

# Only the largest terrestrial carnivores increase their dietary breadth with increasing prey richness

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## Abstract

1. Animals should adapt their foraging habits, changing their dietary breadth in response to variation in the richness and availability of food resources. Understanding how species modify their dietary breadth according to variation in resource richness would support predictions of their responses to environmental changes that alter prey communities.
2. We evaluated relationships between the dietary breadth of large terrestrial carnivores and the local richness of large prey (defined as the number of species). We tested alternative predictions suggested by ecological and evolutionary theories: with increasing prey richness, species would (1) show a more diverse diet, thus broadening their dietary breadth, or (2) narrow their dietary breadth, indicating specialisation on a smaller number of prey.
3. We collated data from 505 studies of the diets of 12 species of large terrestrial mammalian carnivores to model relationships between two indices of dietary breadth and local prey richness.

4. For the majority of species, we found no evidence for narrowing dietary breadth (i.e. increased specialisation) with increasing prey richness. Although the snow leopard and the dhole appeared to use a lower number of large prey species with increasing prey richness, larger sample sizes are needed to support this result.
5. With increasing prey richness, the five largest carnivores (puma *Puma concolor*, spotted hyaena *Crocuta crocuta*, jaguar *Panthera onca*, lion *Panthera leo*, and tiger *Panthera tigris*), plus the Eurasian lynx *Lynx lynx* and the grey wolf *Canis lupus* (which are usually top predators in the areas from which data were obtained), showed greater dietary breadth and/or used a greater number of large prey species (i.e. increased generalism).
6. We suggest that dominant large carnivores encounter little competition in expanding their dietary breadth with increasing prey richness; conversely, the dietary niche of subordinate large carnivores is limited by competition with larger, dominant predators. We suggest that, over evolutionary time, resource partitioning is more important in shaping the dietary niche of smaller, inferior competitors than the niche of dominant ones.

**Keywords:** Canidae, Felidae, food habits, interspecific competition, large carnivores, predator-prey relationships

## INTRODUCTION

Variation in richness and availability of food resources is expected to affect foraging habits and diet composition of species (e.g. Jarman 1974, Macdonald 1983, Hofmann 1989), in turn influencing their dietary breadth (e.g. Birkhofer & Wolters 2012, Forister et al. 2015, Creel et al. 2018). Environmental changes and anthropogenic alterations of natural communities have profound ecological consequences (e.g. Walther et al. 2002, 2009), often influencing the richness and availability of resources available to foragers. The extent to which species modify their diet according to variation in food availability is influenced by anatomical, physiological, and behavioural traits, as well as by ecological determinants (e.g. Hofmann 1989, Forister et al. 2015, Creel et al. 2018). Understanding whether and how species modify their foraging habits according to variation in food resources should help us to predict their responses and ability to adapt to the effects of environmental changes (Forister et al. 2015).

Large terrestrial carnivores play fundamental roles in ecosystems and are ecologically, culturally, and economically important worldwide (Ripple et al. 2014). Changes in the abundance of large terrestrial carnivores can trigger cascading effects with impacts on lower trophic levels (e.g. Hebblewhite et al. 2005, Estes et al. 2011, Ripple et al. 2014). Additionally, many are threatened with extinction (Macdonald et al. 2010). Usually, they depend on medium to large terrestrial vertebrates for prey (Carbone et al. 1999, 2007), and this dependence tends to increase with carnivore body size (Carbone et al. 2010). Their food habits – and, thus, their dietary breadth – are expected to be strongly influenced by variation in the richness of large prey (see also Estes et al. 2011, Hatton et al. 2015, Creel et al. 2018).

Ecological and evolutionary theories, as well as empirical studies, invite opposing expectations about the dietary response of foragers to changing richness of their food resources. When a greater diversity of resources is available, foragers may respond by expanding their dietary breadth (Birkhofer & Wolters 2012). However, we might expect to observe a more diverse community of herbivores, which are prey to carnivores, in nutrient-rich areas (e.g. Danell et al. 1996, Olff et al. 2002). In richer environments, optimal foraging theory predicts that species should become increasingly specialised (MacArthur & Pianka 1966, Charnov 1976), narrowing their niches to concentrate on the most profitable resources. Thus, when the richness of food resources is greater, we would expect a narrower dietary breadth (MacArthur & Pianka 1966, Schoener 1971, Forister et al. 2015).

Variations in prey communities can be triggered by natural or anthropogenic drivers (e.g. Sinclair et al. 2003, Wegge et al. 2009, Creel et al. 2018). Poaching, intensive hunting, and/or habitat manipulation can reduce prey abundance and diversity, posing significant threats to carnivore populations, as well as affecting their food habits (e.g. Estes et al. 2011, Sandom et al. 2017, Creel et al. 2018). Additionally, environmental or climatic changes can influence species' distributions (e.g. Walther et al. 2002, 2009), which is expected to trigger a re-arrangement of communities in the medium to long term. Natural or human-driven variations in prey communities influence the food ecology of carnivores (e.g. Meriggi & Lovari 1996, Bagchi & Mishra 2006, Khorozyan et al. 2015, Creel et al. 2018, Khan et al. 2018). Thus, assessing whether and how the dietary breadth of large terrestrial carnivores varies with changing prey diversity has important theoretical and practical implications. Despite this, a global evaluation of how the dietary breadth of large carnivores varies with prey richness is lacking.

