Mammal Review

Continent-wide differences in diet breadth of large terrestrial carnivores: the effect of large prey and competitors

1   **Title:** Continent-wide differences in diet breadth of large terrestrial carnivores: the effect of large

2   prey and competitors

3

4   **Abstract**

5   1. Despite their importance for understanding consumer-resource dynamics, the dietary

6   responses of large terrestrial predators to variations in prey richness and competition

7   pressure are unclear. While a greater predator selectivity along with increasing prey

8   abundance would be expected under an optimal foraging scenario, there is some evidence

9   that predators may broaden their diet where there is a greater resource diversity.

10   Furthermore, the use of large prey may be limited by increasing presence of competitors.

11   2. We considered three widespread large carnivores (the grey wolf *Canis lupus*, the puma

12   *Puma concolor* and the leopard *Panthera pardus*), whose distribution range encompasses

13   different continents, with different communities of prey/competitors. We expected that the

14   potential to modulate their use of large prey according to prey richness would vary

15   according to different levels of potential competition.

16   3. We collated data from more than 240 studies of the diets of wolf, puma and leopard to

17   model whether the relationships between the diversity of used large prey (i.e., the Large

18   Prey Index) and prey richness was modulated by carnivore richness, in different continents.

19   4. The wolf showed an increase in the Large Prey Index with prey richness across its

20   distribution range, where it is usually the apex predator in areas from which data are

21   available. Conversely, the leopard showed this pattern in Asia, but not in Africa, where it

22   often coexists with a greater array of potential competitors. For the puma, the Large Prey

23   Index increased with prey richness throughout its distribution range, except in the areas

24   where the larger and dominant jaguar also occurred.

25   5. By emphasising the complex relationships between prey richness and predator diets, our

26   results testify to the suppressive effects of larger competitors over the use of large prey by

27   subordinate carnivores.

28 **Keywords:** apex predators; competition; diet breadth; food habits; predator-prey relationships; prey

29 diversity.

30 **Running head:** Large carnivore diet breadth

31 **Word count:** 6403

Introduction

Spatiotemporal variation in the diversity of food resources influences consumer-resource dynamics, affecting community-to-ecosystem-level processes. Unequivocal evidence of the responses of foragers to variation in resource diversity is lacking. In more productive systems, with higher abundances and diversities of resources (Danell et al. 1996; Olff et al. 2002; Bailey et al. 2014; Youngentob et al. 2015; but see Mittlebach et al. 2001; Santini et al. 2019), consumers would be expected to specialise on the most profitable resources, increasing their selectivity and adopting a narrower diet breadth (MacArthur et al. 1966; Shoener 1971; Charnov 1976; Forister et al. 2015). Conversely, opportunistic foragers may take advantage of a greater diversity of food resources by broadening their diet (Borkhofer & Wolters 2012; Ferretti et al. 2020). Both outcomes may occur, depending on local environmental conditions, but information at broad scales is scarce. Understanding which of these two expectations is supported by data would provide insights into consumer-resource dynamics, and improve our ability to predict the responses of animals to changes in their communities.

Large terrestrial carnivores are fundamental components of ecosystems, and their persistence is driven by the availability of large prey. The dependence of large carnivores on large prey is founded on bio-energetics (Carbone et al. 1999, 2007), and has strong ecological and conservation implications (Hebblewhite et al. 2005; Carbone et al. 2010; Estes et al. 2011; Sandom et al. 2017). A diverse spectrum of prey is expected to influence food habits and diet breadth of predators (Estes et al. 2011; Hatton et al. 2015; Creel et al. 2018), to buffer them against prey population decreases, and to reduce the effects of competitive interactions (Garrott et al. 2007; Steinmetz et al. 2021). Avoidance of interspecific interference is a major determinant of behaviour and ecology of subordinate species (Palomares & Caro 1999; Donadio & Buskirk 2006; Ritchie & Johnson 2009; Curveira-Santos et al. 2022). Assuming appropriate husbandry of domestic stock, an adequate spectrum of large wild prey is one factor that could limit carnivore attraction to livestock

57   and human facilities reducing predation on livestock, attacks on humans and retaliatory killing of

58   carnivores (Meriggi & Lovari 1996; Packer et al. 2005; Khorozyan et al. 2015; Khan et al. 2018).

59   In the presence of a diverse spectrum of large prey, only the largest and dominant

60   carnivores, but not subordinate predators, have been shown to use a greater number of large prey

61   species (Ferretti et al. 2020). These findings suggest that competition with larger predators limits

62   the potential for subordinate carnivores to broaden their diet of large prey where local prey richness

63   is higher. Some carnivores have extensive distributions, encompassing areas with different

64   communities of prey/competitors. For those carnivores, we would expect that the potential to

65   modulate their use of large prey according to prey richness would vary according to different levels

66   of potential competition.

67   We considered the three most widespread large predators in the world, whose distribution

68   ranges encompass different continents, i.e., the grey wolf *Canis lupus*, the puma *Puma concolor*

69   and the common leopard *Panthera pardus*. We modelled the diversity of large prey used against

70   prey richness in separate continents (wolf: North America and Eurasia; puma: North America and

71   Central-South America; common leopard: Africa and Asia). The wolf is the dominant predator in

72   most habitats that it occupies (Mech & Boitani 2003). The puma has been reported as subordinate

73   to the wolf and to the jaguar *Panthera onca* (occurring in 20% and 37% of studies included in our

74   analyses in North and Central-South America, respectively), whereas relationships with bear

75   species are equivocal (Elbroch & Kusler 2018; LaBarge et al. 2022). In Asia, after the near-

76   extinction of the Asiatic lion *Panthera leo persica*, the major competitors for common leopard are

77   the larger and solitary tiger *Panthera tigris* (Odden et al. 2010; Harihar et al. 2011), and the

78   smaller, but gregarious, dhole *Cuon alpinus* (Srivathsa et al. 2023), that are presently quite range

79   restricted. Conversely, major competitors for the common leopard in Africa include larger and

80   gregarious lions *Panthera leo* and spotted hyaenas *Crocuta crocuta*, and other large predators such

81   as cheetah *Acinonyx jubatus* and gregarious African wild dogs *Lycaon pictus* (Palomares & Caro

82   1999; Vanak et al. 2013). For the common leopard, the strength of interspecific competitive

83   interactions would thus be expected to be greater in Africa than in Asia (Balme et al. 2017). If the

84   variation of predator diet is modulated by interspecific competition, the dietary responses to

85   changing prey diversity would be expected to be consistent across continents for the wolf and the

86   puma, but not for the common leopard. Thus, we predict a positive relationship between the

87   number of large prey used and prey species richness in both continents for the wolf and the puma,

88   irrespective of the number of other carnivore species present, but only in Asia for the common

89   leopard.

90

91   **Methods**

92   We analysed the data collated on food habits of large terrestrial carnivores obtained from peer

93   reviewed scientific papers, books/book chapters, publicly accessible PhD and MSc theses, and

94   conference proceedings (Appendix S1). For the literature review and selection of studies, we

95   adopted the criteria followed in Ferretti et al. (2020). The dataset included only studies where the

96   carnivore and prey communities were described in the primary source or could be assessed through

97   other official sources (e.g., other contemporary papers or official checklists) and where carnivore

98   food habits were studied through analyses of scat content or kills (Ferretti et al. 2020). A 'study'

99   was considered as an account of food habits of a carnivore species in a particular area. If a study

100   reported both scats and kills, only results obtained through the method based on the greatest sample

101   size were considered. The dataset included studies where food habits of carnivores were quantified

102   through absolute or relative occurrences, i.e., the most widely used methods that can be employed

103   to evaluate dietary breadth (Ferretti et al. 2020). Data were also pooled across different studies

104   conducted in the same study area, to limit pseudoreplication of data (Ferretti et al. 2020).

105   We separated the studies relevant to wolf, puma, and common leopard between continents

106   (wolf: North America *vs*. Eurasia; puma: North America, i.e., USA and Canada, *vs*. Central-South

107 America; common leopard: Africa *vs.* Asia). We defined large terrestrial vertebrate prey (Carbone

108 et al. 2007), as prey heavier than 10 kg (hereafter termed 'large prey'; Ferretti et al. 2020). To

109 investigate the relationship between the use of large prey by carnivores and local prey richness, for

110 each study we considered the number of locally available large prey as a measure of local prey

111 richness. Since very large mega-herbivores may not be prey for some carnivores, we only

112 considered as potential prey those species that have been reported – or are known from literature –

113 to be preyed on by that carnivore (Ferretti et al. 2020). Livestock types are frequently pooled in a

114 single 'livestock' category and reported inconsistently across studies. Thus, we pooled all livestock

115 types into a single category of large prey (i.e., as a single species), to ensure a consistent treatment

116 across studies (Ferretti et al. 2020). In cases where several species of prey were reported as a

117 cumulative prey category (e.g., 'deer', 'peccaries', or 'duikers'), we included that category as a

118 single 'species'. All wild prey smaller than 10 kg were pooled into a single 'other' category. Total

119 sample size comprised 246 studies, after study pooling (Wolf, Eurasia: $N = 62$; Wolf, North

120 America, $N = 40$; Puma, North America, $N = 25$; Puma, Central-South America, $N = 38$; Common

121 leopard, Africa, $N = 37$; Common leopard, Asia, $N = 44$). Then, for each study, we estimated the

122 'Large Prey Index', i.e., the number of frequently used large terrestrial vertebrate prey (Ferretti et

123 al. 2020). This index represents the number of large prey used with a relative frequency of

124 occurrence of at least 5% (Krebs 1999).

