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Prey Preferences of the Jaguar *Panthera onca* Reflect the Post-Pleistocene Demise of Large Prey

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Documenting the impacts of the Pleistocene megafaunal extinctions on predator-prey interactions is a challenge because of the incomplete fossil record and depauperate extant community structure. We used a comparative ecological approach to investigate whether the existing prey preference patterns of jaguars *Panthera onca* were potentially affected by the Pleistocene extinctions in the Americas compared with large felids in Africa and Asia. We reviewed the literature and found 25 studies reporting 3214 jaguar kills recorded throughout the species' distribution. We found that jaguars significantly preferred capybara *Hydrochaeris hydrochaeris* and giant anteater *Myrmecophaga tridactyla*, and avoided agoutis, carnivorans, primates, black-eared opossum *Didelphis marsupialis* and tapirs. Generalized linear models showed that jaguars select prey primarily based on socio-ecological and behavioral traits (abundance and herd size), rather than morphological characteristics (body size). Nonetheless, their accessible prey weight range was 6–60 kg, preferred prey weight range was 45–85 kg, and mean mass of significantly preferred prey was 32 ± 13 kg leading to a predator to prey body mass ratio of 1:0.53, which is much less than that of other solitary felids (although 1:0.84 may be the relationship with the smallest jaguars). Compared with other large, solitary felids, jaguars have an unusual predator to prey body mass ratio, show limited effect of prey morphology as a driver of prey selection, lack evidence of optimal foraging beyond their preferred prey, and a lack of preferential hunting on Cetartiodactyla herbivores. These features, coupled with the reduction in jaguar body mass since the Pleistocene, suggest that the loss of larger potential prey items within the preferred and accessible weight ranges at the end-Pleistocene still affects jaguar predatory behavior. It may be that jaguars survived this mass extinction event by preferentially preying on relatively small species.

Keywords: predator-prey interactions, apex predator, optimal foraging theory, Pleistocene megafaunal extinction, capybara, giant anteater, accessible prey, preferred prey weight range

INTRODUCTION

Understanding how foraging individuals decide upon what to feed is essential for predicting links and feedbacks among individuals at the population level and amongst trophic levels (Railsback and Harvey, 2013). Morphological and behavioral characteristics of prey have previously been shown to be drivers of large predator prey selection (Hayward and Kerley, 2005). However, these elements may not contribute uniformly across all predators particularly given the different evolutionary histories of the New and Old World. Consequently, we studied the trait-mediated interactions between jaguars and their prey in the Americas. The jaguar is the largest felid in the Americas (Nowell and Jackson, 1996) and is currently listed on the IUCN Red List as *Near Threatened* based on a high likelihood of persistence over most of its wide (8.75 million km^2) distribution (Caso et al., 2008), although they will soon qualify for *Vulnerable* status given current rates of habitat loss, reductions of their prey base, and human persecution (Caso et al., 2008; H. Quigley pers. comm.).

The jaguar evolved in the Old World ~2.5–3 million years before present and migrated into North America about 2 million years ago (Kurtén and Anderson, 1980). During much of the Pleistocene, its range extended much further north than at present (reaching Nebraska and Oregon in the U.S.A. (ibid) and southern England and the Netherlands in Europe also; Hemmer et al., 2001; Mol et al., 2011). Historically, the jaguar was found from the south-western U.S. to southern Argentina (Seymour, 1989), but its current distribution is considerably smaller (**Figure 1**). This dramatic range reduction over the last million or so years has led some to describe the jaguar today as a relictual population (Kurtén and Anderson, 1980). The decline in range since the mid-Pleistocene was accompanied by a 15–20% reduction in body mass and a change in limb proportions, such that extant jaguars have shorter metapodials,

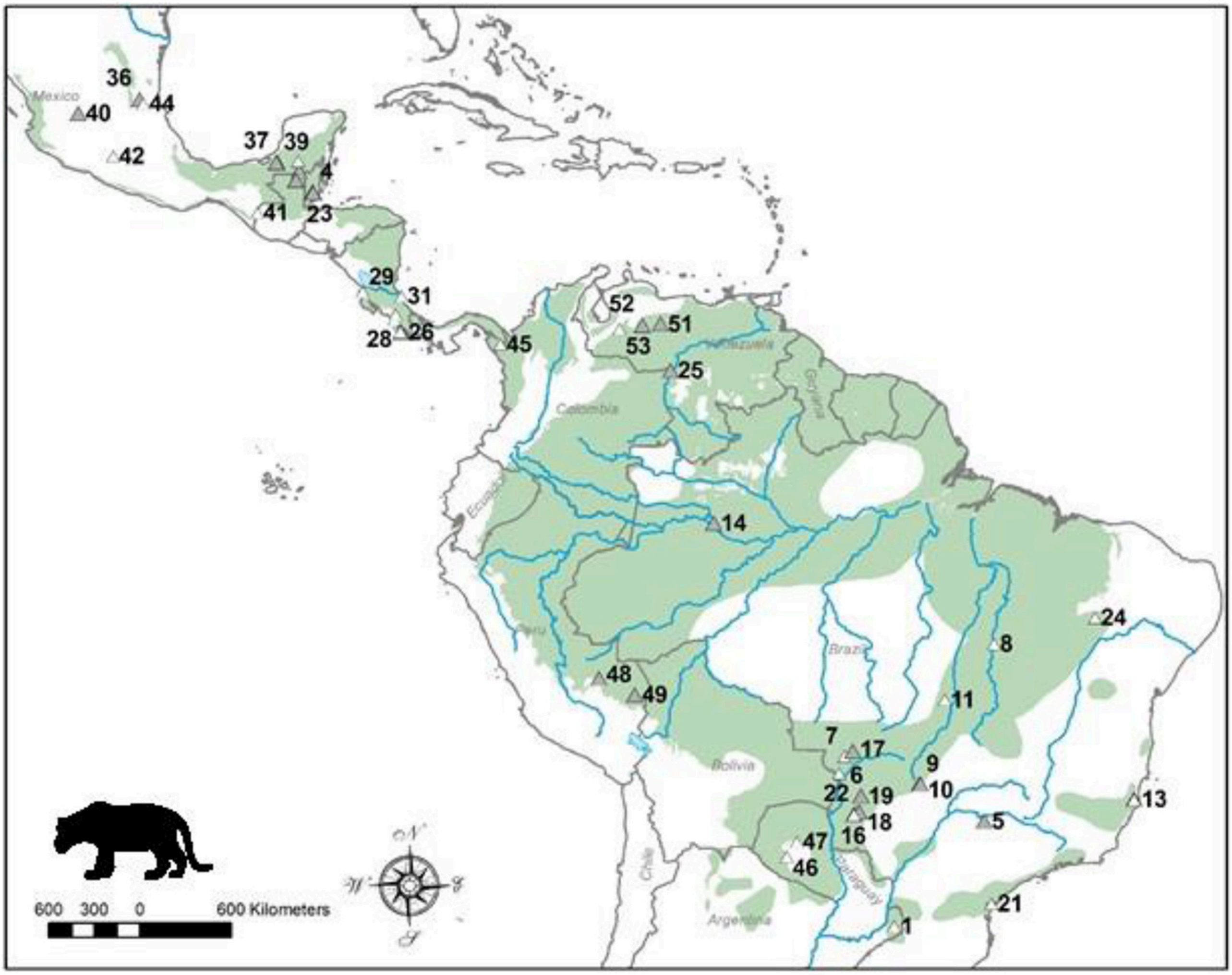

FIGURE 1 | Distribution map of the jaguar and location of study sites. Current jaguar distribution is shaded and these data were obtained from the IUCN Red List. Sites where dietary studies of jaguars have been conducted are shown as triangles, and the shaded triangles represent the sites of studies that had data used in the analyses. Site numbers refer to those in **Table 1**. Note there are alternative maps on jaguar distribution from panthera.org and the U.S. Fish and Wildlife Service that differ from that of the IUCN.

perhaps as a response to hunting in more closed habitats (Kurten, 1973).

The morphology and behavior of other large predators have evolved to enable them to optimally kill a limited number of prey species within a specific prey weight range (Hayward et al., 2006b, 2014). This weight range also corresponds to the age classes of prey killed (Gervasi et al., 2015). Jaguars are solitary hunters (Sunquist and Sunquist, 2002) and so their prey preferences could be expected to be similar to those of leopards *Panthera pardus* (Hayward et al., 2006a), given that the two species have been considered to be ecological analogs in the New and Old Worlds, respectively (Sunquist and Sunquist, 2002). However, jaguars differ markedly from leopards in being about twice the mass with shorter, more robust limb bones, and relatively wider forepaws that are comparable in relative dimensions to those of lions *Panthera leo* (Gonyea, 1976; Meachen-Samuels and Van Valkenburgh, 2009b). Moreover, jaguars are more similar to lions than leopards in having both absolutely and relatively larger upper canines and lateral incisors (Meachen-Samuels and Van Valkenburgh, 2009a). In fact, jaguars appear to have the most robust canine teeth of any living felid for their body size (Meachen-Samuels and Van Valkenburgh, 2009a). These morphological characteristics indicate a specialization on strength relative to mass suggesting that jaguars should be killing larger prey than leopards, on average.

Across their range, jaguars exhibit up to 100% variation in body mass (Sunquist and Sunquist, 2002) and this is likely to impact their hunting decisions, with the smallest forms being more similar to leopards in the size of their prey. For example, Hoogesteijn and Mondolfi (1996) found that floodplain jaguars were significantly larger [body mass: Llanos = 104.5 kg (males), 66.9 kg (females) and Pantanal = 99.5 kg (males), 76.7 kg (females)] than forest jaguars [body mass: Amazon = 83.6 kg (males), no data for females and Central American = 56.1 kg (males), 41.4 kg (females)]. This variability was also reflected in the diet of the populations, with the forest jaguars having a significantly lower mean weight of vertebrate prey at 5.8 kg, compared to 89 kg (including livestock) for floodplain jaguars (Hoogesteijn and Mondolfi, 1996).