We reviewed information on the food habits of large terrestrial carnivores to evaluate intra-specific variation in dietary breadth in relation to prey richness. In particular, we assessed support for the following alternative predictions: (1) with increasing prey richness, carnivores use a larger spectrum of prey, thus showing a broader dietary breadth, or (2) with increasing prey richness, carnivores tend to specialise on the most profitable prey, thus showing a narrower dietary breadth. Body size of carnivores influences their dependence on large prey (Carbone et al. 2010), so we would expect that (3) the strength of the relationships between dietary breadth and richness of large prey increases with carnivore body mass.

## **METHODS**

### **Study species and definitions**

We focused on large terrestrial carnivores (Mammalia: Carnivora), with a diet mainly based on large terrestrial vertebrate prey. In particular, we included carnivores heavier than 14.5 kg (mean body mass), the body mass threshold at which carnivores switch to an obligate carnivorous diet based on large prey (according to Carbone et al. 2007). We excluded Ursidae, which typically have diets dominated by non-vertebrate foods. Considering mean adult body masses taken from the PanTheria database (Jones et al. 2009; see Table 1), 15 carnivore species were initially selected: clouded leopard *Neofelis nebulosa*, dhole *Cuon alpinus*, Eurasian lynx *Lynx lynx*, African wild dog *Lycaon pictus*, grey wolf *Canis*

*lupus*, snow leopard *Panthera uncia*, striped hyaena *Hyaena hyaena*, brown hyaena *Hyaena bruna*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, puma *Puma concolor* spotted hyaena *Crocuta crocuta*, jaguar *Panthera onca*, lion *Panthera leo*, and tiger *Panthera tigris*. Among them, the brown hyaena (43.0 kg) and the striped hyaena (35.1 kg) were excluded because they are mainly scavengers (e.g. Kruuk 1976, Owens & Owens 1978, Stein et al. 2013, Yarnell et al. 2013), with food habits dependent on carrion left by other carnivores. Additionally, the clouded leopard (14.9 kg) was excluded because of the very limited number of studies on its food habits (Rabinowitz et al. 1987, Grassman et al. 2005). Thus, we based our review on 12 species (Table 1).

**Table 1.** Numbers of studies included in the analysis for each species of large terrestrial carnivore (ordered by increasing body mass) and for each sample type (kills or scats), before and after filtering and pooling (see Methods)

Species	Body mass (kg)	Before filtering/pooling			After filtering/pooling		
		Kills	Scats	Total	Kills	Scats	Total
Dhole <i>Cuon alpinus</i>	15.8	1	19	20	0	14	14
Eurasian lynx <i>Lynx lynx</i>	19.3	13	7	20	11	6	17
African wild dog <i>Lycaon pictus</i>	22.0	21	1	22	16	0	16
Grey wolf <i>Canis lupus</i>	31.8	10	86	96	8	81	89
Snow leopard <i>Panthera uncia</i>	32.5	0	24	24	0	22	22
Cheetah <i>Acinonyx jubatus</i>	50.6	21	3	24	14	3	17
Leopard <i>Panthera pardus</i>	52.4	20	71	91	13	62	75
Puma <i>Puma concolor</i>	54.0	20	47	67	19	40	59
Spotted hyaena <i>Crocuta crocuta</i>	63.3	10	17	27	7	16	23
Jaguar <i>Panthera onca</i>	83.9	2	25	27	1	22	23
Lion <i>Panthera leo</i>	158.6	39	9	48	29	6	35
Tiger <i>Panthera tigris</i>	161.9	2	37	39	0	25	25
Total		159	346	505	118	297	415

Large terrestrial carnivores rely mainly on large terrestrial prey (Carbone et al. 2007). So, we considered the richness (number of species) of large terrestrial vertebrate prey (hereafter ‘large prey’) that we defined as being heavier than 10 kg, following Carbone et al. (2007). Livestock types are often inconsistently reported across studies, being frequently pooled in a single ‘livestock’ category. To ensure a consistent treatment across studies, all livestock types were pooled into a single category of large prey (as a single ‘species’). In some cases, several species of prey were reported in the literature as a cumulative prey category (e.g. ‘deer’, ‘peccaries’, or ‘duikers’): in these cases, we considered the cumulative prey category

as a single 'species'. Wild prey smaller than 10 kg were pooled together into a single 'other' category.

### **Literature review**

We searched ISI Web of Science and Google Scholar with combinations of keywords that included the common or scientific name of the focal carnivore species, and either 'diet', 'food habit', 'prey use', 'prey selection', or 'predation'. We considered only documents published in English, up to January 2019. In particular, we considered peer-reviewed scientific papers, books/book chapters, PhD and MSc theses, and conference proceedings. We also considered literature cited in papers found through this search, to locate any papers that were not detected in the first step. Studies were included only when both the carnivore and prey communities were described. For each study, we defined the spectrum of available potential large prey by considering information reported in primary sources. In some cases – especially in prey-rich areas, such as African national parks – the description of the prey community was incomplete in the primary sources. Therefore, we evaluated other official sources (e.g. other contemporary papers or official checklists) to assess the number of potential prey species. Very large mega-herbivores may not be prey for some carnivores (e.g. elephants *Loxodonta africana*, for African wild dogs). Thus, for each carnivore we only considered those species that have been reported – or are known from literature – to be preyed on by that carnivore as potential large prey (see Appendix S1 for a list of excluded prey species for each carnivore). We only considered studies based on analyses of scat contents or kills. If a study reported both scats and kills, we only used results obtained through the method based on the greatest sample size.

