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Functional responses of cougars (*Puma concolor*) in a multiple prey-species system

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Abstract

The study of predator-prey interactions is commonly analyzed using functional responses to gain an understanding of predation patterns and the impact they have on prey populations. Despite this, little is known about predator-prey systems with multiple prey species in sites near the equator. Here we studied the functional response of cougars (*Puma concolor*) in Sierra Nanchititla Natural Reserve (Mexico), in relation to their main prey, armadillo (*Dasypus novemcinctus*), coati (*Nasua narica*) and white-tailed deer (*Odocoileus virginianus*). Between 2004 and 2010, cougar scats were collected along five transects to estimate the consumption of different prey species. A relative abundance index (*RAI*) was calculated for each prey species and cougar using 18 camera traps. We compared Holling type I, II and III functional response models to determine patterns in prey consumption based on the relative abundance and biomass of each prey species consumed. The three main prey species comprised 55% (armadillo), 17% (coati) and 8% (white-tailed deer) of the diet. Type I and II functional responses described consumption of the two most common prey species armadillos and coati similarly well, while a type I response best characterized consumption of white-tailed deer. A negative correlation between the proportions of armadillo versus coati and white-tailed deer biomass in cougar scats suggests switching to consume alternative prey, confirming high foraging plasticity of this carnivore. This work represents one of the few studies to compare functional responses across multiple prey species, combined with evidence for prey-switching at low densities of preferred prey.

Keywords: cougar, functional responses, Holling, multiple prey, model comparison.

INTRODUCTION

For most obligate carnivores, changes in prey availability can be one of the main drivers influencing their behavior and population dynamics, as prey availability influences their main demographic parameters (abundance, fertility, survival and dispersal). Conversely, predators also have a fundamental role in the diversity of ecosystems due to the effect that they have on prey populations (Ruth & Murphy 2010). Thus, a crucial aspect in the ecology of carnivores is an understanding of the interactions predators have with their prey (Gittleman *et al.* 2001; Bowyer *et al.* 2005; Boitani & Powell 2012).

Predator-prey interactions have commonly been analyzed using functional responses, which describe predator consumption rates as a function of prey densities or abundance (Holling 1959; Ricklefs & Miller 2000). These responses have been used to understand predation patterns and the effect they have on prey populations (Joly & Patterson 2003). Models to determine the functional response of predators were initially applied to invertebrates and they have improved our understanding of the responses of other animal groups, including large carnivores (Bowyer *et al.* 2005). Holling (1959) described and quantified the concepts initially formulated by Solomon (1949), about the components of the predation process and the types of functional response shaped by predators (Fig. 1). Type I functional responses show a linear association with a positive slope between predator consumption rate and prey density up to a maximum consumption rate, above which the relationship is horizontal. The type I relationship is more frequent among filter feeders, but has also been described for wolves (Jeschke *et al.* 2004; Cariappa *et al.* 2011). The type II response describes a hyperbolic relationship in the predator consumption rate with increasing prey density, a response typical of wolves, coyotes and lynxes in some parts of their distribution (Dale *et al.* 1994; O' Donoghue *et al.* 1998). Type III responses are sigmoidal, where the maximum

consumption rate is reached at intermediate prey densities, before decreasing at higher densities. In this type of response, prey find a refuge at low densities, which has also been suggested in wolf and European polecat populations (Lode 2000; Cariappa *et al.* 2011).

Several studies have analyzed the functional response in simple predator-prey systems, from parasites and hosts (Morales *et al.* 2001; Flores *et al.* 2010) to vertebrate species such as nocturnal birds (Boutin 1995), feral cats (Harper 2005), Asiatic lions (Sundararaj *et al.* 2012), lynxes, coyotes and wolves (Dale *et al.* 1994; O' Donoghue *et al.* 1998; Cariappa *et al.* 2011). Systems with multiple prey species provide the opportunity for prey switching by generalist carnivores, but this has seldom been studied, unlike single prey systems, and data have previously been too limited for such an assessment for cougars (*Puma concolor*; Ruth & Murphy 2010). In latitudes close to the poles and with prey greater than 15 kg, cougars can replace their preferred prey with other species when the former is scarce (Sweitzer *et al.* 1997; Novaro *et al.* 2000; Wittmer *et al.* 2005a,b). However, for other sites nearer the equator, where cougar prey may be less than 15 kg (Iriarte *et al.* 1990) and where there is a high diversity of potential prey, the functional responses and the impact that cougars have on the prey populations remains unknown.