Prey is fundamental to the existence of large predators (Fuller and Sievert, 2001; Karanth et al., 2004; Hayward et al., 2007b), but in the case of the jaguar, it is not clear from existing reviews what the key prey base is or even whether they are reliant on large prey species (López Gonzalez and Miller, 2002). The currently prevailing view is that jaguars are opportunistic predators whose diet simply reflects the available prey community at a site (Mondolfi and Hoogesteijn, 1986; Rabinowitz and Nottingham, 1986; Emmons, 1987; Sunquist and Sunquist, 2002; Harmsen et al., 2010). Not surprisingly given their wide distribution and habitat tolerance, the jaguar's diet is diverse with at least 85 species listed as prey (Weckel et al., 2006b) ranging from cattle weighing more than 200 kg to small rodents (Harmsen et al., 2010). Their prey is unusually diverse and includes species such as arboreal primates (Peetz et al., 1992), ocelots (Gonzalez-Maya et al., 2010), marine and river turtles (Carrillo et al., 2009; Salera et al., 2009; Veríssimo et al., 2012), tortoises and fish (Emmons, 1989), crocodilians and their eggs (da Silveira et al., 2010) and dolphins (Castañeda et al., 2013). The diversity of aquatic prey reflects the jaguar's habitat use and ability to swim (Guggisberg, 1975). The majority of these prey are killed, but jaguars readily scavenge from carcasses for up to 17 days after death (López González and Lorenzana Piña, 2002). Despite this diversity of prey and their apparent strength, jaguars tend to kill prey slightly smaller than themselves (predator:prey ratio = 1:0.6–0.9; de Oliveira, 2002; if domestic livestock are excluded).

Hoogesteijn and Mondolfi (1996) describe the hunting technique frequently used by jaguars to kill cattle, whereby they jump on the back or side of the cattle, pull the animal's head around, unbalancing it and causing it to fall to the ground—often causing the animal to break its neck. The name jaguar is linked to their hunting technique: it comes from one of the Tupi-Guarani languages, deriving from the word "yaguara," meaning "wild beast that overcomes its prey in a bound" (Seymour, 1989). Other hunting techniques used by jaguars include using the forepaws to hit smaller prey species (such as capybaras) to the ground and using a single bite to the nape of the neck to puncture the skull (Sunquist and Sunquist, 2002). This behavioral evidence suggests the jaguar has mechanisms by which to successfully kill large prey.

Reviews have indicated that medium and large prey are critical prey resources for jaguars (López Gonzalez and Miller, 2002), and that these vary depending on biome, competitor levels and prey availability (Sunquist, 2002). This study aimed to determine what the critical prey resources of jaguars are by determining the preferred prey of the species, and to investigate the impact of the Pleistocene extinctions on jaguar predatory ecology. There has been extensive research on the human-wildlife conflict arising from jaguar depredation on livestock (Rabinowitz, 1986; Quigley and Crawshaw, 1992; Hoogesteijn et al., 1993; Dalponte, 2002; Polisar et al., 2003; Michalski et al., 2006; Palmeira and Barrella, 2007; Hoogesteijn and Hoogesteijn, 2008; Rosas-Rosas et al., 2008; Soto-Shoender and Giuliano, 2011; Jêdrzejewski et al., 2014), so we focus predominately on wild prey in this study.

METHODS

We searched Google Scholar and Web of Science for literature on the diet of jaguars, as well as gray literature (dissertations, theses) and the reference lists of any publications found. Keyword searches were for "jaguar" OR "*Panthera onca*" OR "onça" OR "onça-pintada" OR "onza" OR "yaguar" OR "yaguareté" OR "tigre Americano" AND "diet" OR "fezes" OR "presas" OR "heces" OR "disponibilidad" OR "alimentación" OR "dieta" OR "hábitos alimentarios" OR "depredación" OR "ecología alimentar." Study sites that were surveyed over different years or in different treatments (hunting vs. non-hunting sections) were treated as separate data (**Table 1**). We included unpublished data if the raw data were obtained using standard, widely used analysis methods (scat analysis), as was done previously (Hayward et al., 2014; Lyngdoh et al., 2014).

Due to the cryptic nature of jaguars (Harmsen et al., 2010), scat analysis is the primary method researchers have used to determine diet (**Table 1**). Scat analysis may under-represent

TABLE 1 | Details on studies found and used in this meta-analysis including location, sample sizes, diet analysis method, and any assumptions made.

Country	Site	Number	Data collection years	Scats/Gut contents	Kills	Assumption/ Comments	References
Argentina	*Colileuga National Park*	*1*	*1991–1995*	*246*		*No prey*	Perovic, 2002
Belize	Cockscomb Basin	2	1983–1984	189			Rabinowitz and Nottingham, 1986
		3	2002	23			Weckel et al., 2006a,b
		4	2003–2006	364		Abundance from Weckel et al. (2006a)	Foster et al., 2010
Brazil	Acurizal Ranch	5	1977–1978		25		Schaller, 1983
	Area de Jofre	*6*	*1988–1994*	*13*		*Sample size*	Dalponte, 2002
	Area de Paraguaizinho	*7*	*1988–1994*	*15*	*30*	*No prey*	Dalponte, 2002
	Área de Proteção Ambiental do Lajeado e na do Rio Tocantins	*8*	*2000–2001*	*18*		*Sample size*	Trovati et al., 2008
	Emas National Park	9	2000–2003	18	20		Silveira, 2004
		10	2004–2009	35			Sollmann, 2011; Sollmann et al., 2013
	Goiás	*11*	*1998–2003*		*242*	*Cattle only*	Palmeira et al., 2008
	Iguaçu NP	*12*	*1997–2001*	*51*		*Cattle only*	de Azevedo, 2008
	Linhares	13	1996	101		Prey availability from Chiarello (1999, 2000)	Garla et al., 2001
	Mamirauá Ecological Reserve	14	2004–2005	29	10		Ramalho, 2006
	Miranda Ranch, Pantanal	*15*	*1980–1984*	*48*	*59*	*No prey*	Crawshaw and Quigley, 2002
	Pantanal	16	2003–2004	149	114		de Azevedo and Murray, 2007
		17	2001–2006	160	431		Perili, 2009
		18	2007–2008	134	50		Porfirio, 2009
		19	2001–2004		438		Cavalcanti and Gese, 2010
		20	*2003–2008*		*114*	*Crocodilians only*	Azevedo and Verdade, 2012
	Superagui National Park	*21*	*1995–1997*	*32*		*No prey*	Leite and Galvão, 2002
	Pantanal Matogrossense National Park	*22*	*1988–1994*	*7*	*14*	*No prey*	Dalponte, 2002
	Reserva Florestal da Companhia Vale do Rio Doce	*23*	*1993–1994*	*13*		*Sample size*	Facure and Giaretta, 1996
	Serra da Capivara National Park	*24*	*1990*	*7*		*Sample size*	Olmos, 1993
Colombia	Llanos Orientales	25	2005–2007		60		Garrote, 2012
Costa Rica	Corcovado National Park	26	1993–1994	22			Chinchilla, 1997
		27	1996–1998	18		Sample size	Carrillo et al., 2009
	Finca Las Alturas	*28*	*2008*	*13*		*Sample size*	Gutierrez and Porras, 2008
	Santa Rosa National Park	*29*	*2001–2011*	*5*	*0*	*Sample size*	Guadamuz, 2012
	Talamanca	*30*	*2007*	*15*		*Sample size*	Gonzalez-Maya et al., 2010
	Tortuguero National Park	*31*	*2005–2010*		*676*	*Turtles only*	Veríssimo et al., 2012
Guatemala	*Laguna del Tigre National Park*	*32*	*2005–2008*	*73*		*No prey*	Márquez, 2009
	La Selva Maya	33	1994–2005	206			Hernandez, 2006
	Maya Biosphere Reserve (hunted section)	34	2000–2001	23			Novack et al., 2005
	Maya Biosphere Reserve (unhunted section)	35	2000–2001	53			As above
Mexico	Sierra del Abra-Tanchipa Biosphere Reserve	36	2010–2012	43			Hernández-SaintMartín et al., 2015

(Continued)

TABLE 1 | Continued

Country	Site	Number	Data collection years	Scats/Gut contents	Kills	Assumption/ Comments	References
	Calakmul Biosphere Reserve	37	1989–1993	38			Aranda, 1994; Aranda and Sanchez-Cordero, 1996
		38	*1998–2000*	*84*		Same data as Ceballos et al. (2005)	Amin, 2004
		39	1997–2005	84			Ceballos et al., 2005
	Chamela-Cuixmala Biosphere Reserve	40	1995–1998	50			Núñez et al., 2000
	Sierra Madre de Chiapas	*41*	*1995–2002*	*45*		*No prey*	Cruz et al., 2007
	Sierra Nanchititla Natural Park	*42*	*2002–2009*	*13*		*Sample size*	Gómez-Ortiz and Monroy-Vilchis, 2013
	Sonora	*43*	*1999–2005*	*28*		*Cattle only*	Rosas-Rosas et al., 2008
	Tamasopo	*44*	*2011*	*11*		*Sample size*	Rueda et al., 2013
Panama	*Darien National Park*	*45*	*2004–2007*	*9*	*5*	*Sample size*	Moreno et al., 2006; Moreno Ruiz, 2006
Paraguay	*Chaco*	*46*	*1987–1989*	*106*		*No prey*	Taber et al., 1997
		47	2002	41		No prey	McBride et al., 2010
Peru	Manu National Park	48	1982–1985	25			Emmons, 1987
	Tambopata-Candamo Reserve	49	1997–1998	21			Kuriowa and Ascorra, 2002
Venezuela	*Hato Piñero*	*50*	*1996*	*3*		*Sample size*	Farrell et al., 2000
		51	1996–2002	122	30		Polisar et al., 2003
		52	1996–1998	42	30		Scognamillo et al., 2003
	Los Llanos	*53*	*2002–2006*		*608*	*Cattle only*	Hoogesteijn and Hoogesteijn, 2008