Several indicators can be used to quantify food habits of carnivores (e.g. absolute occurrence, relative occurrence, volumetric estimates, biomass estimates; Kruuk & Parish 1981, Ciucci et al. 1996, Chakrabarti et al. 2016). Among them, absolute or relative occurrences are the most widely used methods and can be employed to evaluate dietary breadth (see below). Additionally, besides uncertainties affecting the calculation of biomass consumed from scats (cf. Chakrabarti et al. 2016, Khorozyan et al. 2017, Lumetsberger et al. 2017), it is usually impossible to know (1) the age class and sex that was preyed upon; (2) whether other carnivores also fed on the carcass; and (3) whether an individual fed alone or with conspecifics (e.g. a pair, a pack or a female with pups or cubs; Bocci et al. 2018, Khan et al. 2018). Thus, to ensure consistent treatment across studies and species, we considered studies (1) which included absolute occurrences of given prey species in the diet, i.e. the ratio of the total number of occurrences of that prey over the total number of scats or kills analysed; (2) for which absolute occurrence could be derived from relative occurrences (the ratio of the total number of occurrences of that prey over the total number of prey items) reported in the study; or (3) reporting relative occurrences.

We defined as a 'study' an account of food habits of a carnivore species in a given study area. We selected an initial total of 505 studies (out of 351 sources) and compiled a data set including the following information: paper title, year of publication, author(s), journal (if peer-reviewed), study area, study period (in years or months), carnivore focal species, sample type (scats or kills), sample size (number of scats or kills analysed), and absolute

occurrence (or relative, if the absolute figure was not provided) of each prey reported in the primary source.

### Data analyses

We (1) pooled together all livestock types and summed up their occurrences; and (2) pooled together all smaller prey into the 'other' category and summed up their occurrences. For each predator, multiple studies conducted in the same study area were pooled (i.e. absolute occurrences of each prey, as well as sample sizes, were summed up across studies), to avoid pseudo-replication of data obtained in the same study areas. Although changes in prey communities may occur between different periods, the number of available prey species – the predictor used in the analyses – is most unlikely to vary across several studies conducted in the same study area; consequently, pooling should not affect our conclusions. Only studies conducted with the same method (scats or kills) were pooled; in cases where the two methods had been used at different times in the same area, only results obtained through the method based on the higher number of observations were considered. When necessary, we added additional prey species available in the study area, but not reported in the paper(s), and assigned them zero occurrence ( $n = 81$  studies, after pooling). The list of studies selected for the analyses ( $N = 415$ ) is reported in Appendix S2. A summary of the number of studies considered per species and sample type, before and after study filtering and pooling, is shown in Table 1.

We calculated relative occurrences (i.e. the relative use) of each prey by dividing their absolute occurrence by the total number of prey items, which is necessary to calculate dietary breadth indices. For each carnivore species, we considered two indices of dietary breadth. First, we considered the total dietary breadth, inclusive of all prey. To estimate total dietary breadth, we considered the Levins Index (Levins 1968) as:  $B = 1/\sum p_j^2$ , where  $p_j$  is the proportion of items in the diet that belong to the food category  $j$ . For this index, the 'other' category was included in the calculation of the overall dietary breadth. Large carnivores mainly depend on large prey for feeding and survival (Carbone et al. 1999, 2007; see Introduction). Thus, we evaluated whether variation in the richness of the guild of large prey would influence the use of large prey, prompting consideration of a second, additional index focused on large prey only. Specifically, we determined the number of frequently used resources (Krebs 1999) restricted to large prey showing a relative occurrence in scats of at least 5% (this second index is the Large Prey Index; Krebs 1999). The Levins Index and the Large Prey Index can vary from zero to the maximum number of available prey (with a maximum of 20 for Large Prey Index, which is theoretically possible if 20 prey are used, each with a frequency of 5%). For both indices, increasing values indicate increasing dietary breadth.

The Standardised Levins Index is frequently used to quantify dietary breadth (Colwell & Futuyama 1971, Hurlbert 1978, Krebs 1999). The calculation of this index includes both the proportional use of resources and the number of available potential resources (Colwell & Futuyama 1971, Hurlbert 1978, Krebs 1999). For this index, values are expected to be influenced by the number of potential resources available (i.e. resource states), so it is unsuitable for comparisons between populations using different resource matrices (Colwell

& Futuyma 1971). Since our major focus was the assessment of variations of dietary niche in relation to variations in prey richness, we did not use the Standardised Levins Index.

We used linear models to evaluate relationships between dietary breadth and richness of large prey. For both indices, the following model was used for each species:

$$\log(\text{dietary breadth index}) \sim \log(N \text{ available large prey}) + \text{sample type}.$$

To account for the greater reliability of studies based on larger samples, we weighted by sample size [using 'weights = sqrt(sample size)' in the model declaration]. To account for studies where no large prey showed a frequency of use greater than 5%, we used a  $\log(x + 1)$  transformation for the Large Prey Index (where  $x$  represents this index for any given species in a given study).

All models were weighted by square root of sample size (i.e.  $N$  scats or kills analysed in each study) because variance typically declines linearly with that measure.