Here we study cougar functional responses to changes in their principal prey species in an area with a high prey diversity (Monroy-Vilchis *et al.* 2009; Gómez-Ortiz *et al.* 2011). Our aim was to determine the functional responses that cougars show in the Sierra Nanchititla Natural Reserve, Mexico, in a multiple prey species system.

MATERIALS AND METHODS

Study area and species

The study was conducted at the Sierra Nanchititla Natural Reserve (SNNR), located in the center of Mexico, in the physiographic region of the Balsas River basin, a subtropical biome (Fig. 2). This mountainous region has altitudes ranging from 410 to 2080 m.a.s.l, with a surface area of 664 km². Here, the Nearctic and Neotropical regions converge, which results in a high diversity of habitats, such as deciduous forests (37% of total surface area), pine-oak forests (48%), grasslands (8%) and cultivated fields (7%). Mammal diversity is also high: 53 species have been recorded, representing 10% of the total Mexican mammalian species richness (Monroy-Vilchis *et al.* 2011a). Five out of the six feline species distributed in Mexico are found in the SNNR: jaguar (*Panthera onca*), margay (*Leopardus wiedii*), ocelot (*L. pardalis*), jaguarundi (*Puma yagouaroundi*) and cougar (*P. concolor*; Sánchez *et al.* 2002; Monroy-Vilchis *et al.* 2008b). Of these, cougars are of particular interest as one of the most abundant felines, with relatively wide knowledge about its trophic ecology (Monroy-Vilchis *et al.* 2009; Gómez-Ortíz *et al.* 2011). Cougar therefore provide a useful model to analyze predator functional responses in a multiple prey species system. Cougars consume a wide variety of vertebrate species, such as reptiles, birds and mammals of different sizes (Currier 1983; Altendorf *et al.* 2001; Logan & Sweanor 2001). In the study area, cougars have been documented feeding on 21 mammal species, mainly armadillo, followed by coati and white-tailed deer, with other species occurrence in the diet each less than 5% (Monroy-Vilchis *et al.* 2009; Gómez-Ortíz *et al.* 2011). We only considered these three main prey species in our analysis.

Scat analysis

Monthly field trips were carried out from December 2004 to October 2007, from October 2008 to September 2009 and from January to July 2010. Scats were collected along five transects established in SNNR. The transect locations were chosen based on accessibility and to cover the area of pine-oak forests in the SNNR. Transects were between 6 and 8 km long, with a separation of around 5 km. Cougar scats were identified based on the extraction of bile acid using thin-layer chromatography (TLC; see Gómez-Ortiz *et al.* 2015), to avoid confusing cougar scats with jaguar, as the scats of both species have similar morphological characteristics. Cougar scats were processed following the method proposed by Monroy-Vilchis *et al.* (2009). Prey identification was carried out using bones and tooth structures, which were compared with samples from the collection available at the SNNR Biological Station. Following predator species verification, hairs were identified according to Monroy-Vilchis and Rubio-Rodríguez's (2003) method, which involves the estimation of both macroscopic (hair length and shape) and microscopic (hair width and medulla type) characteristics. After the taxonomic prey identification, we estimated a proportion of biomass consumed ($PBC_{i,t}$) for each prey species, i , during each sampling block, t . This proportion of biomass was used to determine the consumption rate of cougar for each prey (Harper 2005 and Tobajas *et al.* 2016), which was calculated from the frequency of occurrence in scats (FO), the correction factor of Ackerman *et al.* (1984; Y), and the average mass of each prey species (M_i), suggested by Monroy-Vilchis *et al.* (2013; 4.9 kg for armadillo and coati and 6.13 kg for white tailed deer) and using the following equations:

$$Y_i = 1.98 + 0.035 * M_i \quad (1.1)$$

$$PBC_{i,t} = (FO * Y_i) / \sum(FO * Y_i) \quad (1.2)$$

$$CR_{i,t} = PBC_{i,t} * RAI_{p,t} \quad (1.3)$$

where CR_i is the consumption rate of species i and $RAI_{p,t}$ is the relative abundance of cougar at sampling time t (see following section for further information on RAI).