Sites in italics were excluded (see Assumption/Comments column).

turtles in jaguar diet as only the meat is eaten while the carapace remains intact yielding no evidence of the prey source within the scat (Carrillo et al., 2009), but over-represent reptiles, rodents and mesocarnivores (Martínez-Gutiérrez et al., 2015). However, scats were invariably collected from throughout the study sites, so problems associated with patchily distributed local prey are minimized (Steenweg et al., 2015). Distinguishing jaguar scat from sympatric puma *Puma concolor* scat based on size and other physical characteristics can lead to mis-diagnosis of the depositor (Farrell et al., 2000; Martínez-Gutiérrez et al., 2015), which will reduce the chances of obtaining significant preferences/avoidance in our analyses by broadening the dietary niche to include puma prey (hence our results are conservative). In the jaguar's case, DNA confirmation of the diet indicated that larger prey species are more likely to be present in scats than small prey species (Farrell et al., 2000), counteracting the traditional bias toward detecting smaller prey species from scat analysis (Mills, 1992). Prey availability was obtained from each study site from information presented in the literature (**Table 1**).

We used Jacobs' (1974) index to determine wild prey selectivity of jaguars following previous prey preference studies (Hayward et al., 2012, 2014; Lyngdoh et al., 2014). Where domestic livestock were killed alongside wild prey, we included both, but otherwise excluded studies solely focused on domestic livestock. Positive values of Jacobs' index indicate preference and negative values indicate avoidance (Jacobs, 1974). We calculated a Jacobs' index value for each prey species at each study site and then tested these using t-tests against a mean of zero, where data were normally distributed or a sign test where it was not, to determine significant preferences or avoidance (Hayward and Kerley, 2005). We also plotted Jacobs' index values with error bars to illustrate where a larger sample size was likely to lead to significant preference or avoidance, assuming the existing trend continued. We conducted these analyses for individual species and groups of related species (e.g. primates or *Agouti* spp.).

We developed a set of testable covariates that could potentially influence jaguar prey preferences from our literature review. A generalized linear model with a Gaussian distribution and an identity link function was conducted on these non-correlated variables. The independent variables used were socio-ecological/behavioral (prey relative abundance, habitat type and herd size at a site, and morphological (prey body mass and potential threat to a hunting jaguar; **Table 2**). Prior to model fitting, we standardized all covariates. We evaluated all possible combinations of models derived from the covariates. Model selection occurred using Akaike's information criterion (AIC) in a maximum likelihood framework (Akaike, 1973, 1974). We

TABLE 2 | Preference status (P/A; where –, denotes significantly avoided; +, significantly preferred; and ∼, killed in accordance with relative abundance), mean Jacobs's index value of each jaguar prey species, number of studies recording it as potential prey (n_p) and actual prey (n_a), mean percentage abundance and kills of each prey species, body mass (three-quarters of adult female), and categories of herd size, main habitat and potential threat to a jaguar, based on Nowak (1999).

Species	Scientific name	P/A	n_p	n_a	Jacobs' index (± S.E.)	Abundance	Kills (%)	Body mass (kg)	Herd size	Habitat	Threat
Acouchi, green	*Myoprocta pratti*		1	0	−1	0.07	0				
Agouti	*Dasyprocta sp.*	−	18	13	−0.47 ± 0.12						
Agouti, Azara's	*Dasyprocta azarae*		2	2	−0.42 ± 0.55	0.22	0.14 ± 0.14	3	2	2.5	0
Agouti, black	*Dasyprocta fuliginosa*		2	2	0.24 ± 0.22	0.02 ± 0.01	0.03 ± 0.00	2.6	2	2.5	0
Agouti, Central American	*Dasyprocta punctata*	∼	11	7	−0.52 ± 0.14	0.09 ± 0.03	0.05 ± 0.02	4	2	2.5	0
Agouti, red-rumped	*Dasyprocta leporina*		2	1	−0.99 ± 0.00	0.43 ± 0.42	0.01 ± 0.01	2	2	2.5	0
Anteater, giant	*Myrmecophaga tridactyla*	+	9	8	0.33 ± 0.20	0.06 ± 0.03	0.17 ± 0.08	18	1	1.5	1
Armadillos		∼	17	11	−0.11 ± 0.18						
Armadillo, nine-banded	*Dasypus novemcinctus*	∼	12	9	0.02 ± 0.21	0.14 ± 0.04	0.18 ± 0.06	3	1	2.5	0
Armadillo, southern three-banded	*Tolypeutes matacus*		1	0	−1	0.11	0				
Armadillo, yellow	*Euphractus sexcinctus*		1	0	−1	0.15	0				
Caiman		∼	6	5	−0.62 ± 0.26						
Caiman, black	*Melanosuchus niger*		1	1	−0.92	0.39	0.03				
Caiman, common	*Caiman crocodilus*	∼	3	3	−0.32 ± 0.49	0.43 ± 0.18	0.19 ± 0.07	17	1	2	2
Caiman, yacare	*Caiman yacare*		1	1	−0.82	0.67	0.16				
Canidae		∼	6	4	−0.43						
Capybara	*Hydrochaeris hydrochaeris*	+	8	8	0.46 ± 0.13	0.07 ± 0.03	0.21 ± 0.07	46	5	3	0
Carnivora		−			−0.26 ± 0.11						
Cattle	*Bos indicus/taurus*		2	2	−0.88 ± 0.10	0.73 ± 0.06	0.17 ± 0.15	340	5	1	1
Chachalaca, plains	*Ortalis vetula*		1	1	−0.63	0.08	0.02				
Coati	*Nasua sp.*	∼	14	13	−0.11 ± 0.14						
Coati, South American	*Nasua nasua*	∼	7	6	−0.13 ± 0.21	0.15 ± 0.09	0.10 ± 0.04	3.5	4	2	0
Coati, white-nosed	*Nasua narica*	∼	6	6	−0.26 ± 0.16	0.32 ± 0.10	0.17 ± 0.03	3.5	4	2	0
Coyote	*Canis latrans*		1	0	−1	0.01	0				
Deer	Cervidae	∼	30	25	−0.02 ± 0.11						
Deer, brocket	*Mazama spp.*	∼	15	11	−0.25 ± 0.16	0.07 ± 0.03	0.02 ± 0.01				
Deer, Central American red brocket	*Mazama temama*		1	1	0.30	0.01	0.02				
Deer, gray brocket	*Mazama gouazoubira*		1	1	−1	0.05	0				
Deer, marsh	*Blastocerus dichotomus*	∼	3	3	0.56 ± 0.29	0.02 ± 0.01	0.07 ± 0.02	60	3	2	0.5
Deer, pampas	*Ozotoceros bezoarticus*		2	1	−0.32 ± 0.68	0.02 ± 0.02	0.05 ± 0.05	30	3	1	0.5
Deer, red brocket	*Mazama americana*	∼	9	8	−0.08 ± 0.19	0.06 ± 0.01	0.06 ± 0.01	24	1	2.5	0
Deer, white-tailed	*Odocoileus virginianus*	∼	7	7	0.07 ± 0.18	0.10 ± 0.03	0.12 ± 0.06	41	3	2	0.5
Dog	*Canis familiaris*		1	1	−0.21	0.03	0.02				
Fox, crab-eating	*Cerdocyon thous*	∼	3	3	−0.41 ± 0.47	0.06 ± 0.03	0.01 ± 0.01	5	2	1.5	0
Fox, gray	*Urocyon cinereoargenteus*		1	0	−1	0.04	0				
Fox, hoary	*Pseudalopex vetulus*		1	1	0.39	0.01	0.02				
Horse	*Equus spp*		2	2	−0.07 ± 0.45	0.05 ± 0.01	0.05 ± 0.03	300	4	1	1
Livestock		∼			−0.48 ± 0.3						
Monkey, black-and-gold howler	*Alouatta caraya*		1	0	−1	0.07	0				
Monkey, Geoffroy's spider	*Ateles geoffroyi*		1	0	−1	0.47	0				
Monkey, golden-white bare-ear marmoset	*Callithrix argentata*		1	0	−1	0.02	0				

(Continued)