To evaluate whether the relationship between dietary breadth and prey richness was affected by carnivore body mass, we considered the model coefficients for the relationships between prey richness and each dietary breadth index. Specifically, for both indices, we evaluated the following model:

$$\text{Model coefficient} \sim \log(\text{body mass}).$$

Relationships were considered as statistically supported if the 0.95 confidence intervals of coefficients did not include zero. Analyses were conducted through the RStudio version 1.1.447 software (R Core Team 2018).

## RESULTS

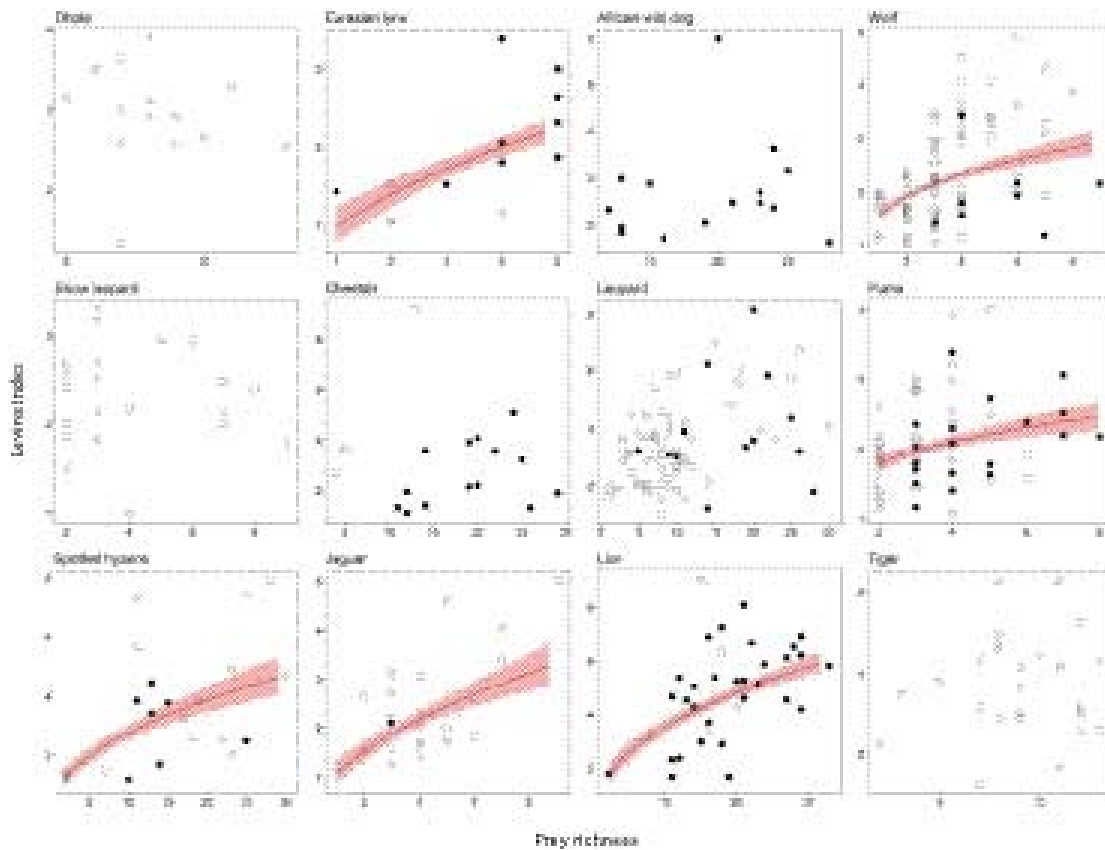
The Levins Index (i.e. the total dietary breadth) increased with increasing prey richness for six carnivore species (lion, jaguar, spotted hyaena, puma, grey wolf, and Eurasian lynx). No association between the Levins Index and prey richness was supported for the other six carnivore species (Table 2; Fig. 1).

Table 2. Model coefficients (and 0.95 confidence intervals, CIs) for relationships between indices of dietary breadth (Levins Index and Large Prey Index) and the number of available large prey species (prey richness) for large terrestrial carnivores. In bold, supported relationships (with confidence intervals not including zero)