We calculated dietary overlap between seasons of the different sampled years, using the MacArthur and Levins index (1967) to determine whether seasonality could have an effect on our results. Niche overlap ranges from 0 to 1, with 0 representing no overlap in diet between seasons and 1 indicating complete overlap.

Relative abundance index of prey

To determine a relative abundance index (RAI) of each species, 18 camera traps were set during scat searches. Due to the rugged topography, accessibility to study sites and the movement distances of the different species analyzed the distance between traps was variable. Twelve camera traps were placed at a distance of 0.5 to 1 km, five cameras from 1 to 2 km and the final camera had a minimum distance of 3.2 km to the nearest other camera. Six camera traps were placed at wide roads, six at small wildlife tracks and six at gorges near water bodies, to increase the probability of photographing the main study species (Harmsen *et al.* 2010). The camera traps were fixed to tree trunks at 20-40 cm above the ground and were programmed to work constantly over a 24-hour

period. The date and time was printed in each photograph and cameras were checked once a month to assess their functionality and battery life.

A relative abundance index (*RAI*) was calculated for cougar and each prey species (armadillo, coati and white-tailed deer), defined as the number of independent photographs of each species per 100 camera-trap days (O' Brien *et al.* 2003), sampling effort was calculated as the sum of trap-days each camera was active plus the records of photographs. Only two cases were considered in the analysis as independent photographs: (1) consecutive photographs of different individuals (where individuals can be distinguished by marks on the coat or sex (e.g., cougars and deer; Soria-Díaz & Monroy-Vilchis 2015) and (2) consecutive photographs of the same species taken with a difference of 24 hours or longer, in individuals who cannot be identified by marks on the coat or sex (e.g., coati and armadillo; Monroy-Vilchis *et al.* 2011b).

Functional responses

To determine the functional responses associated with cougar predation, both the proportion of consumed biomass and the relative abundance obtained monthly for cougar and each prey were grouped in quarterly blocks (Table 1).

We considered type I, II and III functional response models to describe how the consumption of prey biomass varied with prey abundance:

$$CR_{i,t} = a_{i,t} CR_{i,t} + \varepsilon_{i,t} \quad (2.1)$$

$$CR_{i,t} = \frac{a_i CR_{i,t}}{1 + a_i h_i CR_{i,t}} + \varepsilon_{i,t} \quad (2.2)$$

$$CR_{i,t} = \frac{a_i CR_{i,t}^{1+k_i}}{1 + a_i h_i CR_{i,t}^{1+k_i}} + \varepsilon_{i,t} \quad (2.3)$$

where a is the attack rate, h is the handling time, k is the Hill exponent and ε is the residual error. All functional responses were fit using a non-linear least squares approach, with lower bounds of 0 set for each estimated parameter, based on the “port” algorithm in the R software package (R Core Team 2016). Models were compared using AIC_c (corrected for small sample sizes) values, generated by the `AICcmodavg` package (Mazerolle 2016), with the best model(s) considered to be that with the lowest AIC_c score, or the set of models with $\Delta AIC_c < 2$ compared to that lowest score (Burnham and Anderson 2002).

Finally, to investigate the evidence for prey switching, we considered the Spearman’s rank correlation coefficient between the RAI of each pair of prey species, as well as their PBC values at a given sampling block.