125   Presence of potential competitors may influence feeding behaviour of carnivores. Thus, for

126 each carnivore and continent, we evaluated whether the relationship between the use of large prey

127 and prey richness was influenced by the local richness of other large carnivore species (hereafter

128 'carnivore richness'). As for prey richness, carnivore richness was inferred from information

129 included in the primary source or from other official sources (e.g., other contemporary papers or

130 official checklists; Ferretti et al. 2020). We considered all carnivore species larger than 14.5 kg

131 (Carbone et al. 2007; Ferretti et al. 2020), i.e., including Canidae, Felidae, Hyaenidae, brown bear

132 *Ursus arctos*, black bear *Ursus americanus* and Himalayan black bear *Ursus thibetanus*, that could

133   be expected to be potential competitors for our focal species. We initially verified whether

134   carnivore richness increased with local prey richness by fitting the following model for each

135   carnivore in each continent:

136   Model.A1: log (*N* other large carnivore species) ~ log (*N* available large prey), weighted by

137   the sqrt(sample size).

138   To account for studies where no other large carnivores were present, we used a log(x + 1)

139   transformation for the Number of other large carnivore species (where x represents this value for

140   any given species in a given study). For all carnivores and continents, the number of other large

141   predator species increased with local prey richness, with the only exception of the wolf in Eurasia,

142   for which 0.95 confidence intervals of model coefficients included '0' value (Wolf, Eurasia: *B* =

143   0.022, 0.95 CIs: − 0.038, 0.082; Wolf, North America: *B* = 0.159, 0.95 CIs: 0.104, 0.215; Puma,

144   North America: *B* = 0.116, 0.95 CIs: 0.039, 0.194; Puma, Central-South America: *B* = 0.070, 0.95

145   CIs: 0.025, 0.115; Common leopard, Africa: *B* = 0.214, 0.95 CIs: 0.137, 0.290; Common leopard,

146   Asia: *B* = 0.116, 0.95 CIs: 0.047, 0.185).

147   We then modelled the Large Prey Index against local prey richness and carnivore richness

148   using linear models to assess whether the relationship between the use of large prey and prey

149   richness was influenced by the increasing number of other carnivore species. Thus, for each

150   predator and each continent we fitted the following model:

151   Model.B1: Log(Large Prey Index) ~ Log (Number of available large prey) × Number of

152   other large carnivore species, weights(√sample size)

153   and we compared it with four alternative candidate models:

154   Model.B2: Log(Large Prey Index) ~ Log(Number of available large prey) + Number of

155   other large carnivore species, weights(√sample size)

156   Model.B3: Log(Large Prey Index) ~ Log(Number of available large prey), weights(√sample

157   size)

158   Model.B4: Log(Large Prey Index) ~ Number of other large carnivore species,

159 weights(√sample size)

160   Model.B5: Null model

161 Models including the interactive effects of predictors also included their additive effects. Predictors

162 were standardised through 'scale()' in the model declaration to improve the comparability of their

163 coefficients, because they were estimated on different scales, and to limit multicollinearity issues

164 between interaction terms. No substantial multicollinearity issues were detected (i.e., Variance

165 Inflation Factors were ≤ 2.1; Zuur et al. 2010). To account for the greater reliability of studies based

166 on larger samples, we weighted by sample size, i.e., the number of scats or kills reported in the

167 study [using 'weights = sqrt(sample size)' in the model declaration]. To account for studies where

168 no large prey showed a frequency of use greater than 5%, we used a log(x + 1) transformation for

169 the Large Prey Index (where x represents this index for any given species in a given study).

170 Previous work showed that the relationship between the Large Prey Index and prey richness was

171 unaffected by sample type (i.e., scats or kills) (Ferretti et al. 2020), so we did not consider sample

172 type in the analyses. Relationships were considered to be statistically supported if the 0.95

173 confidence intervals of model coefficients did not include zero. Candidate models were compared

174 according to AICc values; we selected for inference those models with ΔAICc ≤ 6 in respect to the

175 best one, and if their AICc value was lower than that of any other simpler, nested alternative

176 (Richards 2008; Richards et al. 2011). A threshold of ΔAICc ≤ 6 has been selected because it has

177 been shown to provide a probability ≥0.95 that the model with the lowest Kullback–Leibler distance

178 is retained (Richards 2008; Richards et al. 2011).

179   We validated models through visual inspection of model fits and residual distributions, as

180 well as regression between predicted and observed values. No major problems were found, except

181 for models relevant to the puma in Central-South America, where visual inspection of residuals

182 suggested the presence of an outlier, relevant to a study conducted in six sheep and cattle ranches in

183 the Neuquén Province (Argentina, Novaro et al. 2000). That area showed very altered ecological

184   conditions, with large wild native prey (i.e., guanaco *Lama guanicoe* and lesser rhea *Rhea pennata*)

185   being defined as "ecologically extinct" and replaced by introduced red deer *Cervus elaphus* and

186   wild boar *Sus scrofa*. Locally, puma diet was dominated by introduced European hare *Lepus*

187   *europaeus* and, in contrast to the other 37 studies, no large prey was used with a frequency greater

188   than 5% (Novaro et al. 2000). Given the relatively unnatural ecological conditions of that area, with

189   a few introduced prey species and virtually free of wild native large prey, we removed this study

190   from subsequent analyses.

191

192   **Results**

193   Global models included an interaction between prey and carnivore richness. These showed that the

194   Large Prey Index tends to increase with increasing prey richness, but the relationship between

195   Large Prey Indices and increasing number of other carnivore species is complex (Fig. 1).

196   Specifically, there was a tendency for large prey indices to increase with the number of other

197   carnivore species in areas of lower prey richness, but to decrease with the number of other carnivore

198   species in areas of higher prey richness (Fig. 1). Although a trend was observed for the decreasing

199   strength of the positive relationship between Large Prey Index and prey richness with increasing

200   number of carnivore species (Figure 1), the interactive effect of carnivore richness and prey

201   richness on Large Prey Index was only selected in the best model for the puma in Central-South

202   America (Table 1).

203   Only the best model was selected for the wolf and for the common leopard in Asia. Two

204   models were selected the puma in North America (i.e., the best one and the null one), and for the

205   puma in Central-South America, whereas the null model was selected for the common leopard in

206   Africa (Table 1). For the wolf and the puma, in both respective continents, the Large Prey Index

207   increased with increasing prey richness (Figs. 1-2; Tables 1-2). For the leopard, a positive

208   relationship between the Large Prey Index and prey richness was supported for Asia, but not for

209   Africa (Fig. 1).

9

210   Effects of competitor richness were retained in the selected models for puma in Central-

211   South America and <mark>common</mark> leopard in Asia (Tables 1-2). For the <mark>common</mark> leopard in Asia, for a

212   given value of prey richness, the <mark>Large Prey Index</mark> was greater in areas with a higher number of

213   other carnivore species (Fig. 1). For the puma in Central-South America, two models were selected

214   including the interactive and additive effects of prey and carnivore richness, respectively (Tables 1-

215   2). The positive relationship between <mark>Large Prey Index</mark> and prey richness was not observed in sites

216   including the jaguar, as supported by both the best model and by averaged parameters between the

217   two selected models (Fig. 1; Tables 1-2).