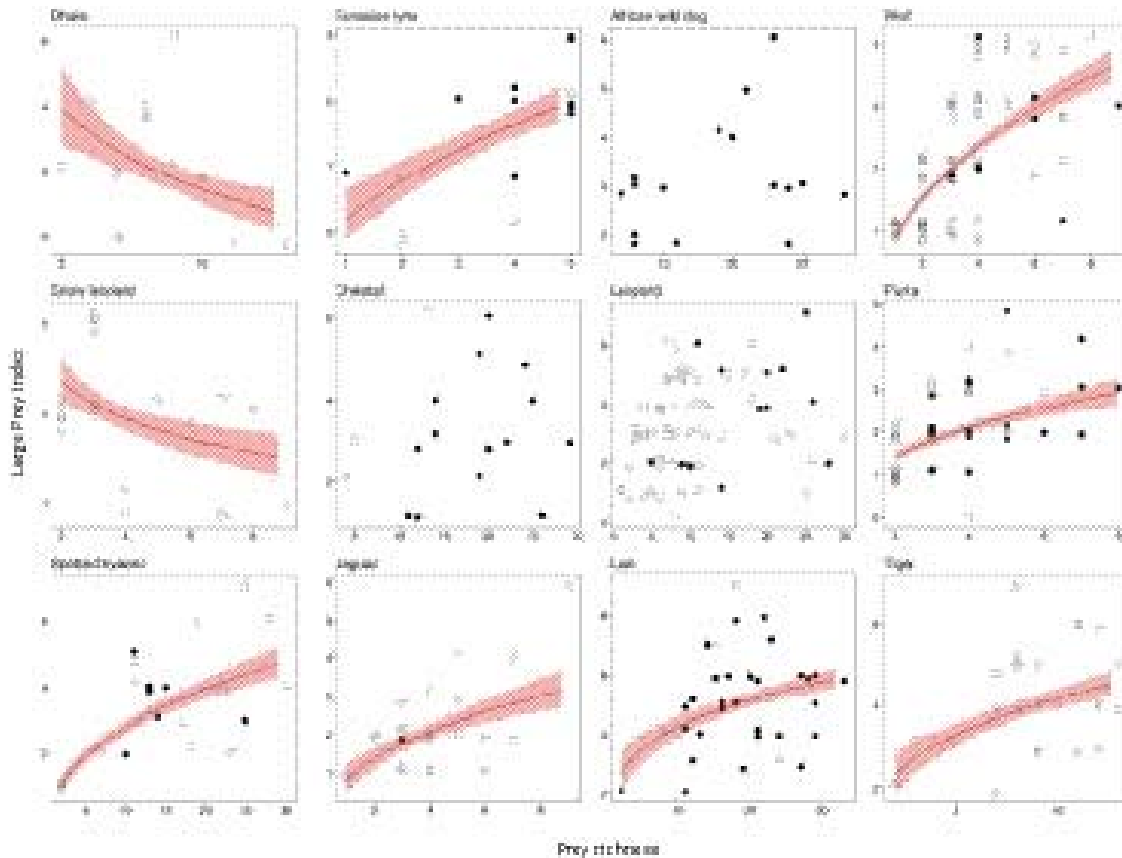
Species	Dietary breadth-prey richness relationships			
	Levins Index		Large Prey Index	
	<i>B</i>	CIs	<i>B</i>	CIs
Dhole	-0.214	±0.468	<b>-0.413</b>	<b>±0.396</b>
Eurasian lynx	<b>0.465</b>	<b>±0.358</b>	<b>0.465</b>	<b>±0.407</b>
African wild dog	-0.223	±0.614	0.180	±0.339
Grey wolf	<b>0.367</b>	<b>±0.125</b>	<b>0.447</b>	<b>±0.098</b>
Snow leopard	0.007	±0.222	<b>-0.194</b>	<b>±0.180</b>
Cheetah	0.443	±0.688	0.370	±0.486
Leopard	0.149	±0.162	0.117	±0.146
Puma	<b>0.279</b>	<b>±0.213</b>	<b>0.319</b>	<b>±0.204</b>
Spotted hyaena	<b>0.505</b>	<b>±0.221</b>	<b>0.381</b>	<b>±0.122</b>
Jaguar	<b>0.520</b>	<b>±0.312</b>	<b>0.386</b>	<b>±0.263</b>
Lion	<b>0.467</b>	<b>±0.195</b>	<b>0.240</b>	<b>±0.158</b>
Tiger	0.150	±0.310	<b>0.276</b>	<b>±0.187</b>

The Large Prey Index (i.e. the dietary breadth limited to the use of large prey) increased with prey richness for seven carnivore species, namely the five largest species considered (tiger, lion, jaguar, spotted hyaena, and puma) plus the grey wolf and the Eurasian lynx (Table 2; Fig. 2). This index decreased with increasing prey richness for the dhole and the snow leopard, although 0.95 confidence intervals were close to zero (Table 2).





**Fig. 1.** Relationships between the total dietary breadth of large carnivores (the Levins Index) and the number of available species of large terrestrial vertebrate prey (body mass > 10kg; prey richness). Fitted relationships and relevant standard errors are shown for supported relationships, i.e. those with confidence intervals not including zero values (see Methods for explanations). White circles: studies based on scats; black circles: studies based on kills.