RESULTS

One hundred and fifty cougar scats were collected over 1980 km of transects covering the trails at the SNNR. Armadillo was the main prey, followed by coati and white-tailed deer (55%, 17% and 8% of occurrence respectively). The proportion of consumed biomass varied for all prey throughout the study: from 0.1 to 0.96 for armadillo, 0.01 to 0.44 for coati, and 0.01 to 0.44 for white-tailed deer (see Table 1). Moreover, there was a niche overlap between seasons using the

MacArthur and Levins (1967) index: $O = 0.87$; suggesting a similarity of cougar diet in both wet and dry seasons throughout the study.

With a total sampling effort of 11,516 trap-days, 895 independent photographs were obtained corresponding to coatis (78% of cases), cougar (20%), white-tailed deer (19%) and armadillos (3%). Coatis showed the highest relative prey abundance, with a temporal variation of *RAI* from 1.23 to 10.95, white-tailed deer from 0.16 to 4.4, and finally armadillo from 0.16 to 1.19 individuals/100 trap days (Table 1). Cougar *RAI* varied from 0.80 to 2.82 (Table 1).

For armadillo, the main prey in cougar diets, the type I and II functional responses showed the best relative fit to consumption data ($AIC_c = 5.45$ and 5.82 , respectively), though there was relatively high uncertainty associated with the handling time estimate for the type II response (0.305 ± 0.175 S.E.; Table 2, Fig. 3A). The mechanistic type III model fit comparatively poorly ($AIC_c = 9.18$), with attack rate and handling time estimates matching the Type II response (Table 2).

The type I and II functional responses also fit the coati consumption data best ($AIC_c = 5.39$ and 5.23 , respectively; Table 2, Fig 3B). The type III response for coati had high levels of uncertainty associated with all parameters (Table 2). The type I model described the consumption of white-tailed deer best ($AIC_c = 5.02$, Table 2).

While the non-linear least squares approach cannot generate r^2 values, we can use the r^2 value from a linear regression based on the type I model (lacking an intercept, to continue to force the functions through the origin) for each species to indicate how well those models perform and give bounds for variance explained by the Type II models for consumption of armadillo (type I $r^2 = 0.91$; upper bound for Type II model) and coati (type I $r^2 = 0.69$; lower bound for type II model) and the type I model for white-tailed deer ($r^2 = 0.31$).

There was a statistically significant negative correlation between armadillo and coati *RA*s across time (Spearman's $r_s = -0.48$, $p = 0.045$) but not between deer and armadillo or coati *RA*s. However, while there were statistically significant negative relationships between the proportions of armadillo and coati ($r_s = -0.52$, $p = 0.027$) and armadillo and deer biomass ($r_s = -0.77$, $p < 0.001$) found in the cougar scats, there was no statistically significant correlation between coati and deer *PBC*. Together, these results indicate that cougar are switching to alternative prey when armadillo are at low relative abundances.

DISCUSSION

To our knowledge, this is the first study carried out in Latin America or in a subtropical region to determine the cougar functional response. This is important because biodiversity and therefore abundance of (prey) species increase as one moves closer to the equator (Mittelbach *et al.* 2007) and cougar responses under these latitudes and conditions were previously unknown. Likewise, we know of no other studies that have explicitly compared cougar functional responses using current information-theoretic model selection approaches (Aho *et al.* 2014). Functional responses are more often studied for single-prey systems with predators such as lynx and wolf (Stenseth *et al.* 1997; O' Donoghue *et al.* 1998; Ruth and Murphy 2010), whereas systems with multiple prey species have received little attention (Dale *et al.* 1994; Novaro *et al.* 2000).

In our study, there was evidence that cougars in the SNNR showed a strong functional response to changes in the abundance of multiple prey species. A type II functional response was found to be either the best or at least a plausible model for armadillo and coati, but not for white-tailed deer, the least consumed of its main prey species. A type II functional response indicates that

cougar has a relatively high consumption rate at low prey densities, declining as prey densities increases (Fig. 3). Cougars may be switching to consume alternative prey at low armadillo abundances (the preferred prey), with our results showing negative correlations between the proportion of armadillo and proportions of both coati and white-tailed deer biomass found in cougar scat. Prey switching has also been observed in other North American cougar populations further north in its range (Sweitzer *et al.* 1997; Wittmer *et al.* 2005a,b). Previous studies in the SNNR have shown that cougars can switch to consume alternative prey when their main prey abundance has decreased under particular environmental conditions. A natural forest fire occurred in May 2003, affecting 10 km² of the pine-oak forests. After this incident, cougars shifted from preying mainly on mid-sized prey less than 6 kg ($N=5$ prey), to a diet including larger number of prey ($N=19$) such as livestock (see Monroy-Vilchis *et al.* 2009).