TABLE 2 | Continued

Species	Scientific name	P/A	n_p	n_a	Jacobs' index (± S.E.)	Abundance	Kills (%)	Body mass (kg)	Herd size	Habitat	Threat
Monkey, Guianan red howler	*Alouatta macconnelli*		1	1	−0.03	0.08	0.08				
Monkey, Guinean brown capuchin	*Sapajus apella*		1	0	−1	0.09	0				
Monkey, mantled howler	*Alouatta palliata*		1	1	−0.10	0.07	0.06				
Monkey, northern night	*Aotus trivirgatus*		1	0	−1	0.01	0				
Monkey, red-bellied titi	*Callicebus moloch*		1	0	−1	0.03	0				
Monkey, white-throated capuchin	*Cebus capucinus*		1	1	−0.18	0.14	0.10				
Monkey, Yucatan black howler	*Alouatta pigra*		1	0	−1	0.05	0				
Ocelot	*Felis pardalis*		1	1	0.17	0.04	0.06				
Opossum	*Didelphis sp.*	∼	7	4	−0.71 ± 0.18						
Opossum, black-eared	*Didelphis marsupialis*	–	4	2	−0.95 ± 0.03	0.21 ± 0.16	0.02 ± 0.02	4	1	2.5	0
Opossum, Virginia	*Didelphis virginiana*		1	1	0.25	0.01	0.02				
Paca, spotted	*Cuniculus paca*	∼	11	10	−0.12 ± 0.16	0.12 ± 0.03	0.10 ± 0.03	6	1	2.5	0
Suids		∼			0.18 ± 0.1						
Peccary spp.		∼	35	32	0.19 ± 0.11						
Peccary, collared	*Pecari tajacu*	∼	18	17	0.24 ± 0.13	0.08 ± 0.01	0.18 ± 0.03	22	5	2	1
Peccary, white-lipped	*Tayassu pecari*	∼	15	13	0.07 ± 0.20	0.13 ± 0.05	0.13 ± 0.04	35	5	2.5	1
Pig, wild	*Sus scrofa*	∼	5	5	0.04 ± 0.37	0.09 ± 0.05	0.20 ± 0.18	47	5	3	1
Primates		–	11	4	−0.75 ± 0.13						
Lagomorphs		∼	11	7	−0.45 ± 0.25						
Rabbit, tapeti	*Sylvilagus brasiliensis*	∼	4	3	−0.48 ± 0.30	0.02 ± 0.00	0.01 ± 0.01	1	1	3	0
Raccoons		∼			−0.36 ± 0.33						
Raccoon, crab-eating	*Procyon cancrivorus*	∼	3	3	0.07 ± 0.37	0.02 ± 0.01	0.02 ± 0.00	5	1	2	0
Raccoon, northern	*Procyon lotor*		2	0	−1 ± 0	0.01 ± 0.00	0 ± 0	5	1	2	0
Rhea	*Rhea americana*		1	1	0.99	0.00	0.7				
Rodents		–			−0.2 ± 0.1						
Skunk, striped hog-nosed	*Conepatus semistriatus*		1	0	−1	0.00	0				
Sloth, brown-throated	*Bradypus variegatus*		1	1	−0.30	0.44	0.3				
Squirrel	*Sciurus langsdorffi*		1	0	−1	0.01	0				
Tamandua		∼	5	5	0.27 ± 0.28						
Tamandua, northern	*Tamandua mexicana*	∼	3	3	0.10 ± 0.47	0.03 ± 0.02	0.04 ± 0.02	5	1	2	0
Tamandua, southern	*Tamandua tetradactyla*		2	2	0.54 ± 0.10	0.02 ± 0.00	0.05 ± 0.00	5	1	2	0
Tapir, Baird's	*Tapirus bairdii*	–*	4	0	−1 ± 0	0.06 ± 0.03	0 ± 0	221	1	2	0.5
Tapir, lowland	*Tapirus terrestris*	–	7	4	−0.55 ± 0.24	0.07 ± 0.03	0.03 ± 0.03	130	1	2	0.5

*Scientific names are based on the IUCN Red List. *Denotes a significant result is likely with a larger sample size.*

used model averaging to derive parameter estimates (Burnham and Anderson, 1998). Strongly supported relationships among individual variables were plotted using linear or loess best fit models.

We estimated prey species body size as three-quarters of adult female body mass to account for juveniles and sub-adult prey killed (Jooste et al., 2013). Body mass, herd size, habitat use, and potential threat data were taken from Nowak (1999). Herd size is assumed to be an indicator of how well prey could detect predators (Hamilton, 1971; Fitzgibbon and Lazarus, 1995) and how the attraction effect of congregating prey affects predator detection of prey (Hebblewhite and Pletscher, 2002), and was a categorical variable with 1 relating to solitary individuals, two to species existing in pairs, three to small family groups, 4 to small herds (10–19) and 5 to large herds (>20; **Table 2**). Habitat type may influence predation as the density of vegetation can affect detectability and catchability, and predator and prey must overlap in habitat to encounter one another (Hayward and Kerley, 2005). A categorical variable of habitat use was used with 1 relating to open environments, 2 to woodlands, and 3 to dense forests (**Table 2**). Threat was a categorical variable where 0 represents no threat, 1 a minor threat, and two a major threat based on body size and the possession of weaponry, such as horns or teeth (**Table 2**).

We identified the *accessible prey weight range* following the break point analysis of Clements et al. (2014). The accessible prey weight range is most likely to encompass the *preferred weight range* of earlier prey preference studies, which we estimated from loess smoothed plots of mean species Jacobs' index scores against body mass (Hayward et al., 2014). We calculated the *ideal mass* as the mean body mass of those species that were significantly preferred. We estimated the body mass of jaguars as 60 kg, which is the lower range of adult female body mass (Nowak, 1999) and used this to determine the predator to prey mass ratio by dividing the *ideal mass* of prey by 60. We also include 38 kg as this is the lowest reported body mass of adult jaguars in Nowak (1999). We recognize jaguar body mass varies substantially throughout their range and these ratios could be affected by site-specific variability, however, we used this as representing the body mass over the entire distribution of the species.

We tested whether jaguar preferences for individual species varied with prey abundance, rainfall or size of prey available at a site (following Kiltie, 1984) using linear regression. We could not run generalized models on these variables because of insufficient sample size for individual species (cf the global models we ran with data from all species). Climate data were obtained from details presented in individual studies or the US National Climatic Data Center (http://www.ncdc.noaa.gov/). Note that the regression of Jacobs' index on prey abundance tests how jaguars respond to changes in the relative abundance of individual species, whereas the inclusion of prey abundance in the generalized linear model is looking at how a species' overall abundance affects its likelihood of being selected by jaguars.

Finally, we tested aspects of optimal foraging theory using linear regression. We hypothesized that (1) jaguars would show greater preferences at sites with higher species richness because there would be sufficient prey for them to specialize on particular species; and (2) jaguars would show greater preferences at sites with higher prey biomass for the same reason. We used total biomass, largest biomass of a single species, and body mass of the most preferred prey at a site as measures for this second hypothesis.

All analyses were conducted in *R* (R Core Development Team, 2008; Barton, 2013). Mean (±1 S.E.) values are presented throughout.

RESULTS

We found 53 studies documenting the diet of jaguars collected over 176 study years and based on 5977 kill records (**Table 1**). These studies were conducted throughout the distribution of the jaguar (**Figure 1**). Twenty-five (25; 47%) of these studies, collected over 75 survey years with 3214 kill records (**Table 1**), had sufficient data for use in this meta-analysis. The remaining 28 studies were excluded due to inadequate prey availability data or a focus on livestock predation (**Table 1**). Brazil, Mexico and Costa Rica had the largest number of jaguar diet studies, while Brazil (9 useable of 20 studies), Guatemala (4 of 4) and Mexico (4 of 9) had most of the studies that could be included in this meta-analysis (**Table 1**). Studies that were used came from the suite of habitats used by jaguars including tropical forest, the Llanos, Cerrado, Pantanal, and Chacos. No studies from Argentina, Panama, or Paraguay could be used in this analysis (**Figure 1**).

Within our meta-analysis there were 111 wild species in the diet of jaguars, ranging in size from 1 kg rabbits to 130 kg lowland tapirs (these results and scientific names of species mentioned in the text are presented in **Table 2**). The species that appeared most frequently in their diet (16–21%) included capybara, wild pig, caiman, collared peccary, nine-banded armadillo, giant anteater and white-nosed coati. In addition, there were species that were always preyed upon if they were present, suggesting a possible preference (capybara, white-tailed deer, white-nosed coati, wild pigs, common caiman, marsh deer, crab-eating fox, crab-eating raccoon, and northern tamandua). In addition, collared peccary, red brocket deer, spotted paca, giant anteater, white-lipped peccary and South American coati were also killed by jaguars more than 85% of the time they were present in the prey community (**Table 2**). Conversely, Baird's tapir was never killed by jaguars in the sampled studies, and primates were killed at only four of 11 sites where they were recorded as present (**Table 2**).

Common caiman, white-nosed coati, Azara's agouti and black-eared opossum constituted over 20% of the available prey community where they were recorded (**Table 2**). Capybara, wild pigs, common caiman, nine-banded armadillo, collared peccary, white-nosed coati, giant anteater, and white-lipped peccary constituted more than 10% of the kills of jaguar where they occurred (**Table 2**).

When the relative abundance of prey species was accounted for, jaguars significantly preferred to prey on only two species: giant anteater [$t_{(8)} = 7.24, p < 0.001$] and capybara [$t_{(7)} = 16.96$, $p < 0.001$; **Table 2**; **Figure 2A**). Southern tamandua and marsh deer may become preferred with a larger sample size (**Table 2**; **Figure 2A**), all but two of the remaining 109 prey species were killed in accordance with their relative abundance within the prey community (**Figure 2A**). Both black-eared opossum [$t_{(4)} = -31.42$, $p < 0.001$] and lowland tapir [$t_{(6)} = -2.66$, $p = 0.038$] were significantly avoided, along with Baird's tapir if sample sizes were larger (**Table 2**; **Figure 2A**).

There was no indication that jaguars prefer a particular group of related prey, such as peccaries or armadillos, but they do significantly avoid carnivorans [$t_{(27)} = -2.86$, $p = 0.008$], the agoutis [$t_{(18)} = -4.09$, $p < 0.001$] and primates (*binomial* test 0/11, $p < 0.001$; **Table 2**; **Figure 2B**). All other broad taxonomic groups were killed in accordance with their abundance (**Figure 2B**).