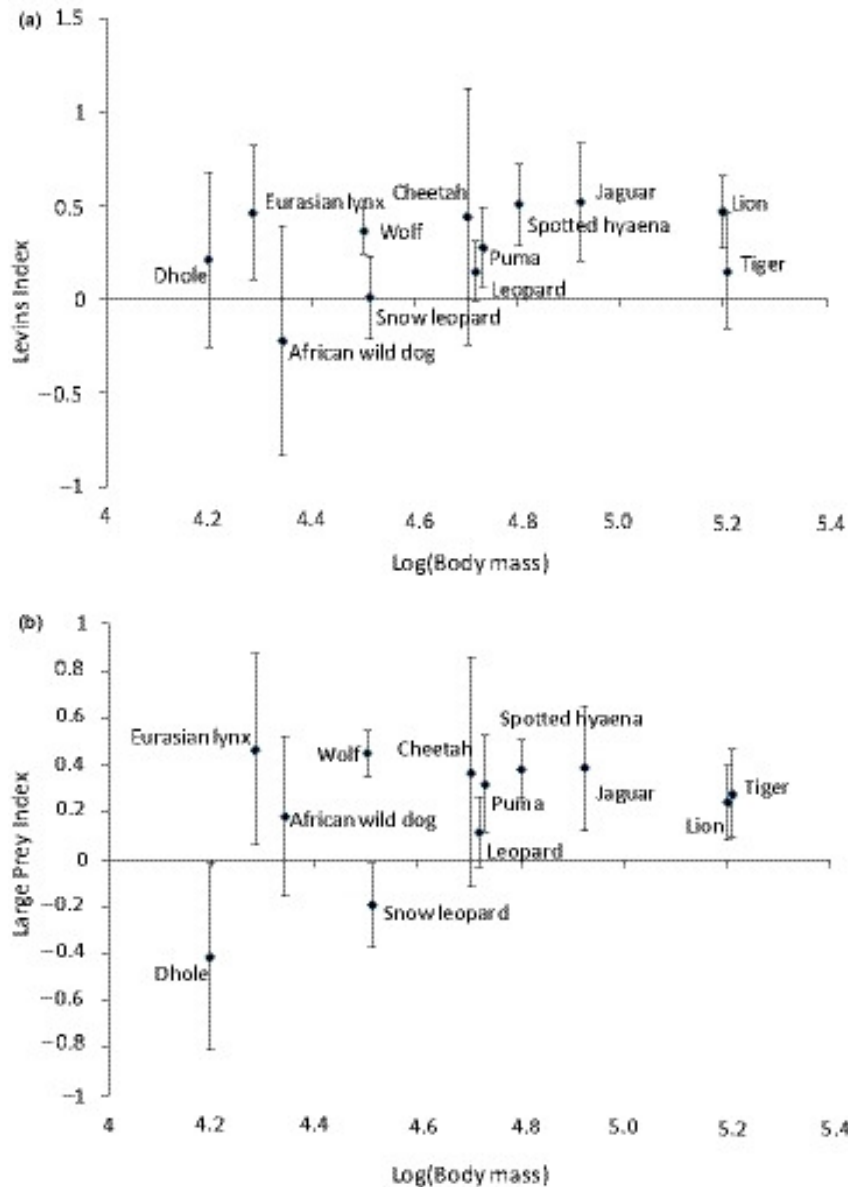


**Fig. 2.** Relationships between the dietary breadth of large carnivores (the Large Prey Index, i.e. the number of frequently used large vertebrate prey) and the number of available species of large terrestrial vertebrate prey (body mass > 10kg; prey richness). Fitted relationships and relevant standard errors are shown for supported relationships, i.e. those with confidence intervals not including zero values (see Methods for explanations). White circles: studies based on scats; black circles: studies based on kills.

We observed that the prey richness–dietary breadth relationship tended to increase only slightly with body mass, with 0.95 confidence intervals always including zero (Table 3; Fig. 3). The fits, model coefficients and 0.95 confidence intervals for linear models of both indices and predictors are shown in Appendix S3.

**Table 3.** Effects of carnivore body mass on the relationships between dietary breadth of large terrestrial carnivores (Levins Index, including all prey, and Large Prey Index, including only large prey species) and prey richness. Model coefficients ( $B$ ), their standard errors (SE), and 0.95 confidence intervals (CIs), as well as  $R^2$  value of models, are shown.

Index	Predictor	$B$	SE	0.95 CIs	$R^2$
Levins Index	Intercept	-1.790	0.975	-2.963 1.383	0.108
	Log (body mass)	0.228	0.208	-0.235 0.692	
Large Prey Index	Intercept	-1.181	1.119	-3.674 1.312	0.135
	Log (body mass)	0.298	0.239	-0.234 0.830	



**Fig. 3.** Estimated coefficients ( $\pm 0.95$  confidence intervals) concerning the relationships between dietary breadth (a: Levins Index; b: Large Prey Index) and the number of species of potential large vertebrate prey available (prey richness), for large carnivores, as a function of logged body mass.

## DISCUSSION

We assembled a large data set to relate the dietary breadth of all large terrestrial mammalian carnivores to the richness of their prey communities. In spite of the heterogeneity of sources, ecosystems, and researchers, our results support the existence of relationships between body mass, dominance in guilds, and niche partitioning. In particular, our results strongly suggest that the five largest carnivores in the world, as well as the grey wolf and the Eurasian lynx, use a greater number of large prey species with increasing prey richness (in agreement with our first prediction, that with increasing prey richness, carnivores use a larger spectrum of prey, thus showing a broader dietary breadth). Furthermore, our findings identify directions for future research into the potential for large

carnivores to adapt their foraging behaviour in the face of changing prey communities. We discuss our findings in relation to these two broad issues.

### **Dietary breadth, niche partitioning and body mass**

Optimal foraging theory suggests that, with increasing environmental productivity, species will specialise on the most profitable food resources, thus narrowing their dietary breadth (MacArthur & Pianka 1966, Charnov 1976). As opposed to totally indiscriminate predation, prey selection has been reported for large carnivores, and it can be influenced by several factors, such as prey abundance, accessibility, and/or vulnerability, as well as prey body size and anti-predator behaviour (e.g. Karanth & Sunquist 1995, Jędrzejewski et al. 2000, Hayward & Kerley 2005, Lovari et al. 2015). We found that most large carnivores do not reduce niche breadth when the richness of large prey increases. The Levins Index and the Large Prey Index provide different information. The Levins Index refers to the whole dietary breadth, including all potential prey, whereas our estimate of Large Prey Index is specifically relevant to prey heavier than 10 kg, i.e. the most substantial prey available to large carnivores (Carbone et al. 2007, 2010). In addition, the Levins Index accounts for evenness of prey consumption. None of our focal carnivore species showed a decrease of dietary breadth, as indexed by the Levins Index, with the increase of large prey richness. Our results do not provide support for our second prediction (that with increasing prey richness, carnivores tend to specialise on the most profitable prey, thus showing a narrower dietary breadth), which would have been expected under an 'optimal foraging' scenario (MacArthur & Pianka 1966, Charnov 1976).