A decrease in the consumption rate at higher armadillo and coati abundances corresponds to the excess of food available to the predator, or the low energy requirement of cougars in the SNNR. Laundré (2005) described that female cougars with no young have lower energy requirements than those with cubs. No cubs were photographed in our study during seven sampling blocks (1, 4, 8, 9, 10, 11 and 13) and a few photographs of male cougars was obtained during periods of high armadillo abundance (sampling blocks 9, 10, 11 and 12; Table 1). In British Columbia, Canada, cougars can switch to alternative prey when its main prey, caribou (*Rangifer tarandus caribou*), occurs in low densities (Wittmer *et al.* 2005a,b). In the Great Basin Desert, U.S.A., the population decline of mule deer (*O. hemionus*) following a long drought, forced cougars to switch to porcupine (*Erethizon dorsatum*; Sweitzer *et al.* 1997). In Patagonia, Novaro *et al.* (2000) found that guanacos (*Lama guanicoe*) were the main prey of cougars but they could also prey on exotic species such as red deer and hares (*Cervus elaphus* and *Lepus europaeus*). These results show the ability of

cougars to consume alternative prey when their main prey availability decreases. This plasticity can help cougars to coexist with other competing predators, as well as to maintain relatively stable prey populations (Ruth & Murphy 2010).

Armadillos were the most important prey item for cougar, being energetically rich (2,399 kcal/kg) in comparison to coati (2,225 kcal/kg) and white-tailed deer (2,166 kcal/kg; Gómez-Ortíz *et al.* 2011). Armadillos are safe to handle and show similar nocturnal activity patterns to cougar, influencing its high predation rates (Soria-Díaz *et al.* 2016). This result contrasts with studies conducted in temperate parts of North America where ungulates comprise the dominant source of energy for cougar (Sweitzer *et al.* 1997; Wittmer *et al.* 2005a,b). Thus, cougar predation is likely to have different impacts on community composition and diversity depending on the degree to which they select ungulate prey.

The ability of cougar to switch to alternative prey can buffer its population dynamics at the SNNR. We do not think that cougar predation is a factor increasing the extinction risk of prey populations, as cougars can predate on other secondary prey, contrary to specialist predators that only consume a single prey species (Stenseth *et al.* 1997; O' Donoghue *et al.* 1998; Ruth and Murphy 2010). Our results can be used in other areas to explain that cougar may have different types of functional response and switch prey in their diet, as other studies indicate that cougar consume a wide variety of vertebrates (Iriarte *et al.* 1990).

Females with cubs, as well as solitary males, were photographed in our study and densities of up to 6.86 individuals/100km² have been estimated (Soria-Díaz *et al.* 2010). At the same time, feeding on alternative prey probably allows cougar and jaguar to coexist in the SNNR despite the large overlap of their diets (Gómez-Ortiz & Monroy-Vilchis 2013). Another advantage of prey

switching is that cougars may have a greater impact upon the dynamics of the populations in which their prey are sympatric. In this case, predation by cougar might regulate populations of primary prey; as a consequence, the pressure of foraging in certain habitats can be alleviated (Hassell 2000).