218 **Table 1** Model selection for models including the effects of Log(*N* available large prey) (referred in the table as 'N prey species') and *N* other large carnivore
219 species (referred in the table as 'N carnivore species') on the Large Prey Index. Models including interactive terms also include the additive effects of predictors.
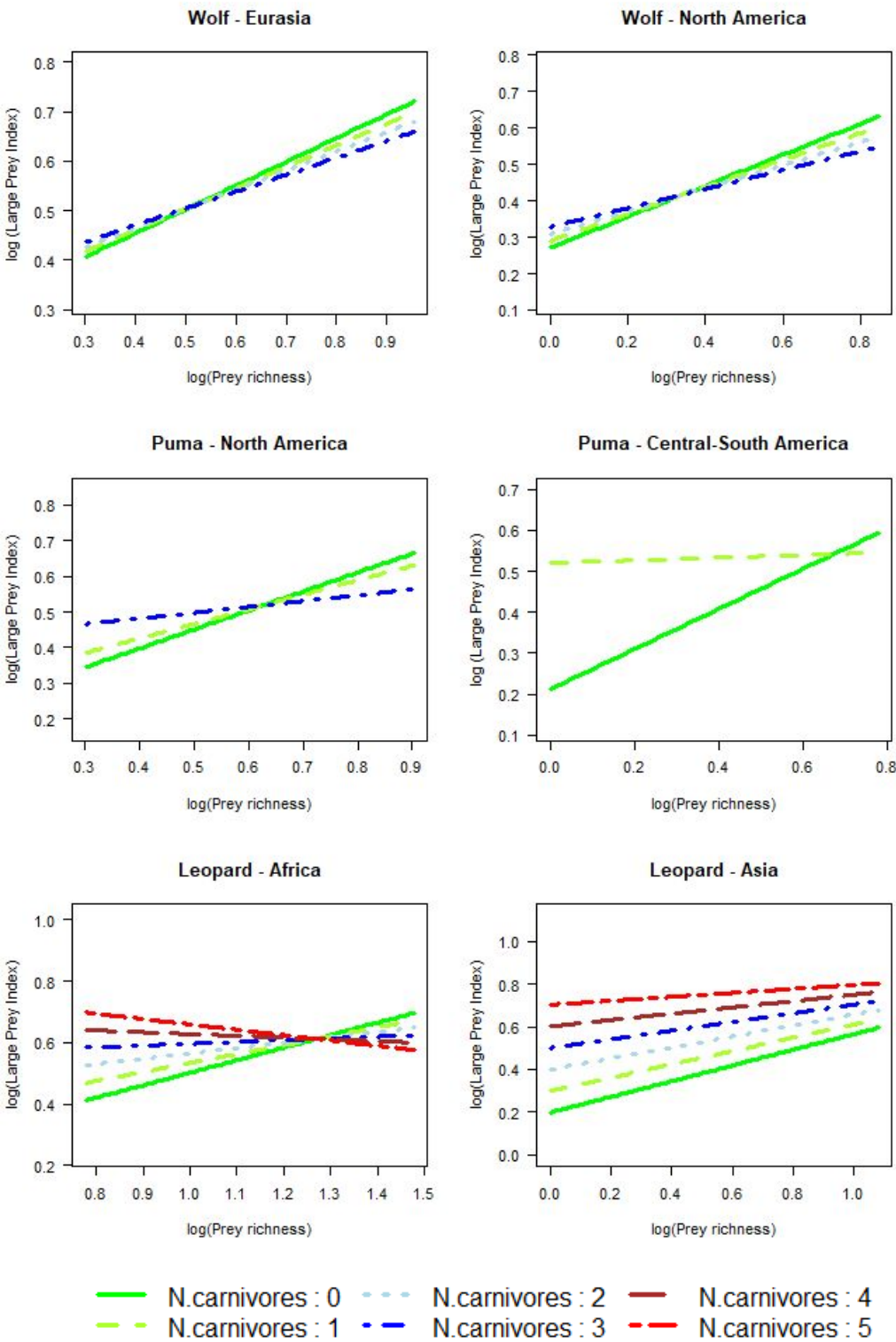220 In bold, selected models.

Predator	Model	Variables	df	logLik	AICc	ΔAICc	Weight	R^2
Wolf_Eurasia	**Best**	**N prey species**	**3**	**52.351**	**-98.3**	**0.00**	**0.666**	**0.33**
	Second	N prey species + N carnivore species	4	52.479	-96.3	2.03	0.241	0.33
	Third	N prey species × N carnivore species	5	52.716	-96.4	3.93	0.093	0.34
	Fourth	Null model	2	39.936	-75.7	22.62	0.000	0.00
	Fifth	N carnivore species	3	39.939	-73.5	24.82	0.000	0.00
Wolf_North America	**Best**	**N prey species**	**3**	**32.869**	**-59.1**	**0.00**	**0.699**	**0.43**
	Second	N prey species + N carnivore species	4	32.932	-56.7	2.35	0.216	0.43
	Third	N prey species × N carnivore species	5	33.311	-54.9	4.21	0.085	0.44
	Fourth	Null model	3	25.703	-44.7	14.33	0.001	0.18
	Fifth	N carnivore species	2	21.792	-39.3	19.81	0.000	0.00
Puma_North America	**Best**	**N prey species**	**3**	**19.475**	**-31.8**	**0.00**	**0.611**	**0.21**
	Second	N prey species + N carnivore species	4	19.519	-29.0	2.77	0.153	0.21
	Third	**Null model**	**2**	**16.576**	**-28.6**	**3.20**	**0.123**	**0.00**
	Fourth	N carnivore species	3	17.155	-27.2	4.64	0.060	0.05
	Fifth	N prey species × N carnivore species	5	20.019	-26.9	4.93	0.052	0.24
Puma_Central-South America	**Best**	**N prey species × N carnivore species**	**5**	**39.434**	**-66.9**	**0.00**	**0.856**	**0.56**
	Second	**N prey species + N carnivore species**	**4**	**36.148**	**-63.0**	**3.89**	**0.123**	**0.48**
	Third	N carnivore species	3	32.492	-58.3	8.68	0.011	0.36
	Fourth	N prey species	3	32.408	-58.1	8.84	0.010	0.36
	Fifth	Null model	2	24.165	-44.0	22.96	0.000	0.00
Leopard_Africa	**Best**	**Null model**	**2**	**7.942**	**-11.5**	**0.00**	**0.331**	**0.00**
	Second	N prey species	3	8.884	-11.0	0.49	0.260	0.05
	Third	N carnivore species	3	8.853	-11.0	0.55	0.252	0.05
	Fourth	N prey species + N carnivore species	4	9.063	-8.9	2.65	0.088	0.06
	Fifth	N prey species × N carnivore species	5	10.174	-8.4	3.12	0.070	0.11
Leopard_Asia	**Best**	**N prey species + N carnivore species**	**4**	**28.027**	**-47.0**	**0.00**	**0.692**	**0.48**
	Second	N prey species × N carnivore species	5	28.384	-45.2	1.84	0.276	0.49
	Third	N carnivore species	3	23.423	-40.2	6.78	0.023	0.36
	Fourth	N prey species	3	22.460	-38.3	8.71	0.009	0.33
	Fifth	Null model	2	13.763	-23.2	23.79	0.000	0.00

221

223 **Table 2** Model coefficients for the effects of Log(N available large prey) (referred in the table as 'N prey species') and N other large carnivore species (referred
224 in the table as 'N carnivore species') on the Large Prey Index in different continents for the wolf, the puma and the leopard. Best models are shown; in bold,
225 supported relationships. For the puma in Central-South America, the main effects were also found in the only other selected model (Intercept: $B = 0.446$, 0.95
226 CIs: 0.417, 0.475; N prey species: $B = 0.047$, 0.95 CIs: 0.012, 0.083; N carnivore species: $B = 0.047$, 0.95 CIs: 0.012, 0.082; ΔAICc = 3.89; weight = 0.123; see
227 Table 1).

| Species	Continent	Variable	B	SE	0.95 Cis	
					-	+
Wolf	Eurasia	Intercept	0.543	0.012	0.519	0.567
		N prey species	**0.066**	**0.012**	**0.041**	**0.090**
	North America	Intercept	0.431	0.016	0.398	0.463
		N prey species	**0.094**	**0.018**	**0.058**	**0.130**
Puma	North America	Intercept	0.500	0.022	0.454	0.546
		N prey species	**0.052**	**0.021**	**0.008**	**0.096**
	Central-South America	Intercept	0.465	0.015	0.434	0.497
		N prey species	**0.057**	**0.017**	**0.023**	**0.091**
		N carnivore species	**0.054**	**0.016**	**0.022**	**0.087**
		N prey species × N carnivore species	**-0.040**	**0.016**	**-0.073**	**-0.008**
Leopard	Asia	Intercept	0.590	0.019	0.551	0.629
		N prey species	**0.073**	**0.023**	**0.025**	**0.119**
		N carnivore species	**0.076**	**0.022**	**0.031**	**0.120**

229

Figure 1 Relationship between Large Prey Index (i.e., number of frequently used large prey species; log-scale) and local prey richness (i.e., number of available large prey species; log-scale) for the wolf, the puma, and the leopard in different continents, in relation to local carnivore richness (i.e., number of other large carnivore species). Relationships estimated through the model 'log(Large Prey Index) ~ log(Prey Richness) × Carnivore Richness, weights = √sample size' are shown.