Jaguars reduced their preference for white-nosed coatis as they became more abundant in the prey community ($r^2 = 0.92$, $n = 7$, $p < 0.001$; **Figure 3**). No other prey species exhibited a significant relationship between their Jacobs' index value and their relative abundance (**Figure 3**). There was no relationship between the degree to which jaguars preferred or avoided a prey species and the mean annual rainfall at each study site where it occurred (**Figure 4**).

A generalized linear model of the drivers of jaguar prey preferences revealed that prey abundance was the most supported predictor variable (sum of Akaike's weights $w_i = 0.93$), with prey herd size also strongly supported ($w_i = 0.74$; **Table 3**).

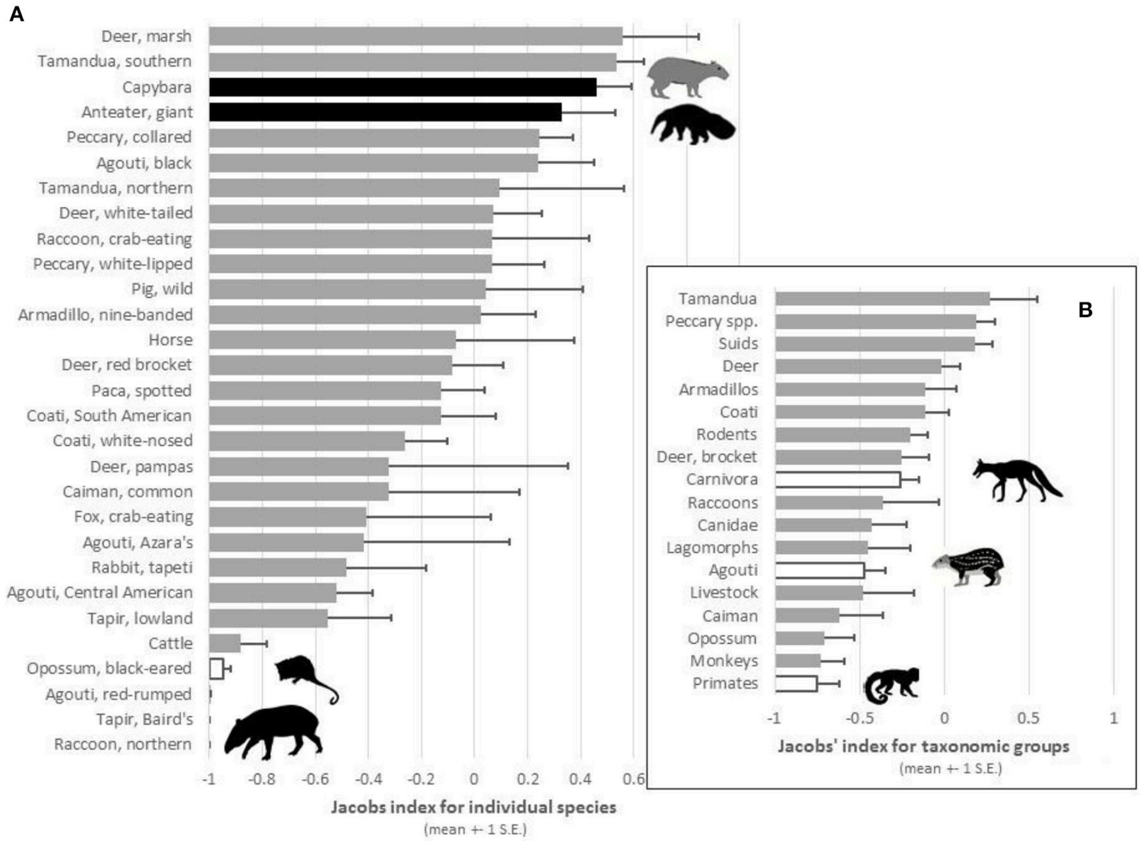

FIGURE 2 | Plot of the mean Jacobs' index values (±1 S.E.) of preference for (A) prey species and (B) taxonomic groups that were reported as potential prey of jaguars in at least two study sites. Black bars represent significantly preferred species, white bars significantly avoided species, and gray bars species killed in accordance with their availability.

Model averaged parameter estimates from the top-ranking model showed that jaguar prey preferences were negatively associated with prey abundance ($\beta = -1.39$) and positively associated with herd size ($\beta = 0.08$; **Table 3**; **Figure 5**). Prey body mass was the next most important variable (**Table 3**), and a regression of Jacobs' index against prey body mass indicated that jaguars significantly preferred larger prey up until 100 kg (**Figure 6**). In our sample, tapirs are the only wild prey that exceed 100 kg and jaguars avoided both species.

Segmented modeling showed strong support for two and four breakpoints in jaguar prey preference and prey body mass relationships (**Table 4**). We use the most conservative of these and discuss the results with two breakpoints hereafter. The segmented modeling showed the accessible prey weight range was from 6 to 60 kg (**Figure 7**). The preferred prey weight range of jaguars is 45 to 85 kg (**Figure 5**). Note that the upper limit of the preferred weight range is larger than that of the accessible weight range due to the loess smoothing function. The body mass of significantly preferred prey (*ideal prey*; capybara and giant anteater) is 32 ± 14 kg. The predator: *ideal prey* ratio for jaguars is therefore 1: 0.53 based on adult female jaguar body mass of 60 kg and 1:0.84 for adult body mass of 38 kg.

Individual prey species within the preferred and accessible weight ranges were invariably increasingly avoided as they became more abundant within the prey community (**Figure 3**). Significantly preferred prey species (mean $b = -0.1 \pm 2.2$), species within the preferred weight range ($b = -7.7 \pm 8.3$) and significantly avoided prey ($b = -1.8 \pm 1.9$) had a mean slope of this relationship with standard error bars crossing 0 (**Figure 3**). Conversely, accessible prey ($b = -3.9 \pm 2.7$) and prey outside the accessible prey weight range ($b = -9.4 \pm 3.8$) had a consistently negative relationship between preference and abundance (**Figure 3**).

There was no support for our hypotheses relating to optimal foraging theory of jaguars (**Figure 8**). Jaguars did not show greater preferences where there was greater prey species richness or where there was a greater biomass of potential prey.

DISCUSSION

Jaguars exhibit trait-mediated foraging interactions with their prey species (Railsback and Harvey, 2013) by significantly preferring capybara and giant anteater, and avoiding species outside their preferred and accessible weight ranges (**Figure 2**). In contrast to other large predators, the traits that mediate

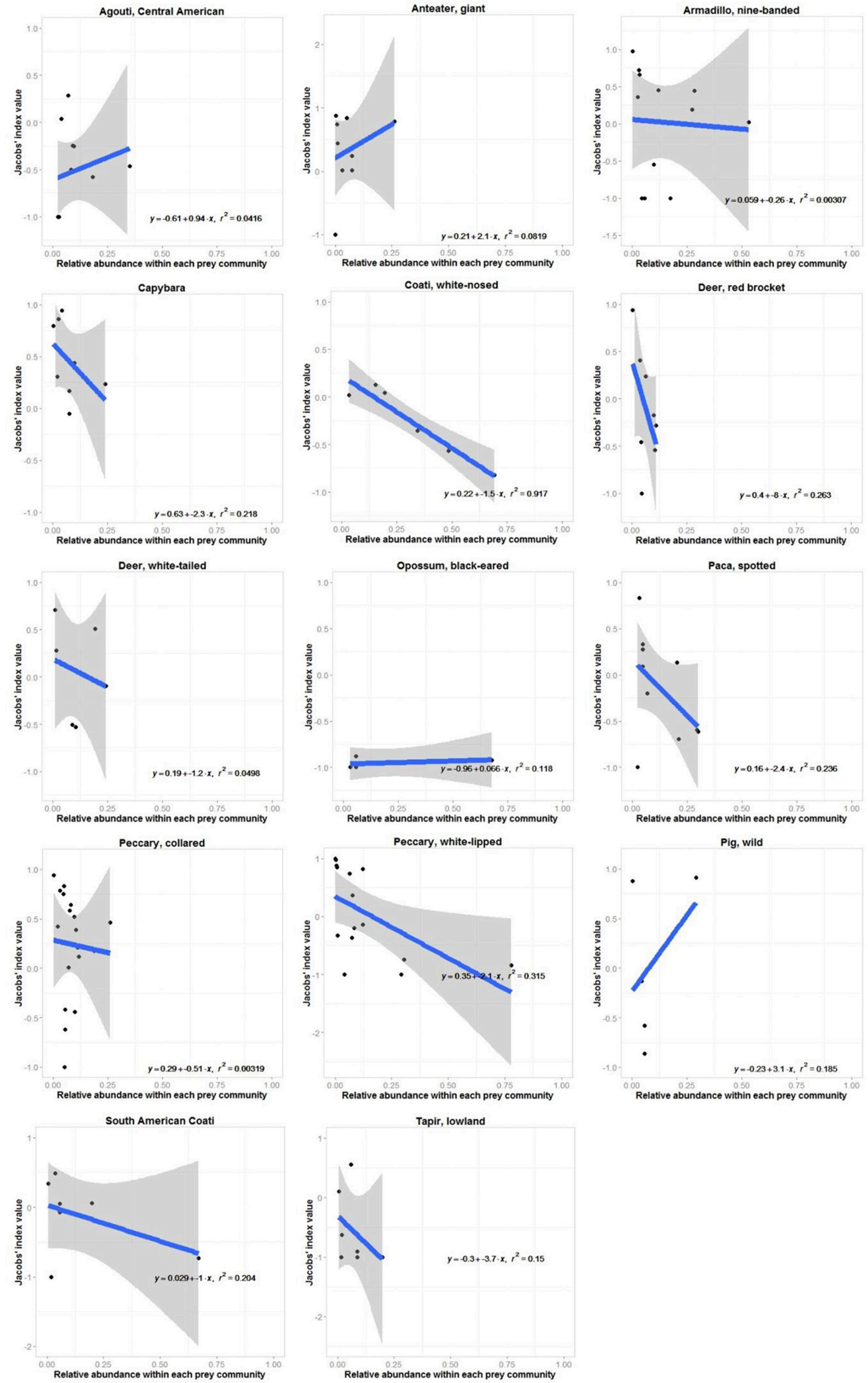

FIGURE 3 | Relationship between site-specific preference (Jacobs' index value) and relative abundance for each prey species of jaguars with four or more Jacobs' index value estimates within the prey community. Ninety-five percent confidence intervals are shown unless they extend to far beyond the y-axis limits.

