P. tajacu* (in > 37 % scats) followed by *O. virginianus* and coatis *Nasua narica* (in > 11 % of scats), and Geoffrey's spider monkeys *Ateles geoffroyi, M. temama* and *D. novemcinctus* (in > 8 % scats) (table 1). The differences between the diets included opossum *Didelphys* sp. remains in puma but not jaguar scats, whilst striped hog–nosed skunks *Conepactus semiestratus,* Central American agoutis *Dasyprocta punctata,* long–tailed weasels, northern tamanduas *Tamandua mexicana* and gray foxes *Urocyon cinereoargenteus* were found in jaguar but not puma scats.

The estimated biomass and number of prey consumed suggest that nearly half the biomass of jaguar diets came from two ungulates, *M. temama* and *P. tajacu*, although their most numerous prey were

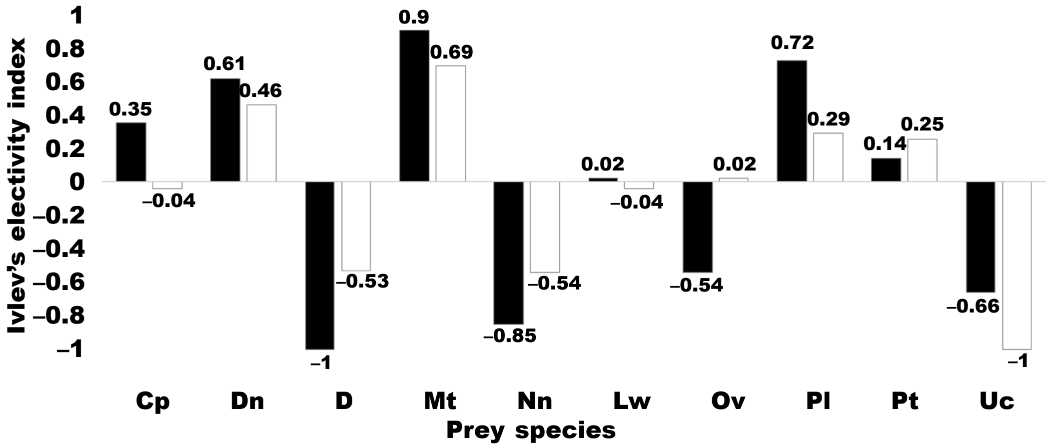

Fig. 3. Prey selection by jaguar (black bars) and puma (white bars) in the Eden Ecological Reserve, Quintana Roo, Mexico, according to Ivlev's electivity index (E) based on prey remains in scats (n = 23 for jaguar and n = 26 for puma). (For the abbreviations of prey species, see figure 2).

Fig. 3. Selección de presas por el jaguar (barras negras) y el puma (barras blancas) en la Reserva Ecológica El Edén, en Quintana Roo, México, según el índice de selectividad de Ivlev (E) basado en los restos de presas encontrados en los excrementos (n = 23 y n = 26 para el jaguar y el puma, respectivamente). (Para las abreviaturas de las especies presa, véase la figura 2).

small mammals, *D. novemcinctus, P. flavus* and *U. cinereoargenteus* (mean live body weights all > 2 and < 4.8 kg, table 1). *P. tajacu* contributed the highest amount of biomass to puma diets (> 36 %) followed by the two deer species, *O. virgineanus* (17.3 %) and *M. temama* (11.8 %), whilst their most numerous prey were *P. tajacu* and *N. narica,* followed by *D. novemcinctus* and *A. geoffroyi* (table 1). Ten of the 16 species recovered from the scats were also recorded in the camera traps (fig. 2) with a high overlap between the animal diversity in camera traps and that of the jaguar (Ss = 0.64) and puma (Ss = 0.60) diets. We also recovered prey items from scats which were not captured in the camera traps, including the arboreal species *A. geoffroyi, P. flavus* and *T. mexicana*, and smaller mammals like *C. semiestratus*, spotted pacas *Cunilicus paca* and Northern raccoons *Procyon lotor*.

Ivlev's electivity indices suggested a degree of prey preference and avoidance by the cats (fig. 2), with *M. temama* preferred by both felids although rarely photographed. *O. virginianus* appeared to be avoided or inaccessible to jaguars but not pumas, whilst *P. tajacu* was frequently photographed and consumed by both felids (fig. 3, table 1). *N. narica* were photographed frequently but were either avoided or inaccessible to jaguars and to a lesser extent pumas, *Didelphys* spp. were avoided by or were inaccessible to jaguars, whilst *U. cinereoargenteus* were avoided by or were inaccessible to pumas and, to a lesser extent, jaguars. Finally, *C. paca* and margays *Leopardus wiedii* appeared to be consumed according to their availability by jaguars, whilst pumas showed a slight preference for *C. paca*.