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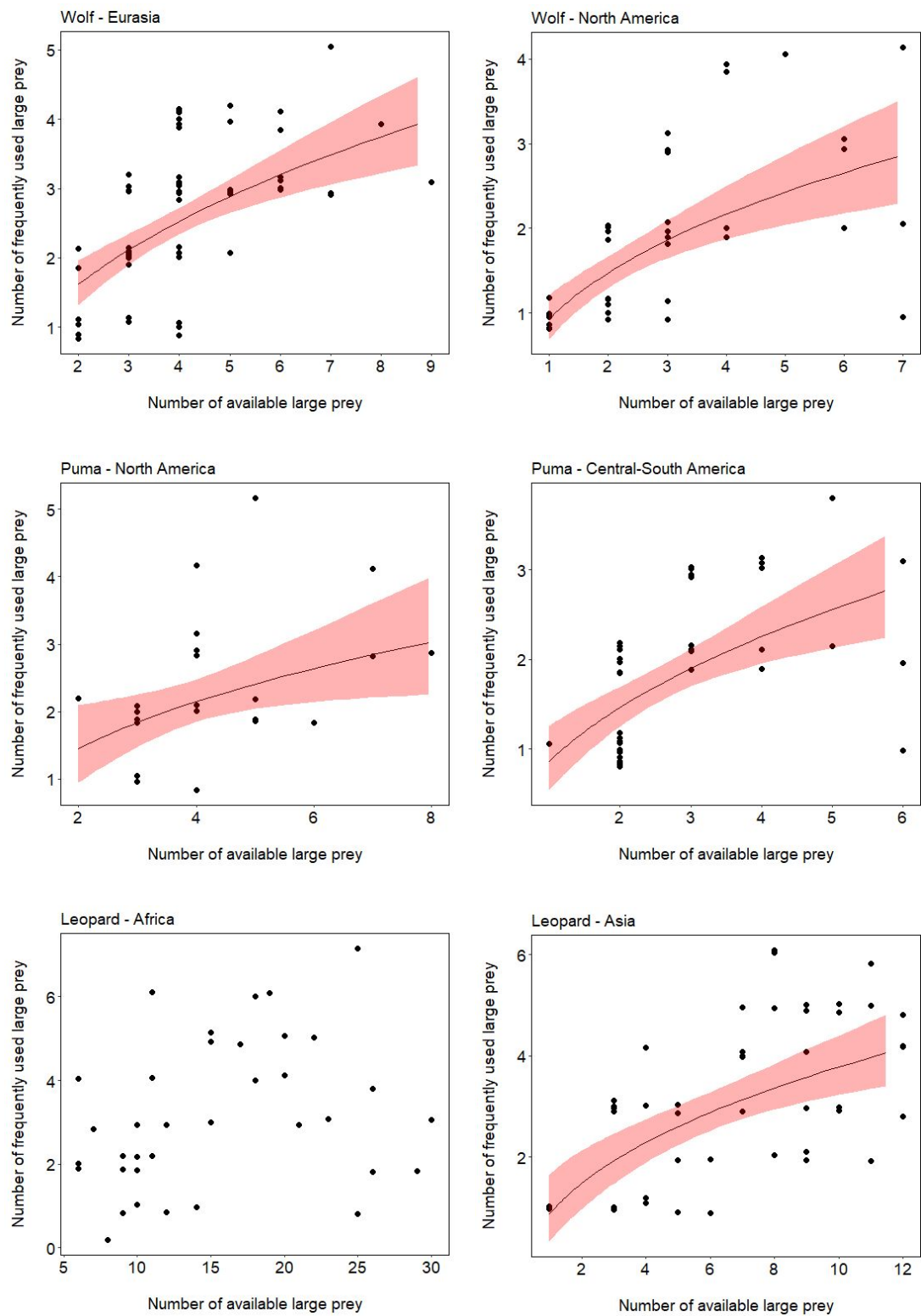
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Fig. 2 Large Prey Index (i.e., number of frequently used large prey) *vs.* local prey richness (i.e., number of
available large prey species) for wolf, puma and leopard in different continents. Black lines indicate fitted
relationships of the model 'log(Large Prey Index) ~ log(Prey Richness), weights = √sample size' are shown;
red shaded areas indicate 0.95 confidence intervals of fitted relationships. Data points were jittered to
improve figure readability.

243

Discussion

A positive relationship between the number of frequently used large prey species and prey richness

was found for the wolf, across its distribution ranges. The common leopard showed this pattern in

Asia but not in Africa. For the puma, the positive relationship between the Large Prey Index and

prey richness was not observed in areas of central-southern America where the jaguar also occurred.

These results emphasise a complex relationship between diet breadth of large carnivores and prey

richness that can be modulated by the influence of competitive pressure (Ferretti et al. 2020;

Steinmetz et al. 2021). These results are generally consistent with larger and most dominant

carnivores exploiting a wider range of prey sizes (Radloff & du Toit 2004; Ferretti et al. 2020).

Relationships between predators are often context-dependent, affected by several ecological

factors (Haswell et al. 2017; Tallian et al. 2021). Spatial, temporal and/or dietary partitioning are

mechanisms allowing interspecific coexistence by limiting competition (Hutchinson 1959; Pianka

1973; Schoener 1974). Interspecific dominance is a relative concept, as the same predator may

behave both as dominant or subordinate in relation to the presence/absence of out-competing

species. Subordinate carnivores can adjust their spatio-temporal and hunting behaviour to limit

encounters with superior competitors (Palomares & Caro 1999; Donadio & Buskirk 2006), which

may lead to a reduced use of large prey (Ferretti et al. 2020; Steinmetz et al. 2021). The wolf was

the carnivore showing the most consistent behaviour across continents. This gregarious,

ecologically flexible and generalist carnivore is mainly a predator of medium-to-large sized

ungulates, and is usually the apex predator in ecosystems where it is found (Mech & Boitani 2003;

Ripple et al. 2014; Newsome et al. 2016). Although kleptoparasitism of wolf prey by bears has been

reported (Tallian et al. 2017, 2021), there is no clear evidence of wolf subordination to other

carnivores (Palomares & Caro 1999), except the tiger (which occurred in only one out of the 58

sites from which we obtained data: Miquelle et al. 2005). Support for wolf dominance or potential

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268   dominance over other carnivores is more common (Mech & Boitani 2003; Bocci et al. 2018;

269   Elbroch et al. 2018; LaBarge et al. 2022).

270   The common leopard expanded its use of large prey with large herbivore richness only in Asia,

271   but not in Africa. Leopards may have a greater need to adapt to local ecological conditions and

272   competition pressure in Africa, where the array of potentially competing species is larger than in

273   Asia (Vanak et al. 2013; Balme et al. 2017). Accordingly, food caching in trees by common

274   leopards has been suggested to be greater in African sites than in Asiatic ones, suggesting a lower

275   intensity of kleptoparasitism in the latter than in the former (Balme et al. 2017). In Asia,

276   comparably limited diet partitioning has been detected between syntopic common leopards and

277   tigers or lions, indicating a substantial dietary overlap despite potential for interference (Lovari et

278   al. 2015; Zehra et al. 2017; Steinmetz et al. 2021), with larger predators using large prey more often

279   and small prey less often than the leopard did (Hayward et al. 2005, 2006, 2012), and with

280   interference potentially emphasising leopard predation on livestock (Franchini & Guerisoli 2023).

281   Asiatic leopards have been reported to concentrate on larger ungulates in prey-richer areas,

282   increasing their use of smaller prey in depleted areas (Steinmetz et al. 2021), which would fit our

283   results (see also Newsome et al. 2016 for the wolf and Guerisoli et al. 2021 for the puma).

284   Our interpretation is supported by findings on puma, for which the relationship between the use

285   of large prey and prey richness was affected in areas where the jaguar occurred (Elbroch et al. 2018;

286   LaBarge et al. 2022). Jaguars have been reported to kill pumas, to displace them spatially and

287   temporally, and to trigger shifts in their diet, leading to an increased use of smaller prey (Iriarte et

288   al. 1990; Elbroch et al. 2018). Similarly, the wolf has been reported as dominant over puma,

289   through killing and kleptoparasitism, leading to potential displacements or prey switching (Iriarte et

290   al. 1990). Wolves occurred in only 20% of study areas for which data are available: this small

291   sample size probably reduced the potential to detect significant effects of wolf presence on the use

292   of large prey by the puma. The potential for wolves to trigger changes in puma diet at broader scale

293   requires further tests.

294   Over an evolutionary scale, predators would be expected to narrow their diet in relation to

295   increased prey availability, and the resulting specialisation should promote coexistence among

296   potential competitors. A high specialisation to particular prey has been suggested as a determinant

297   of the extinction of Nimravids and saber-toothed Felids (Machairodontinae), while extant, less

298   specialised carnivores could adapt to alternative prey (Van Valkenburgh et al. 2007; but see

299   DeSantis et al. 2012). Although our results might be suggestive of no increase of predator

300   selectivity along with increasing prey richness, data on prey density would be necessary to support

301   that (Steinmetz et al. 2021). Moreover, under a selective predation scenario, we may expect that

302   increasing prey richness will lead to less widening of diet breadth than would be the case under

303   unselective predation. Further work is necessary to evaluate changes in predators' selectivity in

304   relation to variations in prey richness.

305   The current human-induced biodiversity crisis is characterized, among other phenomena, by the

306   collapse of populations of many large herbivore species worldwide (Ripple et al. 2015). Human

307   encroachment on natural habitats is expected to favour carnivore contact with anthropogenic food.

308   Together with prey depletion, it would increase human-carnivore conflicts further endangering

309   predators (Bagchi et al. 2006; Khan et al. 2018). Habitat conservation, direct protection of wild

310   prey, their sustainable management, or restoration of extinct populations, appropriate livestock

311   management, as well as adequate measures to prevent predation on losses and compensate

312   economic losses, are fundamental to ensuring large carnivore persistence (Treves et al. 2003, 2016).

313   Our results testify that large prey depletion would emphasise the negative consequences of

314   competition between carnivores, leading to niche shrinking of subordinate species and/or increased

315   use of smaller, sub-optimal prey (Creel et al. 2018; Ferretti et al. 2020; Steinmetz et al. 2021),

316   posing an additional significant threat to carnivore conservation in the Anthropocene.