Camera traps have shown reliability and efficiency in estimating abundance (Silveira *et al.* 2003; Alves & Andriolo 2005; Harmsen *et al.* 2010). The distance between our traps varied from 0.5 to 3.2 km, due to the rugged topography, accessibility to study sites and the movement distances of the focal species. For example, we had separation distances <1 km, because the home range radius of all focal prey have been estimated at <1 km² (white tailed deer, Marchinton & Hirth 1984; coati, Valenzuela & Ceballos 2000; armadillo, McBee & Baker 1982). Other camera traps ranged from 1 to 3.2 km separation, because the local geography (cliffs and canyons) did not permit shorter distances. One hundred percent of independent photographs of cougar, white tailed deer and 75% of coati were obtained on large roads. 15% of coati photographs and 38% of armadillo were obtained at small wildlife trails, and 10% of coati and 62% of armadillo photographs were obtained at gorges near water bodies. Our camera locations aimed to optimize the possibility of recording all species analyzed in this study.

Finally, we can conclude that cougars in the SNNR show a type I or II functional response for armadillo and coati but there is limited support for anything other than a linear (type I) response for white-tailed deer. It is important to note that armadillo seems to be a key species in the study area for both cougars and jaguars, while it is the third most hunted mammal by the local human populations (Monroy-Vilchis *et al.* 2008a). Human exploitation of species is expected to lead to changes within the ecosystem, increasing the extinction risk of both the harvested and other (non-target) interacting species (Enberg *et al.* 2006). Human hunting may have an additive or compensatory interaction with cougar predation. However, while these are interesting possibilities

to explore further, a lack of detailed records of human hunting effort over the study period means commenting about the impact of human hunting on the SNNR food web would be purely speculative. These facts underscore the importance of carrying out further study to monitor the populations of armadillo and determine their long-term viability under such intense predation and hunting pressure.

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Table 1 Quarterly blocks of biomass proportion (BP) consumed, obtained from cougar scat, and Relative Abundance Index (RAI) obtained with camera traps, for armadillo (*D. novemcinctus*), coati (*N. narica*), white-tailed deer (*O. virginianus*) and cougar (*Puma concolor*), in the Sierra Nanchititla Natural Reserve

Sampling blocks	BP coati	RAI coati	BP		BP armadillo	RAI	RAI
			white-tailed deer	RAI white-tailed deer		armadillo	Cougar
1	0.2	6.35	0.44	3.86	0.1	0.16	2.33
2	0.3	2.06	0.36	0.16	0.1	0.16	1.33
3	0.16	3.2	0.1	1.53	0.38	0.38	1.22
4	0.44	10.95	0.01	4.4	0.48	0.16	1.45
5	0.4	4.2	0.15	1.54	0.43	0.16	1.42
6	0.2	2.93	0.01	0.16	0.76	0.5	1
7	0.25	1.23	0.01	1.53	0.7	0.5	1
8	0.15	1.23	0.01	2.16	0.84	0.85	1.01
9	0.3	4.23	0.1	1.32	0.6	1.19	2.74
10	0.01	1.6	0.01	1.76	0.96	0.82	1.08
11	0.1	2.93	0.01	1.41	0.87	0.82	1.08
12	0.26	2.93	0.1	2.83	0.43	0.44	0.95
13	0.22	5.06	0.01	2.71	0.76	0.44	0.95
14	0.33	4.93	0.01	1.87	0.6	0.44	1.21
15	0.2	4.93	0.17	0.66	0.6	0.26	0.86

16	0.35	3.56	0.01	0.84	0.6	0.26	0.80
17	0.36	3.56	0.1	1.02	0.35	0.26	1.05
18	0.36	3.56	0.1	1.44	0.51	0.56	2.82

Table 2 Parameter estimates from the model sets compared to estimate the consumption of armadillo (*D. novemcinctus*), coati (*N. narica*) and white-tailed deer (*O. virginianus*) estimated from cougar (*P. concolor*) scat. The number of estimable parameters in each functional response model are: Type I = 2; Type II = 3; Type III = 4.