Discussion

Despite some evidence of dietary overlap, jaguars and pumas can coexist at Eden due to differences in their prey preferences, their indiviudal niche breadths, and the relative amount of biomass of each prey species they consume. The dietary overlap of the felids found in this study (0.37) was similar to that found in regions such as Campeche (Mexico), Costa Rica and Peru (0.26–0.39). However, intermediate (Brazil and Abra–Tanchipa, Mexico, 0.49–0.57) and high dietary overlaps have been reported elsewhere, including other parts of Mexico, Jalisco, Brazil, and Paraguay (0.78–0.84) (Oliveira, 2002). Diet breadths at Eden were low (both ≤ 0.32) and are similar to those of other studies in Mexico (Gómez and Monroy–Vilchis, 2013; Hernández–Saint Martin et al., 2015), with both felids consuming relatively few species, which is typical of animals with specialist diets (≤ 0.6, Krebs, 1999).

Jaguars preyed upon a slightly higher number of species than pumas, with four prey species recovered from jaguar but not puma scats, and one species recovered in puma but not jaguar scats. Ivlev's indices suggested that both felids showed preferences for and avoidance of particular prey species, including their high consumption of *M. temama* which was rarely recorded in the camera traps, and of *P. tajacu* which was frequently photographed. These two ungulates contributed about half of the jaguars' dietary biomass, whilst *P. tajacu* and *O. virginianus* together contributed more than half of the pumas' prey biomass, including more than a third of this from *P. tajacu* alone. *O. virginianus* was consumed by pumas in proportion

Table 1. Frequency and relative consumption of prey species by jaguar (Po, *Panthera onca*) and puma (Pc, *Puma concolor*) in the Eden Ecological Reserve, Quintana Roo, Mexico, estimated from their remains in scats (n = 26 and 23 respectively).

Tabla 1. Frecuencia y consumo relativo de especies presa por el jaguar (Po, Panthera onca*) y el puma (Pc,* Puma concolor*) en la Reserva Ecológica El Edén, en Quintana Roo, México, estimados a partir de excrementos (n = 26 y 23, respectivamente).*

	Frequency of occurence		Frequency in the scats		Percentage of prey		Biomass consumed		Number consumed	
	Po	Pc	Po	Pc	Po	Pc	Po	Pc	Po	Pc
Ateles geoffroyi	3	3	13	11.5	6.1	8.6	5.5	7	4.1	12.1
Conepatus semiestratus	3	0	8.7	0	4.1	0	3.5	0	4.5	0
Cuniculus paca	3	1	8.7	3.9	4.1	2.9	4	2.6	1.4	2.1
Dasyprocta punctata	3	3	8.7	11.5	4.1	8.6	3.5	6.8	4.8	15
Dasypus novemcinctus	4	0	17.4	0	8.2	0	7.2	0	6.7	0
Didelphys sp.	0	1	0	3.9	0	2.9	0	2.2	0	9.3
Leopardus wiedii	1	1	4.3	3.9	2	2.9	1.8	2.3	2	5.9
Mazama temama	9	3	39.1	11.5	18.4	8.6	27.9	11.8	2.5	2.5
Mustela frenata	3	0	13	0	6.1	0	NA	0	NA	0
Nasua narica	2	4	4.3	15.4	2	11.4	1.8	9.1	1.7	19.6
Odocoileus virginianus	2	4	4.3	15.4	2	11.4	3.4	17.3	0.3	3
Potos flavus	4	1	17.4	3.9	8.2	2.9	7.1	2.2	8.6	6.3
Procyon lotor	3	1	13	3.9	6.1	2.9	5.5	2.3	4.5	4.4
Tamandua mexicana	2	0	8.7	0	4.1	0	3.6	0	3.2	0
Pecari tajacu	9	13	39.1	50	18.4	37.1	19.9	36.4	4.7	20
Urocyon cinereoargenteus	3	0	13	0	6.1	0	5.3	0	6	0

to its high relative abundance in the camera traps, but it appeared to be avoided by or inaccessible to jaguars. This may suggest differences in the felids' use of prey species and habitat, since *O. virginianus* tolerates open terrain, including pasture and areas under cultivation which have expanded in the Yucatan Peninsula where they are associated with its recent population increases (Fitos–Santos et al., 2012). The absence of livestock remains in scats at Eden is significant, and because an abundant supply of wild prey is thought to reduce the incidence of felid attacks on livestock (Amit et al., 2013) our results suggest there are sufficient natural prey to support both felids, despite Eden's small size and the occasional presence of livestock in the reserve.