317

318   **References**

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481

482

483 **Title:** Continent-wide differences in diet breadth of large terrestrial carnivores: the effect of large

484 prey and competitors

485

486 **Abstract**

487 1. Despite their importance for understanding consumer-resource dynamics, the dietary

488   responses of large terrestrial predators to variations in prey richness and competition

489   pressure are unclear. While a greater predator selectivity along with increasing prey

490   abundance would be expected under an optimal foraging scenario, there is some evidence

491   that predators may broaden their diet where there is a greater resource diversity.

492   Furthermore, the use of large prey may be limited by increasing presence of competitors.

493 2. We considered three widespread large carnivores (the grey wolf *Canis lupus*, the puma

494   *Puma concolor* and the leopard *Panthera pardus*), whose distribution range encompasses

495   different continents, with different communities of prey/competitors. We expected that the

496   potential to modulate their use of large prey according to prey richness would vary

497   according to different levels of potential competition.

498 3. We collated data from more than 240 studies of the diets of wolf, puma and leopard to

499   model whether the relationships between the diversity of used large prey (i.e., the Large

500   Prey Index) and prey richness was modulated by carnivore richness, in different continents.

501 4. The wolf showed an increase in the Large Prey Index with prey richness across its

502   distribution range, where it is usually the apex predator in areas from which data are

503   available. Conversely, the leopard showed this pattern in Asia, but not in Africa, where it

504   often coexists with a greater array of potential competitors. For the puma, the Large Prey

505   Index increased with prey richness throughout its distribution range, except in the areas

506   where the larger and dominant jaguar also occurred.

507   5. By emphasising the complex relationships between prey richness and predator diets, our

508   results testify to the suppressive effects of larger competitors over the use of large prey by

509   subordinate carnivores.

510   **Keywords:** apex predators; competition; diet breadth; food habits; predator-prey relationships; prey

511   diversity.

512   **Running head:** Large carnivore diet breadth

513   **Word count:** 6403

514   **Introduction**

515   Spatiotemporal variation in the diversity of food resources influences consumer-resource dynamics,

516   affecting community-to-ecosystem-level processes. Unequivocal evidence of the responses of

517   foragers to variation in resource diversity is lacking. In more productive systems, with higher

518   abundances and diversities of resources (Danell et al. 1996; Olff et al. 2002; Bailey et al. 2014;

519   Youngentob et al. 2015; but see Mittlebach et al. 2001; Santini et al. 2019), consumers would be

520   expected to specialise on the most profitable resources, increasing their selectivity and adopting a

521   narrower diet breadth (MacArthur et al. 1966; Shoener 1971; Charnov 1976; Forister et al. 2015).

522   Conversely, opportunistic foragers may take advantage of a greater diversity of food resources by

523   broadening their diet (Borkhofer & Wolters 2012; Ferretti et al. 2020). Both outcomes may occur,

524   depending on local environmental conditions, but information at broad scales is scarce.

525   Understanding which of these two expectations is supported by data would provide insights into

526   consumer-resource dynamics, and improve our ability to predict the responses of animals to

527   changes in their communities.

528   Large terrestrial carnivores are fundamental components of ecosystems, and their

529   persistence is driven by the availability of large prey. The dependence of large carnivores on large

530   prey is founded on bio-energetics (Carbone et al. 1999, 2007), and has strong ecological and

531   conservation implications (Hebblewhite et al. 2005; Carbone et al. 2010; Estes et al. 2011; Sandom

532   et al. 2017). A diverse spectrum of prey is expected to influence food habits and diet breadth of

533   predators (Estes et al. 2011; Hatton et al. 2015; Creel et al. 2018), to buffer them against prey

534   population decreases, and to reduce the effects of competitive interactions (Garrott et al. 2007;

535   Steinmetz et al. 2021). Avoidance of interspecific interference is a major determinant of behaviour

536   and ecology of subordinate species (Palomares & Caro 1999; Donadio & Buskirk 2006; Ritchie &

537   Johnson 2009; Curveira-Santos et al. 2022). Assuming appropriate husbandry of domestic stock, an

538   adequate spectrum of large wild prey is one factor that could limit carnivore attraction to livestock

539   and human facilities reducing predation on livestock, attacks on humans and retaliatory killing of

540   carnivores (Meriggi & Lovari 1996; Packer et al. 2005; Khorozyan et al. 2015; Khan et al. 2018).

541   In the presence of a diverse spectrum of large prey, only the largest and dominant

542   carnivores, but not subordinate predators, have been shown to use a greater number of large prey

543   species (Ferretti et al. 2020). These findings suggest that competition with larger predators limits

544   the potential for subordinate carnivores to broaden their diet of large prey where local prey richness

545   is higher. Some carnivores have extensive distributions, encompassing areas with different

546   communities of prey/competitors. For those carnivores, we would expect that the potential to

547   modulate their use of large prey according to prey richness would vary according to different levels

548   of potential competition.

549   We considered the three most widespread large predators in the world, whose distribution

550   ranges encompass different continents, i.e., the grey wolf *Canis lupus*, the puma *Puma concolor*

551   and the common leopard *Panthera pardus*. We modelled the diversity of large prey used against

552   prey richness in separate continents (wolf: North America and Eurasia; puma: North America and

553   Central-South America; common leopard: Africa and Asia). The wolf is the dominant predator in

554   most habitats that it occupies (Mech & Boitani 2003). The puma has been reported as subordinate

555   to the wolf and to the jaguar *Panthera onca* (occurring in 20% and 37% of studies included in our

556   analyses in North and Central-South America, respectively), whereas relationships with bear

557   species are equivocal (Elbroch & Kusler 2018; LaBarge et al. 2022). In Asia, after the near-

558   extinction of the Asiatic lion *Panthera leo persica*, the major competitors for common leopard are

559   the larger and solitary tiger *Panthera tigris* (Odden et al. 2010; Harihar et al. 2011), and the

560   smaller, but gregarious, dhole *Cuon alpinus* (Srivathsa et al. 2023), that are presently quite range

561   restricted. Conversely, major competitors for the common leopard in Africa include larger and

562   gregarious lions *Panthera leo* and spotted hyaenas *Crocuta crocuta*, and other large predators such

563   as cheetah *Acinonyx jubatus* and gregarious African wild dogs *Lycaon pictus* (Palomares & Caro

564   1999; Vanak et al. 2013). For the common leopard, the strength of interspecific competitive

565   interactions would thus be expected to be greater in Africa than in Asia (Balme et al. 2017). If the

566   variation of predator diet is modulated by interspecific competition, the dietary responses to

567   changing prey diversity would be expected to be consistent across continents for the wolf and the

568   puma, but not for the common leopard. Thus, we predict a positive relationship between the

569   number of large prey used and prey species richness in both continents for the wolf and the puma,

570   irrespective of the number of other carnivore species present, but only in Asia for the common

571   leopard.

572

573   **Methods**

574   We analysed the data collated on food habits of large terrestrial carnivores obtained from peer

575   reviewed scientific papers, books/book chapters, publicly accessible PhD and MSc theses, and

576   conference proceedings (Appendix S1). For the literature review and selection of studies, we

577   adopted the criteria followed in Ferretti et al. (2020). The dataset included only studies where the

578   carnivore and prey communities were described in the primary source or could be assessed through

579   other official sources (e.g., other contemporary papers or official checklists) and where carnivore

580   food habits were studied through analyses of scat content or kills (Ferretti et al. 2020). A 'study'

581   was considered as an account of food habits of a carnivore species in a particular area. If a study

582   reported both scats and kills, only results obtained through the method based on the greatest sample

583   size were considered. The dataset included studies where food habits of carnivores were quantified

584   through absolute or relative occurrences, i.e., the most widely used methods that can be employed

585   to evaluate dietary breadth (Ferretti et al. 2020). Data were also pooled across different studies

586   conducted in the same study area, to limit pseudoreplication of data (Ferretti et al. 2020).

587   We separated the studies relevant to wolf, puma, and common leopard between continents

588   (wolf: North America *vs*. Eurasia; puma: North America, i.e., USA and Canada, *vs*. Central-South

589   America; common leopard: Africa *vs.* Asia). We defined large terrestrial vertebrate prey (Carbone

590   et al. 2007), as prey heavier than 10 kg (hereafter termed 'large prey'; Ferretti et al. 2020). To

591   investigate the relationship between the use of large prey by carnivores and local prey richness, for

592   each study we considered the number of locally available large prey as a measure of local prey

593   richness. Since very large mega-herbivores may not be prey for some carnivores, we only

594   considered as potential prey those species that have been reported – or are known from literature –

595   to be preyed on by that carnivore (Ferretti et al. 2020). Livestock types are frequently pooled in a

596   single 'livestock' category and reported inconsistently across studies. Thus, we pooled all livestock

597   types into a single category of large prey (i.e., as a single species), to ensure a consistent treatment

598   across studies (Ferretti et al. 2020). In cases where several species of prey were reported as a

599   cumulative prey category (e.g., 'deer', 'peccaries', or 'duikers'), we included that category as a

600   single 'species'. All wild prey smaller than 10 kg were pooled into a single 'other' category. Total

601   sample size comprised 246 studies, after study pooling (Wolf, Eurasia: $N = 62$; Wolf, North

602   America, $N = 40$; Puma, North America, $N = 25$; Puma, Central-South America, $N = 38$; Common

603   leopard, Africa, $N = 37$; Common leopard, Asia, $N = 44$). Then, for each study, we estimated the

604   'Large Prey Index', i.e., the number of frequently used large terrestrial vertebrate prey (Ferretti et

605   al. 2020). This index represents the number of large prey used with a relative frequency of

606   occurrence of at least 5% (Krebs 1999).