Parameters: a is the attack rate, h is the handling time and k is the Hill exponent. Parameter subscripts correspond to each species, indicated by Genus

Prey Species	Model	Resid. Df	AIC _c	Akaike weight	Deviance	Parameter	Estimate	S.E.	t-value	p-value
Armadillo	Type I	17	5.45	0.5	1.093	a_D	1.392	0.110	12.73	<0.001
	Type II	16	5.82	0.42	0.948	a_D	2.051	0.514	3.99	0.001
						h_D	0.305	0.175	1.74	0.101
	Type III	15	9.18	0.08	0.948	a_D	2.051	2.531	0.81	0.430
						h_D	0.305	0.631	0.48	0.636
						k_D	0.000	0.727	0.00	1.000
Coati	Type I	17	5.39	0.44	1.089	a_N	0.083	0.013	6.14	<0.001

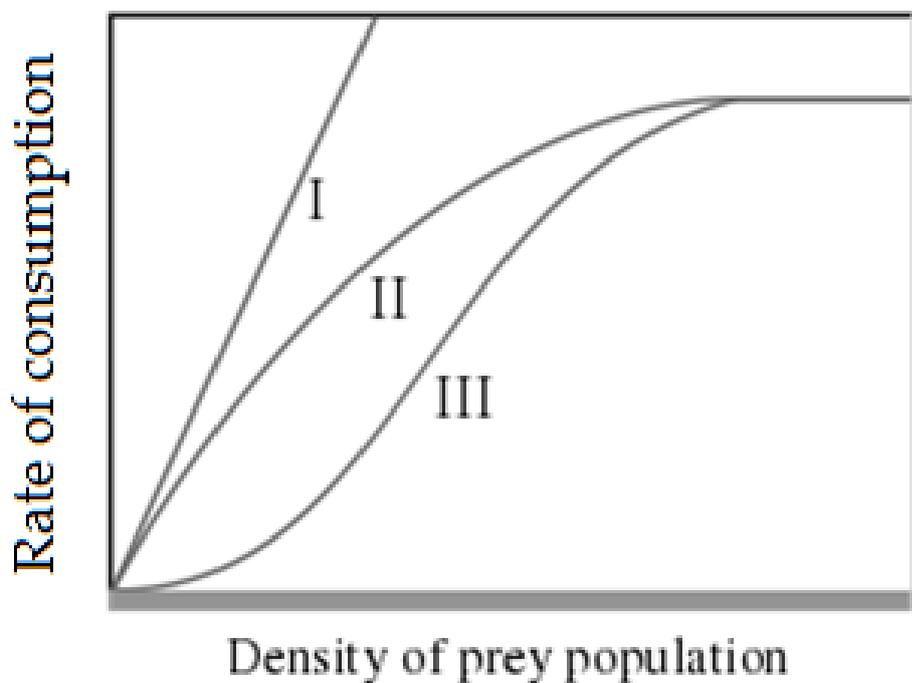
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Deer	Type II	16	5.23	0.47	0.918	a_N	0.178	0.111	1.57	0.130
						h_N	1.114	0.777	1.43	0.171
	Type III	15	8.53	0.09	0.915	a_N	0.138	0.189	0.73	0.478
						h_N	1.512	1.272	1.19	0.253
						k_N	0.469	1.850	0.25	0.803
	Type I	17	5.02	0.78	1.067	a_o	0.079	0.029	2.74	0.014
	Type II	16	7.93	0.18	1.067	a_o	0.079	0.082	0.96	0.352
						h_o	0.000	4.111	0.00	1.000
	Type III	15	11.29	0.03	1.066	a_o	0.074	0.189	0.73	0.478
						h_o	0.000	18.056	0.00	1.000
					k_o	0.106	4.097	0.03	0.980	

Figure legends

Figure 1 Theoretical functional response (Holling 1959) of predator consumption rates relative to prey density.



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Figure 2 Geographical location of Sierra Nanchititla Natural Reserve (SNNR) in Balsas River basin, Mexico.