The frequency of prey in the diet and the relative biomass of each prey species consumed by the two predators varies widely across their range (Oliveira, 2002). At Eden, small mammals (< 10 kg) contributed 35–41 % and large mammals contributed 59–65 % of the felids' dietary biomass, in contrast to the Southern Yucatan Peninsula where four large prey species, *M. temama* and *P. tajacu*, *O. virginianus* and *T. pecari,* contributed 86–95 % of the dietary biomass (Chávez et al., 2007). This emphasizes the need for accurate local data on prey preferences and availability especially where felids occur in close proximity to human populations, since hunting for wild–meat could create conflict and competition. The hunting rates reported for human populations in the Northern Yucatan (Fitos–Santa et al., 2012) and the prey consumption patterns of felids in this study suggest that ungulates, armadillos and coatis are major dietary components of both humans and felids. Further evidence for potential competition between felids and humans is that across the whole of Southern Mexico the ungulates are the most commonly used animals for food, medicine and decoration (Contreras–Moreno et al., 2012; Naranjo et al., 2010; Retana–Guiascón et al., 2011; Tejeda–Cruz et al., 2014; Toledo et al., 2008). There are reports of some hunters taking up to 4,900 kg wild–meat yr^{-1} (Ojasti, 2000; Pug–Gil and Guiascón, 2012), and in Chiapas State the main prey species of felids reported here are widely hunted for human consumption, with over 450 *O. virginianus, M. temama, P. tajacu* and *D. punctata,* plus many *D. novemcinctus* and *N.*

narica taken by one community in a single year (Ávila–Gómez, 2003). Contemporary hunters, including those in the Northern Yucatan, are less dependent on wild–meat and usually target larger game such as deer and peccaries (Santos–Fita et al., 2012), which are also the preferred prey of felids (this study and Chávez et al., 2007; Núñez et al., 2000). Therefore, the relatively high number of small prey recorded for felids in Eden may be a response to competition with hunters for large prey and/or their avoidance of areas frequented by humans.

There are some limitations to this study. First, most jaguar scats were confirmed as originating from male cats, probably reflecting an inherent collecting bias because female jaguars rarely use open tracks (Palomares et al., 2012). However, there are few viable options for finding scats from wild felids in the natural vegetation prevalent at Eden. The mean body mass of males of both felids species is higher than for females, and most scats at Eden were from male felids that appeared to hunt small prey compared with studies from other parts of the Yucatan Peninsula (Chávez et al., 2007), which could indicate that they were smaller individuals, less likely to hunt larger prey. In addition, some species recovered in the scats were under–recorded by the camera traps, including arboreal or small mammals (*A. geoffroyi*, *P. flavus* and *T. mexicana*, *C. semiestratus*, *C. paca* and *P. lotor*), which is likely to increase their electivity indices. We did not study seasonal differences in diet and prey availability between dry and rainy seasons because previous experience during heavy rains resulted in camera malfunctions and scats being washed away. Other limitations in this study include the low number of scats collected, although this is consistent with estimated population densities of up to 3.6 jaguar and 5.2 puma for Eden (Ávila–Nájera et al., 2015).

Despite their small size, Eden and similar reserves may play a disproportionate role in maintaining the overall populations of large felids because these animals require large territories and safe access to sufficient prey, and regularly move across both protected and unprotected areas. In the Northern Yucatan (Santos–Fita et al., 2012) and other parts of Latin America, felid predation of wild–meat species has been used to justify their persecution, even though there is no evidence to confirm that they reduce the population density of their natural prey (Foster et al., 2014). At Eden we found no evidence that they consume livestock. However, as their main prey species are those also favored as wild–meat, long–term conservation management plans of the endangered jaguar can only be achieved by co–managing the sustainable harvesting of wild–meat in the Northern Yucatan Peninsula, in close collaboration with rural communities (Rodríguez–Soto et al., 2011).

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