607   Presence of potential competitors may influence feeding behaviour of carnivores. Thus, for

608   each carnivore and continent, we evaluated whether the relationship between the use of large prey

609   and prey richness was influenced by the local richness of other large carnivore species (hereafter

610   'carnivore richness'). As for prey richness, carnivore richness was inferred from information

611   included in the primary source or from other official sources (e.g., other contemporary papers or

612   official checklists; Ferretti et al. 2020). We considered all carnivore species larger than 14.5 kg

613   (Carbone et al. 2007; Ferretti et al. 2020), i.e., including Canidae, Felidae, Hyaenidae, brown bear

614   *Ursus arctos*, black bear *Ursus americanus* and Himalayan black bear *Ursus thibetanus*, that could

615   be expected to be potential competitors for our focal species. We initially verified whether

616   carnivore richness increased with local prey richness by fitting the following model for each

617   carnivore in each continent:

618   Model.A1: log (N other large carnivore species) ~ log (N available large prey), weighted by

619   the sqrt(sample size).

620   To account for studies where no other large carnivores were present, we used a log(x + 1)

621   transformation for the Number of other large carnivore species (where x represents this value for

622   any given species in a given study). For all carnivores and continents, the number of other large

623   predator species increased with local prey richness, with the only exception of the wolf in Eurasia,

624   for which 0.95 confidence intervals of model coefficients included '0' value (Wolf, Eurasia: $B =$

625   0.022, 0.95 CIs: − 0.038, 0.082; Wolf, North America: $B = 0.159$, 0.95 CIs: 0.104, 0.215; Puma,

626   North America: $B = 0.116$, 0.95 CIs: 0.039, 0.194; Puma, Central-South America: $B = 0.070$, 0.95

627   CIs: 0.025, 0.115; Common leopard, Africa: $B = 0.214$, 0.95 CIs: 0.137, 0.290; Common leopard,

628   Asia: $B = 0.116$, 0.95 CIs: 0.047, 0.185).

629   We then modelled the Large Prey Index against local prey richness and carnivore richness

630   using linear models to assess whether the relationship between the use of large prey and prey

631   richness was influenced by the increasing number of other carnivore species. Thus, for each

632   predator and each continent we fitted the following model:

633   Model.B1: Log(Large Prey Index) ~ Log (Number of available large prey) × Number of

634   other large carnivore species, weights(√sample size)

635   and we compared it with four alternative candidate models:

636   Model.B2: Log(Large Prey Index) ~ Log(Number of available large prey) + Number of

637   other large carnivore species, weights(√sample size)

638   Model.B3: Log(Large Prey Index) ~ Log(Number of available large prey), weights(√sample

639   size)

640   Model.B4: Log(Large Prey Index) ~ Number of other large carnivore species,

641   weights($\sqrt{}$sample size)

642   Model.B5: Null model

643   Models including the interactive effects of predictors also included their additive effects. Predictors

644   were standardised through 'scale()' in the model declaration to improve the comparability of their

645   coefficients, because they were estimated on different scales, and to limit multicollinearity issues

646   between interaction terms. No substantial multicollinearity issues were detected (i.e., Variance

647   Inflation Factors were ≤ 2.1; Zuur et al. 2010). To account for the greater reliability of studies based

648   on larger samples, we weighted by sample size, i.e., the number of scats or kills reported in the

649   study [using 'weights = sqrt(sample size)' in the model declaration]. To account for studies where

650   no large prey showed a frequency of use greater than 5%, we used a log(x + 1) transformation for

651   the Large Prey Index (where x represents this index for any given species in a given study).

652   Previous work showed that the relationship between the Large Prey Index and prey richness was

653   unaffected by sample type (i.e., scats or kills) (Ferretti et al. 2020), so we did not consider sample

654   type in the analyses. Relationships were considered to be statistically supported if the 0.95

655   confidence intervals of model coefficients did not include zero. Candidate models were compared

656   according to AICc values; we selected for inference those models with ΔAICc ≤ 6 in respect to the

657   best one, and if their AICc value was lower than that of any other simpler, nested alternative

658   (Richards 2008; Richards et al. 2011). A threshold of ΔAICc ≤ 6 has been selected because it has

659   been shown to provide a probability ≥0.95 that the model with the lowest Kullback–Leibler distance

660   is retained (Richards 2008; Richards et al. 2011).

661   We validated models through visual inspection of model fits and residual distributions, as

662   well as regression between predicted and observed values. No major problems were found, except

663   for models relevant to the puma in Central-South America, where visual inspection of residuals

664   suggested the presence of an outlier, relevant to a study conducted in six sheep and cattle ranches in

665   the Neuquén Province (Argentina, Novaro et al. 2000). That area showed very altered ecological

666   conditions, with large wild native prey (i.e., guanaco *Lama guanicoe* and lesser rhea *Rhea pennata*)

667   being defined as "ecologically extinct" and replaced by introduced red deer *Cervus elaphus* and

668   wild boar *Sus scrofa*. Locally, puma diet was dominated by introduced European hare *Lepus*

669   *europaeus* and, in contrast to the other 37 studies, no large prey was used with a frequency greater

670   than 5% (Novaro et al. 2000). Given the relatively unnatural ecological conditions of that area, with

671   a few introduced prey species and virtually free of wild native large prey, we removed this study

672   from subsequent analyses.

673

674   **Results**

675   Global models included an interaction between prey and carnivore richness. These showed that the

676   Large Prey Index tends to increase with increasing prey richness, but the relationship between

677   Large Prey Indices and increasing number of other carnivore species is complex (Fig. 1).

678   Specifically, there was a tendency for large prey indices to increase with the number of other

679   carnivore species in areas of lower prey richness, but to decrease with the number of other carnivore

680   species in areas of higher prey richness (Fig. 1). Although a trend was observed for the decreasing

681   strength of the positive relationship between Large Prey Index and prey richness with increasing

682   number of carnivore species (Figure 1), the interactive effect of carnivore richness and prey

683   richness on Large Prey Index was only selected in the best model for the puma in Central-South

684   America (Table 1).

685   Only the best model was selected for the wolf and for the common leopard in Asia. Two

686   models were selected the puma in North America (i.e., the best one and the null one), and for the

687   puma in Central-South America, whereas the null model was selected for the common leopard in

688   Africa (Table 1). For the wolf and the puma, in both respective continents, the Large Prey Index

689   increased with increasing prey richness (Figs. 1-2; Tables 1-2). For the leopard, a positive

690   relationship between the Large Prey Index and prey richness was supported for Asia, but not for

691   Africa (Fig. 1).

692   Effects of competitor richness were retained in the selected models for puma in Central-

693   South America and common leopard in Asia (Tables 1-2). For the common leopard in Asia, for a

694   given value of prey richness, the Large Prey Index was greater in areas with a higher number of

695   other carnivore species (Fig. 1). For the puma in Central-South America, two models were selected

696   including the interactive and additive effects of prey and carnivore richness, respectively (Tables 1-

697   2). The positive relationship between Large Prey Index and prey richness was not observed in sites

698   including the jaguar, as supported by both the best model and by averaged parameters between the