A major caveat to our interpretation is that richness may represent an array of suitable or unsuitable prey with varying levels of population abundance across studies. Prey numerical or biomass densities affect the food habits of carnivores (e.g. Karanth & Sunquist 1995, Hayward & Kerley 2005, Jędrzejewski et al. 2000, Lovari et al. 2015). Ecological factors such as predation, interspecific competition, and climate, or human-driven factors such as poaching, over-hunting and habitat manipulation may influence prey populations differently across studies (e.g. Karanth & Sunquist 1995, Arsenault & Owen-Smith 2002, Sinclair et al. 2003, Owen-Smith 2008, Ferretti et al. 2015, Sandom et al. 2017), which may lead to non-linear relationships between prey richness and density. Environmental productivity, which may influence herbivore diversity (Danell et al. 1996, Prins & Olf 2002), is not always associated with prey density or biomass (e.g. if one or more prey species are rare). Productive environments may have more finely partitioned niches, so that individuals in any given niche are no more abundant than they would be in environments of lower productivity. Moreover, productive environments may allow the persistence of species that are more easily preyed on (by allowing them to have higher reproductive rates that offset the mortality caused by predation). Additionally, within the same prey species, individuals belonging to different age/weight classes can also show different vulnerability to predation (e.g. Kruuk & Turner 1967, Fuller 1989, Foster et al. 2010), so that they may be considered as different 'resource states' (Krebs 1999). However, data on use and availability of different age/mass classes are seldom available, and the use by predators of individuals belonging to different age/mass classes can be particularly difficult to assess in the field, especially for studies based on scat analyses.

Studies relating dietary breadth and prey density in areas with different prey richness are desirable. Densities of all potential large prey species are needed to evaluate the relationships between dietary breadth, prey density, and prey richness. Unfortunately, estimates of the densities for all potential prey species – especially for rare ones – are sparse and heterogeneous across studies. It is seldom possible to describe the whole prey spectrum and define actual prey availability, preventing us from accounting for that in our analyses. Nevertheless, positive relationships between productivity and herbivore abundance/biomass have been reported at local (Coe et al. 1976, Danell et al. 1996) and continental scales (Pettorelli et al. 2009, but see Santini et al. 2018), which supports our conclusions. Additionally, prey diversity has been shown to be a fundamental determinant of food habits, potentially more than prey density (Service et al. 2019). Our review represents a first test of the relationships between dietary breadth and prey richness for an important group of large mammals. Further work is necessary to explore relationships between environmental productivity, prey density, prey diversity, and carnivore food habits and dietary breadth, especially in the light of globally increasing anthropogenic pressure and its potential effects on prey communities (Sandom et al. 2017).

Inferences from analyses of the Levins Index were largely confirmed by restricting the analysis to the use of large prey. Potential exceptions were the snow leopard and dhole, for which the Large Prey Index seemed to decrease with increasing richness of large prey. This finding may indicate that these carnivores increase specialisation with increasing prey richness. However, caution is required in the interpretation of these results, because of the relatively small sample size and because of the confidence intervals associated with the estimated coefficients, which were very close to including values of zero. The snow leopard is a solitary carnivore, adapted to inaccessible habitats with low productivity and steep, rocky terrain where prey density is typically low (McCarthy et al. 2017). Over evolutionary time, the presence of potentially superior competitors, such as the grey wolf (Bocci et al. 2018), leopard (Lovari et al. 2013a), and tiger (Wang & Macdonald 2009), may have forced the snow leopard into marginal areas that are hardly accessible for its competitors and forced it to specialise on prey living in those areas (Lovari et al. 2013b, Lovari & Mishra 2016). This specialisation may be associated with greater selectivity in prey-rich areas where, presumably, competitors are present; in turn, that would favour coexistence with other large predators. However, not surprisingly, especially earlier studies on this large cat were based on a relatively small number of samples (10 out of 22 studies included less than 50 scats: Schaller 1977, Schaller et al. 1988a, 1998b, Bagchi & Mishra 2006, Wegge et al. 2012), suggesting that more data are needed to support our results. The dhole usually coexists with larger predators such as the leopard and the tiger (e.g. Karanth & Sunquist 1995, Andheria et al. 2007, Wang & Macdonald 2009), and it has extensive overlap in dietary preferences with these two species (Hayward et al. 2014). Our analyses show that the tiger increases its use of large ungulates in prey-rich communities. These large cats are dominant over dhole and can kill them (Schaller 1967, Johnsingh 1992). Thus, dholes may be expected to limit the risk of encounters with dominant competitors by selecting different prey, thus increasing their specialisation, which would ultimately favour interspecific coexistence (Karanth & Sunquist 1995). If this is correct, the reduction in the number of large prey used by the dhole with increasing prey richness would be a result of greater specialisation triggered by prey partitioning with larger, superior competitors.