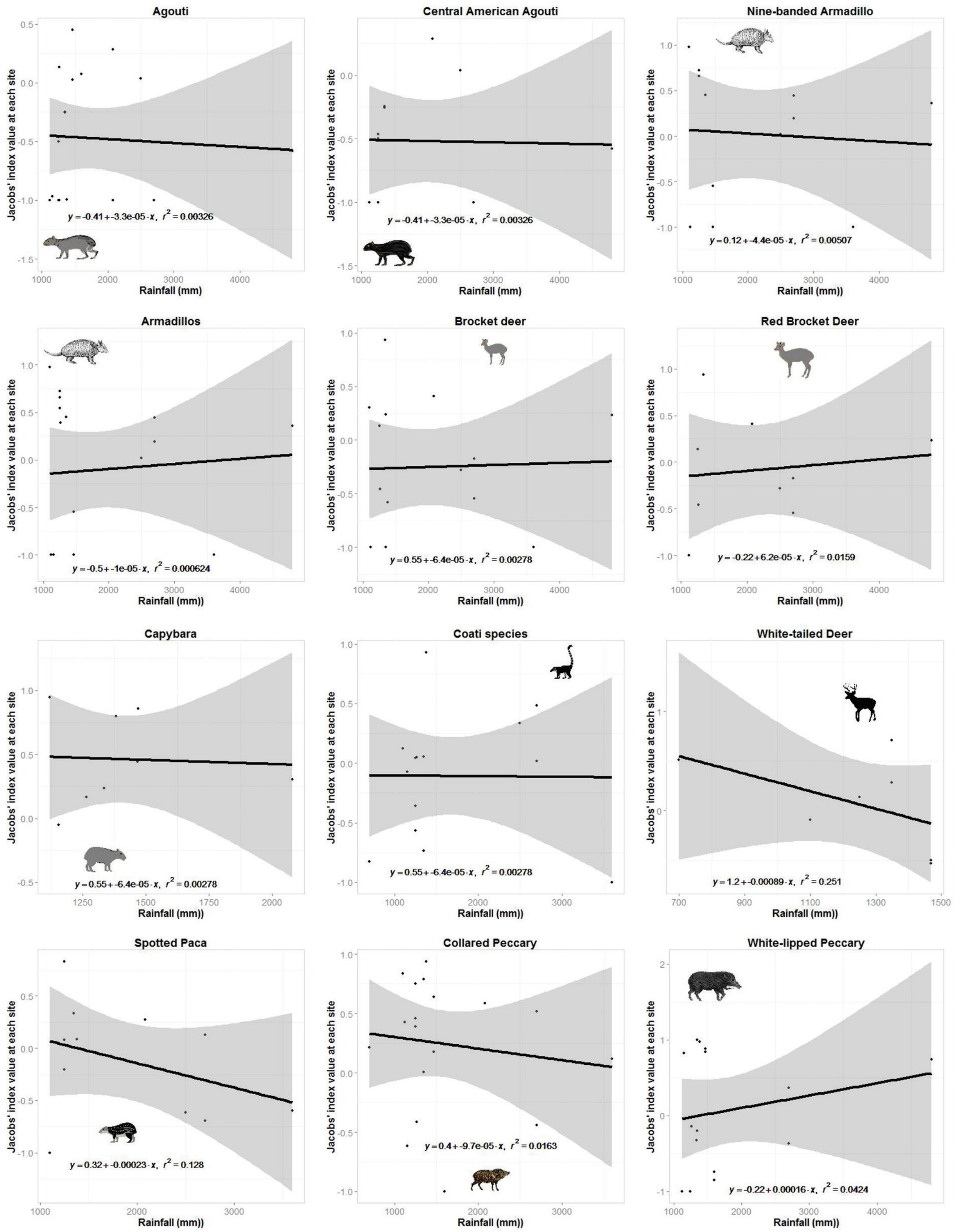

FIGURE 4 | Plots of the relationship between prey preference of jaguar prey species or taxonomic groups with more than six site records and the mean annual rainfall at each site.

TABLE 3 | Model selection statistics for the 10 most supported models of drivers of jaguar prey selection, including model averaged parameter estimates and summed Akaike's weights for each variable.

Intercept	Abundance	Body mass	Habitat	Herd size	Threat	d.f.	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	Akaike's weight
−0.256	−1.567			0.111		4	35.0	0	0.246
−0.263	−1.379	−0.001		0.128		5	36.0	0.98	0.151
−0.276	−1.505	−0.002		0.114	0.225	6	36.9	1.92	0.094
−0.263	−1.682			0.098	0.143	5	37.0	2.02	0.089
−0.029	−1.289					3	37.5	2.46	0.072
−0.321	−1.551		0.029	0.112		5	37.9	2.89	0.058
−0.080	−1.522				0.227	4	38.0	3.04	0.054
−0.072	−1.381	−0.002	−0.086	0.131		6	38.8	3.85	0.036
−0.068	−1.364	−0.001			0.299	5	39.3	4.29	0.029
−0.014	−1.172	−0.001				4	39.7	4.72	0.023
Model averaged parameter estimates	−1.386 ± 0.618	−0.001 ± 0.001	0.001 ± 0.073	0.084 ± 0.067	0.070 ± 0.140				
Sum of Akaike's weights	0.93	0.40	0.19	0.74	0.34				

jaguar foraging decisions are ecological (prey abundance) and behavioral (herd size) more than morphological (body mass; **Table 3**). Thus, jaguars are not generalist predators as once thought, but prey specifically on particular species and according to certain prey characteristics.

During the late Pleistocene, there were more than 50 additional species of large (>40 kg) herbivores in the Americas (Kurtén and Anderson, 1980; Greenwood, 2009), and so jaguars evolved in ecosystems with a much higher diversity and availability of potential prey than found today. This is in contrast to Africa, where extant large carnivores prey upon herbivore communities that were similar in abundance, richness and diversity to those which occurred at the end of the Pleistocene (Lyons et al., 2004). This difference likely explains why the predator to prey body mass of jaguars is much smaller than other large solitary felids (**Figure 9**). For example, jaguars are often considered to be ecologically similar to leopards (Sunquist and Sunquist, 2002), yet jaguars preferentially prey on smaller species than leopards (**Figure 9**), despite jaguars having a larger body size. The lack of diverse large herbivores in the Holocene also likely explains why jaguars do not have prey selection driven by prey morphology (**Figure 5**), do not show any evidence of optimal foraging (**Figure 8**), are the only large felid not preferentially hunting Cetartiodactyla herbivores, and have reduced body mass compared to the Pleistocene (Seymour, 1989). The larger prey species that survived the Pleistocene extinctions in South America, such as tapirs, are currently above the upper limits of the accessible weight range of jaguars. Those Cetartiodactyla species that persist today are likely to have been kept at lower density than jaguars evolved with due to continual hunting pressure from humans since the Holocene. Thus, jaguars may be persisting on sub-optimal prey, as is the case for some puma (Yanez et al., 1986; Iriarte et al., 1990) and African wild dog *Lycaon pictus* populations (Woodroffe et al., 2007).

Additionally, even though the jaguar is regarded today as the largest and most dominant apex predator in the Americas, it has only occupied that role for the past 10,000 years. Near the end of the Pleistocene, the jaguar in the Americas was sympatric with a least ten carnivore species that were larger than itself (Cione et al., 2009). Thus, similar to that reported for the gray wolf (*Canis lupus*; Tedford et al., 2004), the jaguar was somewhat of a mesocarnivore rather than an apex carnivore for most of its evolutionary existence, so its predatory behavior should be viewed in that context. Indeed, the jaguar's ability to function as a mesopredator by preying on a wide range of different-sized species, particularly smaller species, is probably why this large felid species, together with the puma (*P. concolor*), survived the end-Pleistocene extinction in the Americas, whereas the other five sympatric large felid species went extinct (Van Valkenburgh and Hertel, 1998). The effects of the end-Pleistocene megafaunal extinctions, together with the "ghosts" of more dominant extinct carnivores (Connell, 1980), may explain why jaguars continue to preferentially prey upon species smaller than expected given their body size, especially in comparison to African large carnivores, which continuously had a high diversity of large herbivores on which to prey.