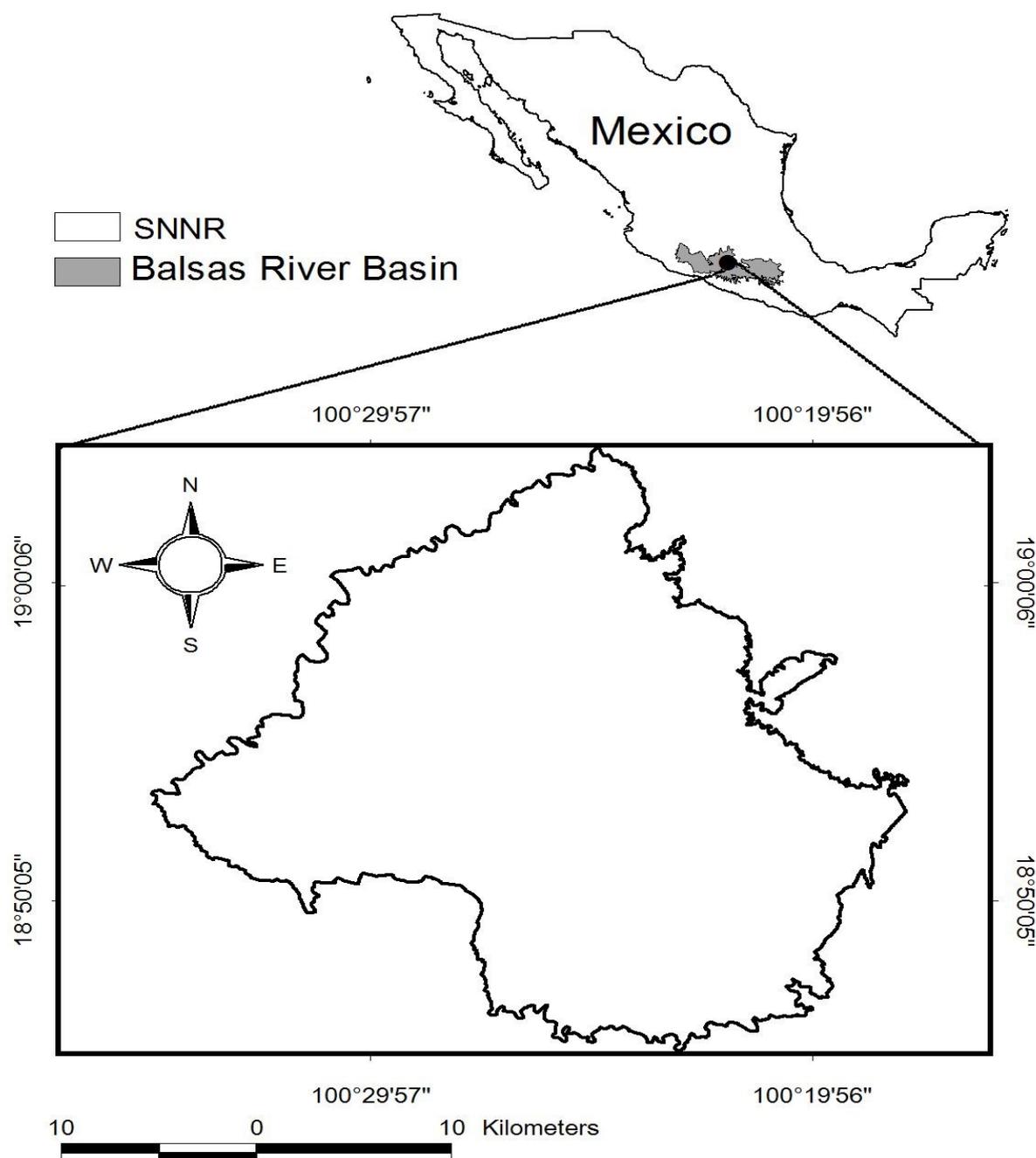


Figure 3 Prey biomass consumed for given relative abundances (circles) and the best fitting functional responses (lines) for cougar (*P. concolor*) feeding on its 3 most common prey species, (a) armadillo (*D. novemcinctus*), (b) coati (*N. narica*) and (c) white-tailed deer (*O. virginianus*), in the Sierra Nanchititla Natural Reserve (SNNR), Mexico. In all cases, 3 different functional responses were tested for each species relative abundance index against the proportion of biomass recorded in cougar scats, with Types I & II performing best for armadillo and coati, while Type I performed best for white-tailed deer.