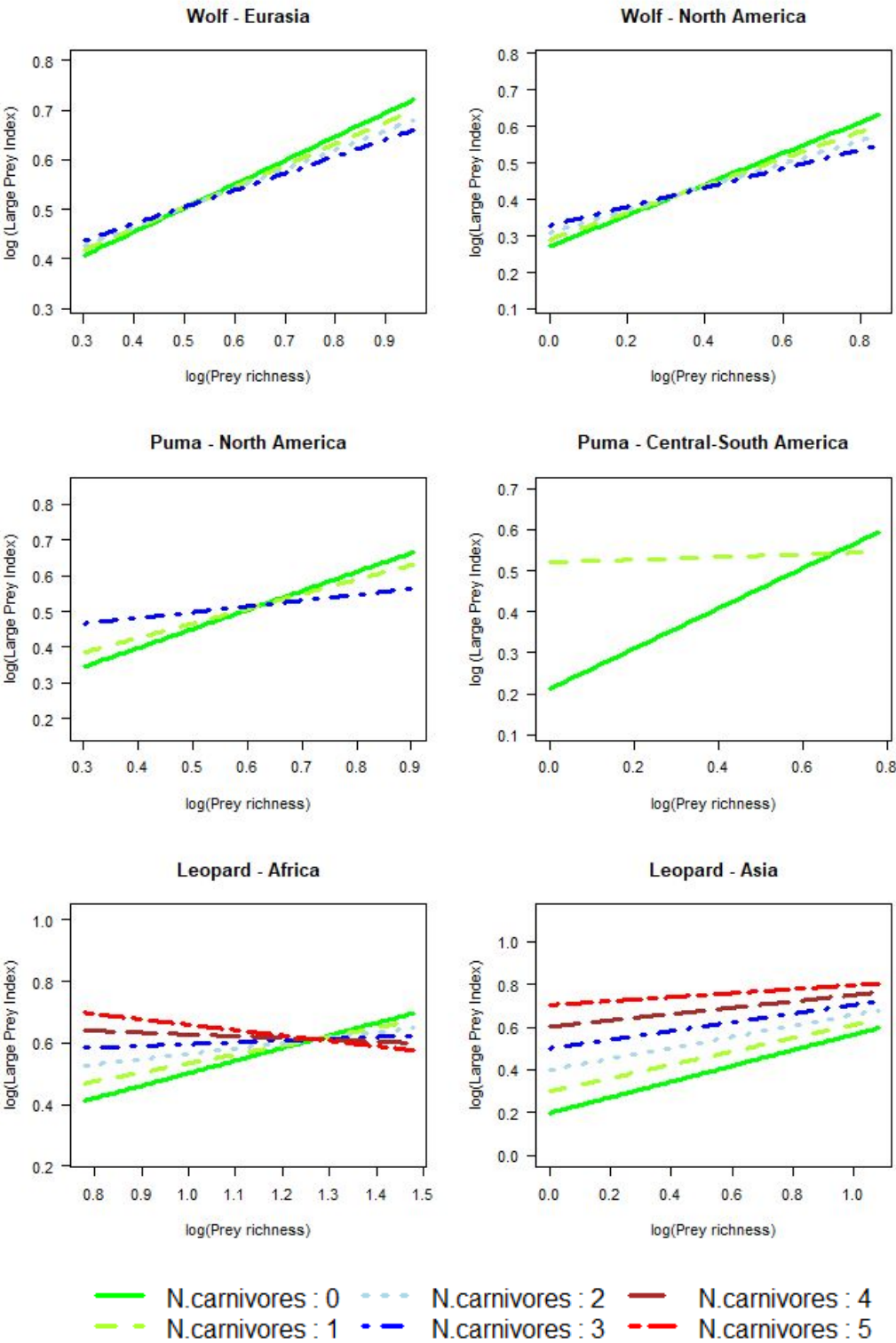699   two selected models (Fig. 1; Tables 1-2).

700 **Table 1** Model selection for models including the effects of Log(N available large prey) (referred in the table as 'N prey species') and N other large carnivore
701 species (referred in the table as 'N carnivore species') on the Large Prey Index. Models including interactive terms also include the additive effects of predictors.
702 In bold, selected models.

Predator	Model	Variables	df	logLik	AICc	ΔAICc	Weight	R^2
Wolf_Eurasia	**Best**	**N prey species**	**3**	**52.351**	**-98.3**	**0.00**	**0.666**	**0.33**
	Second	N prey species + N carnivore species	4	52.479	-96.3	2.03	0.241	0.33
	Third	N prey species × N carnivore species	5	52.716	-96.4	3.93	0.093	0.34
	Fourth	Null model	2	39.936	-75.7	22.62	0.000	0.00
	Fifth	N carnivore species	3	39.939	-73.5	24.82	0.000	0.00
Wolf_North America	**Best**	**N prey species**	**3**	**32.869**	**-59.1**	**0.00**	**0.699**	**0.43**
	Second	N prey species + N carnivore species	4	32.932	-56.7	2.35	0.216	0.43
	Third	N prey species × N carnivore species	5	33.311	-54.9	4.21	0.085	0.44
	Fourth	Null model	3	25.703	-44.7	14.33	0.001	0.18
	Fifth	N carnivore species	2	21.792	-39.3	19.81	0.000	0.00
Puma_North America	**Best**	**N prey species**	**3**	**19.475**	**-31.8**	**0.00**	**0.611**	**0.21**
	Second	N prey species + N carnivore species	4	19.519	-29.0	2.77	0.153	0.21
	Third	**Null model**	**2**	**16.576**	**-28.6**	**3.20**	**0.123**	**0.00**
	Fourth	N carnivore species	3	17.155	-27.2	4.64	0.060	0.05
	Fifth	N prey species × N carnivore species	5	20.019	-26.9	4.93	0.052	0.24
Puma_Central-South America	**Best**	**N prey species × N carnivore species**	**5**	**39.434**	**-66.9**	**0.00**	**0.856**	**0.56**
	Second	**N prey species + N carnivore species**	**4**	**36.148**	**-63.0**	**3.89**	**0.123**	**0.48**
	Third	N carnivore species	3	32.492	-58.3	8.68	0.011	0.36
	Fourth	N prey species	3	32.408	-58.1	8.84	0.010	0.36
	Fifth	Null model	2	24.165	-44.0	22.96	0.000	0.00
Leopard_Africa	**Best**	**Null model**	**2**	**7.942**	**-11.5**	**0.00**	**0.331**	**0.00**
	Second	N prey species	3	8.884	-11.0	0.49	0.260	0.05
	Third	N carnivore species	3	8.853	-11.0	0.55	0.252	0.05
	Fourth	N prey species + N carnivore species	4	9.063	-8.9	2.65	0.088	0.06
	Fifth	N prey species × N carnivore species	5	10.174	-8.4	3.12	0.070	0.11
Leopard_Asia	**Best**	**N prey species + N carnivore species**	**4**	**28.027**	**-47.0**	**0.00**	**0.692**	**0.48**
	Second	N prey species × N carnivore species	5	28.384	-45.2	1.84	0.276	0.49
	Third	N carnivore species	3	23.423	-40.2	6.78	0.023	0.36
	Fourth	N prey species	3	22.460	-38.3	8.71	0.009	0.33
	Fifth	Null model	2	13.763	-23.2	23.79	0.000	0.00

703

705 **Table 2** Model coefficients for the effects of Log(N available large prey) (referred in the table as 'N prey species') and N other large carnivore species (referred
706 in the table as 'N carnivore species') on the Large Prey Index in different continents for the wolf, the puma and the leopard. Best models are shown; in bold,
707 supported relationships. For the puma in Central-South America, the main effects were also found in the only other selected model (Intercept: $B = 0.446$, 0.95
708 CIs: 0.417, 0.475; N prey species: $B = 0.047$, 0.95 CIs: 0.012, 0.083; N carnivore species: $B = 0.047$, 0.95 CIs: 0.012, 0.082; ΔAICc = 3.89; weight = 0.123; see
709 Table 1).

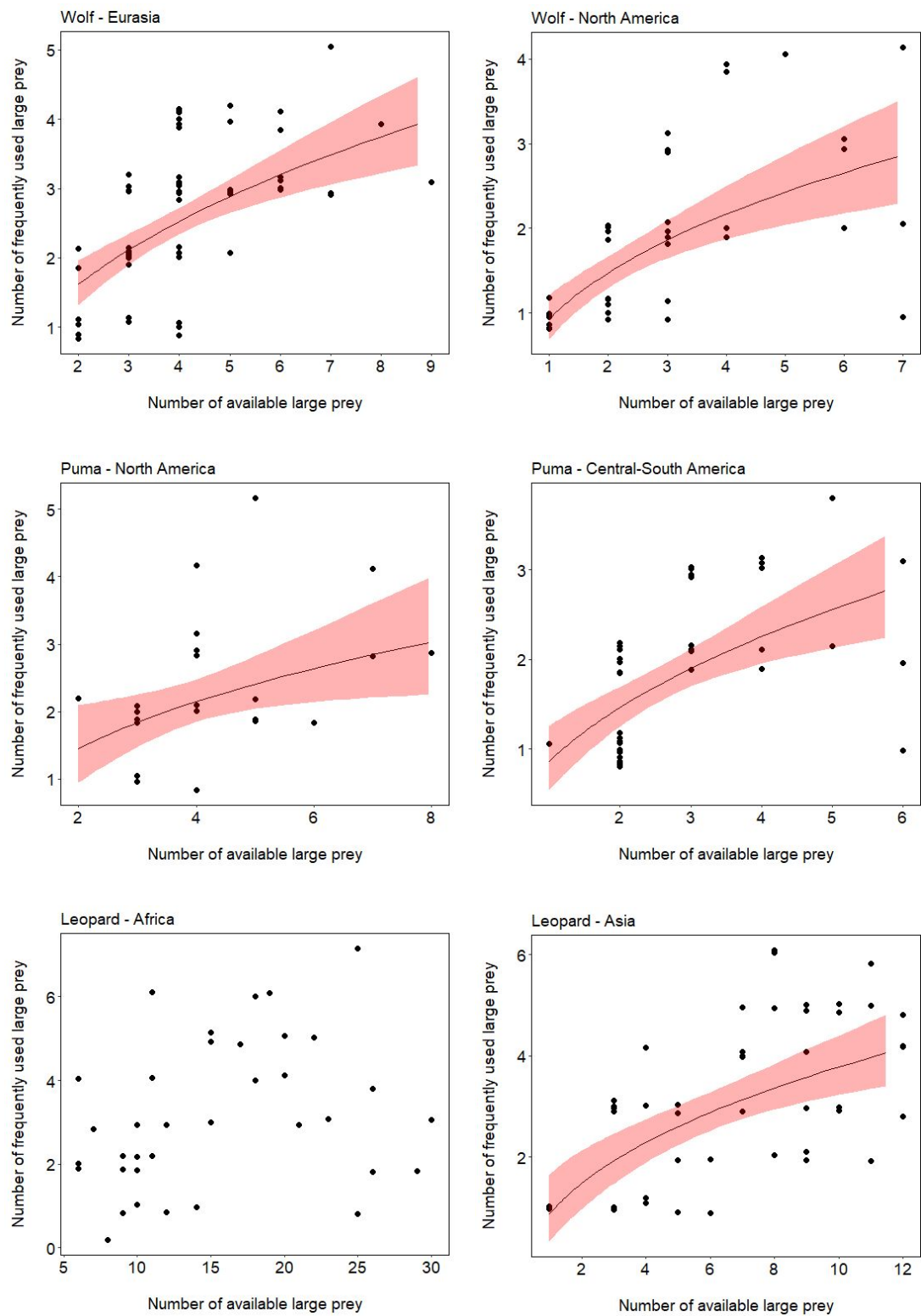| Species	Continent	Variable	B	SE	0.95 Cis	
					-	+
Wolf	Eurasia	Intercept	0.543	0.012	0.519	0.567
		N prey species	**0.066**	**0.012**	**0.041**	**0.090**
	North America	Intercept	0.431	0.016	0.398	0.463
		N prey species	**0.094**	**0.018**	**0.058**	**0.130**
Puma	North America	Intercept	0.500	0.022	0.454	0.546
		N prey species	**0.052**	**0.021**	**0.008**	**0.096**
	Central-South America	Intercept	0.465	0.015	0.434	0.497
		N prey species	**0.057**	**0.017**	**0.023**	**0.091**
		N carnivore species	**0.054**	**0.016**	**0.022**	**0.087**
		N prey species × N carnivore species	**-0.040**	**0.016**	**-0.073**	**-0.008**
Leopard	Asia	Intercept	0.590	0.019	0.551	0.629
		N prey species	**0.073**	**0.023**	**0.025**	**0.119**
		N carnivore species	**0.076**	**0.022**	**0.031**	**0.120**