It is unclear if jaguars also preferentially preyed upon relatively small prey during the Pleistocene, or simply reduced their preferred prey size in the Holocene as a strategy to survive the end-Pleistocene extinctions. Given the high diversity of potential prey species during the Pleistocene in the Americas (higher diversity than contemporary African savannah ecosystems; Lyons et al., 2004), it seems unlikely that jaguars would have restricted themselves to such small prey. In fact, their larger body size in the Pleistocene would have allowed jaguars accessible prey between 30 and 150 kg, with preferred prey around 90 kg (based on the equations in Van Valkenburgh et al., 2015). Interestingly, other carnivore species, ranging from black-footed ferrets *Mustela nigripes* to coyotes *Canis latrans*, appear to have significantly different diets and ecological niches between the Pleistocene and Holocene (Owen et al., 2000; Meachen et al., 2014), probably as an adaptation to survive the end-Pleistocene

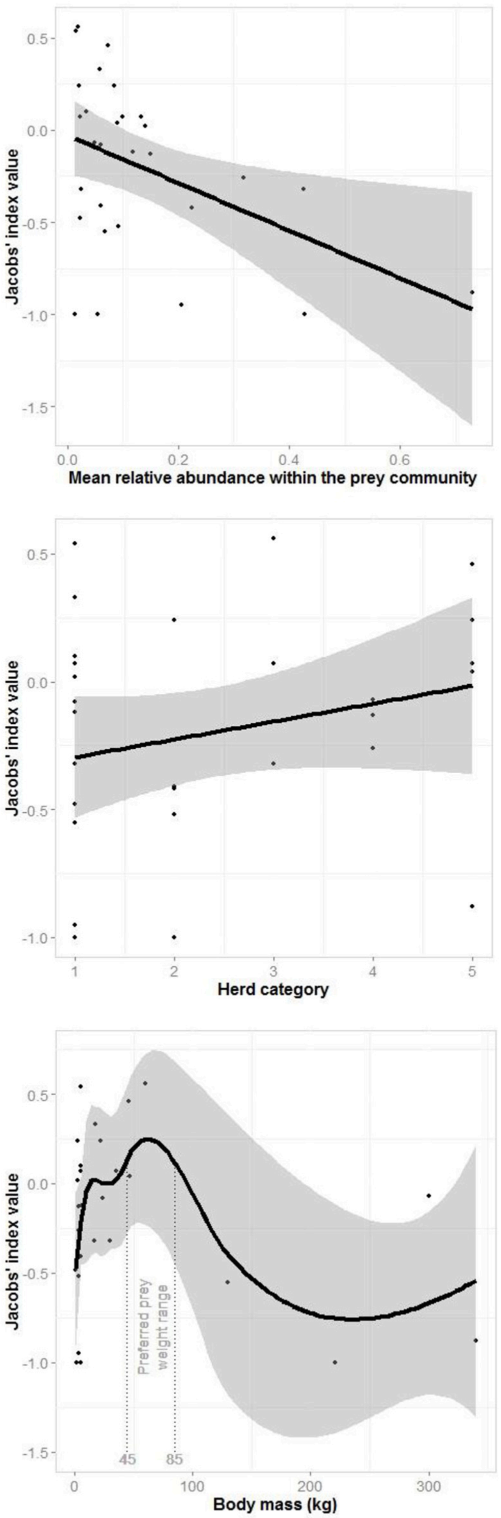

FIGURE 5 | Plots of the relationship between the most important drivers of jaguar prey selection based on the generalized linear model (Table 3): mean prey abundance (linear), prey herd category (1–solitary, 2–pairs, 3–small groups, 4–groups of 5–20, and 5 large groups; linear) and prey body mass (three-quarters of adult female body mass; loess smooth).

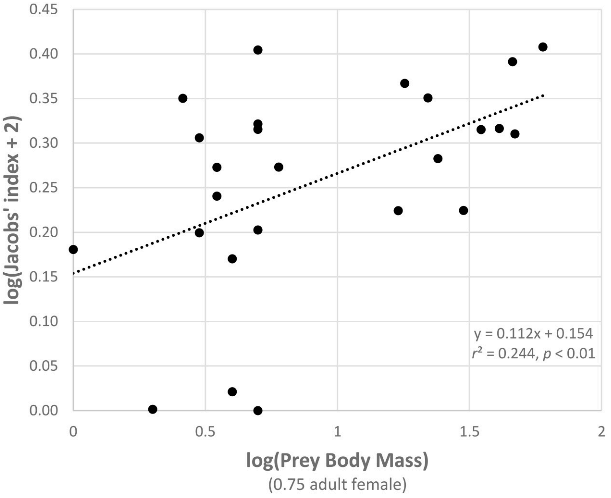

FIGURE 6 | Relationship between the Jacobs' index of each prey species with three or more records and prey body mass (both log transformed).

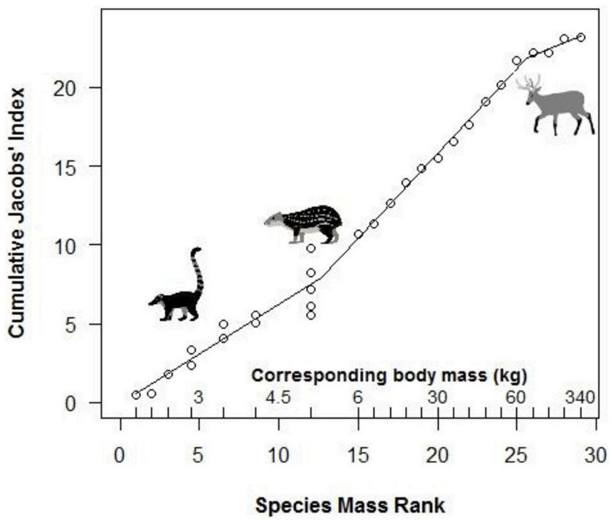

FIGURE 7 | Segmented model of the relationship between the mass rank of each prey species and jaguar preference. Preference is based on cumulative Jacobs' index values (+1 for standardization) following Clements et al. (2014). Actual prey masses corresponding to mass ranks are shown above the *x*-axis. Representative species sitting at breakpoints are shown (coati, paca, marsh deer).

TABLE 4 | Model selection statistics for the segmented model to identify the preferred and accessible prey of jaguars.

Breakpoints	AIC	ΔAIC
2	76.82	0.00
4	76.82	0.00
1	80.93	4.11
5	89.34	12.52
3	93.38	16.56

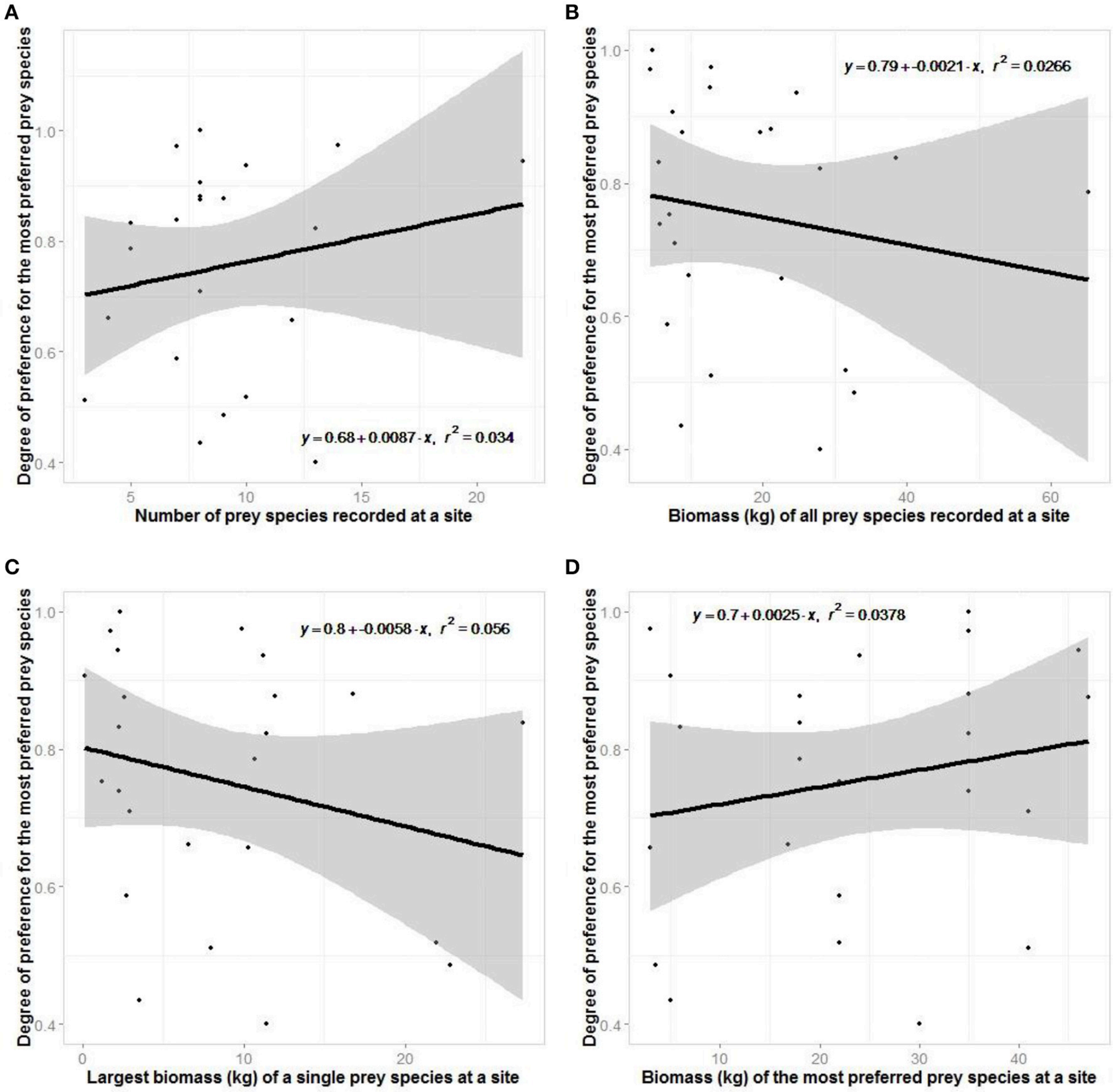

FIGURE 8 | Regression plots testing aspects of optimal foraging theory where the degree of prey preference exhibited at a site is related to (A) the number of species there, (B) the biomass of all prey there, (C) the largest biomass of a species there, and (D) the body mass of the most preferred prey species there.

extinctions, and the same is likely true for jaguars. For the coyotes, the switch to smaller prey species in Holocene coincided with a reduction in body size (Meachen et al., 2014). This suggests that jaguars also could have exhibited adaptive behavioral changes during the Holocene to preferentially prey upon smaller species. Similar to the coyote, this possible behavioral adaptation coincided with a decrease in body size of the jaguar during the Holocene. Furthermore, there is no evidence that canids in North America expanded their dietary niche following the Pleistocene extinctions, possibly because competition with humans outweighed the advantages of niche expansion (Pardi and Smith, 2015).