No linear association was supported between carnivore mean body mass and the dietary breadth-prey richness relationship, thus not supporting our third prediction (that the strength of the relationships between dietary breadth and richness of large prey increases with carnivore body mass). This result suggests that, among large carnivores, body size *per se* is not the main determinant of the increase in dietary breadth with increasing prey richness. Thus, other factors could be influential (e.g. carnivore gregariousness, habitat use by carnivore or prey, and prey abundance). Nevertheless, four out of the five largest carnivore species showed an increase in dietary breadth (as estimated by the Levins Index), and all five showed an increase in the Large Prey Index, with increasing prey richness. For the tiger, results were inconsistent between indices, but the signs of both estimated relationships were positive. Apart from these five species, the grey wolf showed an increase of dietary breadth with increasing prey richness; this result could be easily explained considering the behaviour and ecology of this predator, which is gregarious, very adaptable, and often the top predator in the areas where it lives (Mech 1970, Mech & Boitani 2003). The Eurasian lynx also showed an increase in dietary breadth (Levins Index) and the Large Prey Index with increasing richness of large prey. The Eurasian lynx was often the top predator in the study areas included in this review (65% of 17 studies). However, we recommend caution in interpreting the results for this species, because (1) they are based on a sample of 17 studies; (2) the range of available large prey was only one to five; and (3) for values of one, two, and three large prey available, only one, three, and one studies were found, respectively.

### **Evolutionary implications and future research directions**

Interactions between carnivores are largely shaped by behavioural interference, escalating up to the killing of smaller species by larger competitors, and affecting behaviour, distribution, and numbers of inferior competitors (Palomares & Caro 1999, Linnell & Strand 2000, Donadio & Buskirk 2006). Interspecific dietary overlap is expected to increase the probability of interspecific encounters, thus promoting the occurrence of interspecific killing (Palomares & Caro 1999, Donadio & Buskirk 2006). Our results strongly suggest that top predators use a greater number of large prey with increasing prey richness. These carnivores are expected to encounter little competition in selecting areas with high prey density, whereas movements, activity, space, and prey of sub-dominant carnivores are expected to be influenced by those of larger, dominant ones (e.g. Schaller 1967, 1972, Durant 1998, Vanak et al. 2013). Apex predators seem to take advantage of increasing prey richness by increasing their realised dietary breadth by taking both larger and smaller prey (Gittleman 1985, Radloff & du Toit 2004), behaving as generalists, with different degrees of intensity.

The other carnivores we studied showed relatively stable dietary breadths with increasing prey richness; dietary breadth may even have decreased in snow leopards and dholes. Interspecific competition may strongly affect carnivore guilds (Palomares & Caro 1999, Linnell & Strand 2000). Over evolutionary time, inferior competitors are expected to have developed behavioural tactics to limit encounters with superior ones, involving food habits, space and habitat use, and temporal activity patterns (e.g. Mills & Biggs 1993, Durant 1998, Karanth & Sunquist 2000, Odden et al. 2010, Vanak et al. 2013). For example, subordinate carnivores may be forced to select marginal areas with relatively low densities of top

predators, in spite of the local low density of prey (e.g. African wild dog; Mills & Gorman 1997, cheetah; Durant 1998, leopard; Odden et al. 2010). Subordinate species may also show morphological or behavioural adaptations allowing them to capture rapidly consumable prey, maximising the amount of meat that they can consume before kleptoparasites arrive (cheetah; Hayward et al. 2006). Accordingly, our results show that subordinate large carnivores did not increase their dietary breadth with increasing prey richness, suggesting a role of larger competitors in limiting that increase. Loss of large prey, e.g. through poaching, over-hunting or habitat manipulation, is a major threat to the conservation of large carnivores (e.g. Carbone et al. 2010, Estes et al. 2011, Ripple et al. 2014, Sandom et al. 2017). Prey depletion may lead top predators to increase their use of secondary prey, which would further increase niche suppression of subordinate carnivores (Creel et al. 2018). If so, subordinate carnivores may be affected not only by the loss of their main prey, but also by the loss of prey preferred by dominant, apex predators. Further work is required to integrate information on prey diversity, prey abundance (where available), presence or numbers of competitors, spatially explicit proxies for environmental productivity (Pettorelli et al. 2009), and carnivore dietary breadth. Moreover, our results suggest that different carnivores tend to be found in areas showing different ranges of prey richness. Future research should evaluate whether the results observed at the intra-specific level are confirmed at the interspecific one, i.e. whether carnivores living in prey-rich areas tend to take advantage of this richness through a broader dietary breadth or rather by being more selective, thus showing a narrower dietary breadth.

We conclude that (1) there is no evidence that large carnivores increase their selectivity with increasing large prey richness except, possibly, in the snow leopard and the dhole; (2) the largest and most dominant carnivores do increase their dietary breadth with increasing prey richness; and (3) the dietary breadth of subordinate large carnivores appears to be limited by interspecific competition with dominant predators. Consequently, the realised dietary niche of sub-dominant carnivores may tend to show considerable ‘conservatism’ (Wiens & Graham 2005). If so, we suggest that resource partitioning is more important in shaping the dietary niches of smaller, inferior competitors than those of dominant, superior ones.

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