711

Figure 1 Relationship between Large Prey Index (i.e., number of frequently used large prey species; log-scale) and local prey richness (i.e., number of available large prey species; log-scale) for the wolf, the puma, and the leopard in different continents, in relation to local carnivore richness (i.e., number of other large carnivore species). Relationships estimated through the model 'log(Large Prey Index) ~ log(Prey Richness) × Carnivore Richness, weights = √sample size' are shown.

718

719

720 **Fig. 2** Large Prey Index (i.e., number of frequently used large prey) *vs.* local prey richness (i.e., number of
721 available large prey species) for wolf, puma and leopard in different continents. Black lines indicate fitted
722 relationships of the model 'log(Large Prey Index) ~ log(Prey Richness), weights = √sample size' are shown;
723 red shaded areas indicate 0.95 confidence intervals of fitted relationships. Data points were jittered to
724 improve figure readability.

725

Discussion

A positive relationship between the number of frequently used large prey species and prey richness

was found for the wolf, across its distribution ranges. The common leopard showed this pattern in

Asia but not in Africa. For the puma, the positive relationship between the Large Prey Index and

prey richness was not observed in areas of central-southern America where the jaguar also occurred.

These results emphasise a complex relationship between diet breadth of large carnivores and prey

richness that can be modulated by the influence of competitive pressure (Ferretti et al. 2020;

Steinmetz et al. 2021). These results are generally consistent with larger and most dominant

carnivores exploiting a wider range of prey sizes (Radloff & du Toit 2004; Ferretti et al. 2020).

Relationships between predators are often context-dependent, affected by several ecological

factors (Haswell et al. 2017; Tallian et al. 2021). Spatial, temporal and/or dietary partitioning are

mechanisms allowing interspecific coexistence by limiting competition (Hutchinson 1959; Pianka

1973; Schoener 1974). Interspecific dominance is a relative concept, as the same predator may

behave both as dominant or subordinate in relation to the presence/absence of out-competing

species. Subordinate carnivores can adjust their spatio-temporal and hunting behaviour to limit

encounters with superior competitors (Palomares & Caro 1999; Donadio & Buskirk 2006), which

may lead to a reduced use of large prey (Ferretti et al. 2020; Steinmetz et al. 2021). The wolf was

the carnivore showing the most consistent behaviour across continents. This gregarious,

ecologically flexible and generalist carnivore is mainly a predator of medium-to-large sized

ungulates, and is usually the apex predator in ecosystems where it is found (Mech & Boitani 2003;

Ripple et al. 2014; Newsome et al. 2016). Although kleptoparasitism of wolf prey by bears has been

reported (Tallian et al. 2017, 2021), there is no clear evidence of wolf subordination to other

carnivores (Palomares & Caro 1999), except the tiger (which occurred in only one out of the 58

sites from which we obtained data: Miquelle et al. 2005). Support for wolf dominance or potential

750   dominance over other carnivores is more common (Mech & Boitani 2003; Bocci et al. 2018;

751   Elbroch et al. 2018; LaBarge et al. 2022).

752   The common leopard expanded its use of large prey with large herbivore richness only in Asia,

753   but not in Africa. Leopards may have a greater need to adapt to local ecological conditions and

754   competition pressure in Africa, where the array of potentially competing species is larger than in

755   Asia (Vanak et al. 2013; Balme et al. 2017). Accordingly, food caching in trees by common

756   leopards has been suggested to be greater in African sites than in Asiatic ones, suggesting a lower

757   intensity of kleptoparasitism in the latter than in the former (Balme et al. 2017). In Asia,

758   comparably limited diet partitioning has been detected between syntopic common leopards and

759   tigers or lions, indicating a substantial dietary overlap despite potential for interference (Lovari et

760   al. 2015; Zehra et al. 2017; Steinmetz et al. 2021), with larger predators using large prey more often

761   and small prey less often than the leopard did (Hayward et al. 2005, 2006, 2012), and with

762   interference potentially emphasising leopard predation on livestock (Franchini & Guerisoli 2023).

763   Asiatic leopards have been reported to concentrate on larger ungulates in prey-richer areas,

764   increasing their use of smaller prey in depleted areas (Steinmetz et al. 2021), which would fit our

765   results (see also Newsome et al. 2016 for the wolf and Guerisoli et al. 2021 for the puma).

766   Our interpretation is supported by findings on puma, for which the relationship between the use

767   of large prey and prey richness was affected in areas where the jaguar occurred (Elbroch et al. 2018;

768   LaBarge et al. 2022). Jaguars have been reported to kill pumas, to displace them spatially and

769   temporally, and to trigger shifts in their diet, leading to an increased use of smaller prey (Iriarte et

770   al. 1990; Elbroch et al. 2018). Similarly, the wolf has been reported as dominant over puma,

771   through killing and kleptoparasitism, leading to potential displacements or prey switching (Iriarte et

772   al. 1990). Wolves occurred in only 20% of study areas for which data are available: this small

773   sample size probably reduced the potential to detect significant effects of wolf presence on the use

774   of large prey by the puma. The potential for wolves to trigger changes in puma diet at broader scale

775   requires further tests.

776   Over an evolutionary scale, predators would be expected to narrow their diet in relation to

777   increased prey availability, and the resulting specialisation should promote coexistence among

778   potential competitors. A high specialisation to particular prey has been suggested as a determinant

779   of the extinction of Nimravids and saber-toothed Felids (Machairodontinae), while extant, less

780   specialised carnivores could adapt to alternative prey (Van Valkenburgh et al. 2007; but see

781   DeSantis et al. 2012). Although our results might be suggestive of no increase of predator

782   selectivity along with increasing prey richness, data on prey density would be necessary to support

783   that (Steinmetz et al. 2021). Moreover, under a selective predation scenario, we may expect that

784   increasing prey richness will lead to less widening of diet breadth than would be the case under

785   unselective predation. Further work is necessary to evaluate changes in predators' selectivity in

786   relation to variations in prey richness.

787   The current human-induced biodiversity crisis is characterized, among other phenomena, by the

788   collapse of populations of many large herbivore species worldwide (Ripple et al. 2015). Human

789   encroachment on natural habitats is expected to favour carnivore contact with anthropogenic food.

790   Together with prey depletion, it would increase human-carnivore conflicts further endangering

791   predators (Bagchi et al. 2006; Khan et al. 2018). Habitat conservation, direct protection of wild

792   prey, their sustainable management, or restoration of extinct populations, appropriate livestock

793   management, as well as adequate measures to prevent predation on losses and compensate

794   economic losses, are fundamental to ensuring large carnivore persistence (Treves et al. 2003, 2016).

795   Our results testify that large prey depletion would emphasise the negative consequences of

796   competition between carnivores, leading to niche shrinking of subordinate species and/or increased

797   use of smaller, sub-optimal prey (Creel et al. 2018; Ferretti et al. 2020; Steinmetz et al. 2021),

798   posing an additional significant threat to carnivore conservation in the Anthropocene.

799

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