Adding further pressure to a predator with a limited or reduced abundance of suitably sized prey, previous research has highlighted the importance of areas with no human hunting as jaguar prey refugia (Harmsen et al., 2010). For example, important jaguar prey species, such as peccaries, spotted paca and nine-banded armadillo are heavily hunted by humans (Redford, 1992; Jorgenson and Redford, 1993). Given the importance of prey in determining predator densities (Fuller and Sievert, 2001; Karanth et al., 2004; Hayward et al., 2007b), reduced prey abundance has been, and probably still is, keeping jaguar populations below densities at which they evolved. Thus we reiterate that the "empty forests syndrome" (Redford, 1992; Wilkie et al., 2011) can have cascading impacts on all trophic levels, including apex predators (Steinmetz et al., 2013).

Both peccary species are within the accessible and preferred weight ranges of jaguars, however neither is preferred. Although

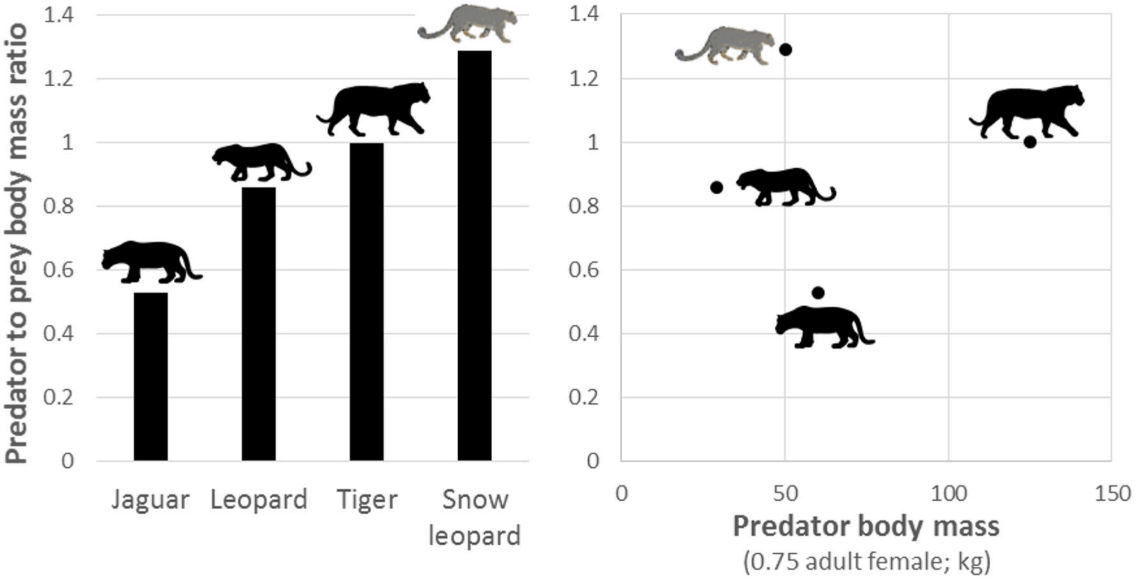

FIGURE 9 | Plot of the predator to prey body mass ratio of solitary members of the genus *Panthera* and how this relates to the body mass of each species (Hayward et al., 2006a, 2012; Lyngdoh et al., 2014).

frequently killed by jaguars, there is no evidence that the predator-prey relationship between jaguars and peccaries is a coevolutionary predator-prey "arms race" given that existing evidence suggests the species evolved at separate times and places (Mayer and Wetzel, 1987). This lack of preference may be because peccaries are formidable opponents that can seriously injure jaguars (Perry, 1970). Furthermore, severe population reductions of peccaries during the late-Pleistocene may have prevented jaguars from optimally foraging on them. In fact, several peccary species did not survive these extinctions (Kurtén and Anderson, 1980; Greenwood, 2009), and those that did likely suffered severe population bottlenecks, similar to that found for other Pleistocene ungulate survivors such as bison *Bison bison* and musk ox *Ovibos moschatus* (Cione et al., 2009) and their loss is likely to have led to a chain of extinction for large scavenging birds such as condors, vultures and teratorns (Van Valkenburgh and Hertel, 1998). Consequently, the surviving jaguars may have been those that preferentially preyed upon species smaller than peccaries, and thus the non-preference for peccaries by modern jaguars could be an artifact from the end-Pleistocene extinctions. Despite this, jaguars can have significant impacts on peccary populations, such as in Iguaçu National Park, Brazil, where half the peccary population was killed by jaguars annually (Crawshaw, 1995). Elsewhere, white-lipped peccaries were found in 89% of jaguar scats along beaches in Corcovado National Park (Carrillo et al., 2009) and collared peccaries were killed almost three-times more frequently than any other prey species in the Sierra Madre de Chiapas of Mexico (Cruz et al., 2007). Our results also support hypotheses that the expanding wild boar population in the Brazilian Atlantic Forest will enable jaguars to recolonize the region (Verdade et al., 2015), because wild boars are killed in accordance with their abundance (**Table 2**) and are expected to function as buffer prey facilitating this expansion.

Jaguars prefer capybara and giant anteaters throughout their range and we assume this is based on optimal foraging of high energy meat yield for minimal investment in handling and processing, and limited injury risk. They are unselective in their predation on capybara age classes, but can kill a substantial proportion of a population over short periods of time (30% of a population within 2 months; Schaller and Vasconcelos, 1978). Just as the heavy predation by leopards *Panthera pardus* on baboons *Papio spp.* does not indicate preferential predation (Hayward et al., 2006a), the high levels of predation on caiman (over 62% of all caiman mortalities; Azevedo and Verdade, 2012) do not mean jaguars preferentially prey on them (**Table 2**). Although previous studies have shown reptiles can constitute up to 54% of a jaguars diet (Ramalho, 2006), a broader review of 19 studies showed that this is closer to 21 ± 3% (although this drops to 0.9 ± 0.1% when means weighted by sample size are used; calculated from da Silveira et al., 2010).

Although we focus this study on wild prey, jaguars are well known predators of livestock (Hoogesteijn et al., 1993; Quigley et al., 2015). Data from Polisar et al. (2003) show that jaguars prefer to kill cattle less than 1 year of age weighing less than 120 kg ($D = 0.60$) and avoid adult cattle ($D = -0.78$). Garrote (2012) showed that jaguars preferred pigs ($D = 0.91$) over horses ($D = 0.38$) and avoided cattle ($D = -0.98$). These results serve to reinforce our prey preference results, but also suggest that the predator naiveté that livestock have evolved through the domestication process allows predators to kill larger individuals than is possible with wild prey.

Other large predators we have studied exhibited reduced preferences for preferred prey species as they became more abundant within the prey community (Hayward, 2011). Conversely, they show increasing preference for non-preferred prey within the preferred weight range as they became more abundant (Hayward, 2011). Jaguars show no such relationship, with non-preferred species also being less preferred as they become more abundant (**Figure 3**). We contend that this is further evidence that jaguar predatory ecology has been substantially altered since the late-Pleistocene extinctions. This is in addition to the unusually small predator to prey body mass ratio of jaguars compared to other solitary felids, the limited effect of prey morphology as a driver of jaguar prey selection, the absence of evidence of optimal foraging by jaguars, the reduction in jaguar body mass since the Pleistocene, and the absence of preferentially hunting on Cetartiodactyla herbivores.

While this meta-analysis highlights the number of studies conducted on jaguar foraging ecology, it illustrates that research exhibits substantial spatial variation across the Americas, being dominated by work in Brazil and Mexico (**Table 1**; **Figure 1**) and data from these sites may be influencing our results. It also concurs with earlier reviews that concluded that research on this species has been limited by small sample sizes and a corresponding lack of information on prey abundance (Sunquist, 2002). In previous research on Africa's large predator guild, we were able to use trait-based aspects of their foraging to predict the number of large predators that could be sustained at a site, the home range sizes, and the diet using the results of prey preference studies similar to this one (Hayward et al., 2007a,b, 2009; Jooste et al., 2013). This was not possible here because jaguar prey abundance data is invariably presented as a relative measure rather than actual densities, which is satisfactory for determining prey preferences (Hayward et al., 2006a) but inadequate for these other purposes. The frequent use of camera traps to monitor prey communities in jaguar territories offers the opportunity to derive population density estimates via entropy modeling (Rowcliffe et al., 2008, 2011) and these would assist predictive ecology for these species.

This research highlights the important prey species and weight ranges of prey that are necessary for the conservation of jaguars and will be useful if plans for reintroduction come to fruition (Galetti et al., 2013). It also highlights areas for focus in future research programmes. Most importantly, however, this study illustrates the predatory response of an apex predator to the Pleistocene extinctions and more recent overhunting in which jaguars exhibit a diverse prey spectrum with minimal evidence of adhering to optimal foraging rules and, where they do, preferentially killing smaller than predicted prey (**Figure 9**).

AUTHOR CONTRIBUTIONS

MH designed, analyzed and wrote up this study. JK collected data and wrote-up this study. RM wrote-up this study. AN collected data and wrote-up this study. SR collected data and wrote-up this study. LS collected data and wrote-up this study. BV wrote-up this study.

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