



Non-linear relationship between body size of terrestrial carnivores and their trophic niche breadth and overlap

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Abstract

Studying food partitioning of mammalian predators is important for understanding trophic structures and interactions between coexisting carnivore species. This is particularly pertinent in the light of expanding ranges of populations of generalist species whose habitat and diet overlap with more specialized species. Here, we tested the resource partitioning hypothesis in terrestrial carnivores, predicting that trophic niche breadth and overlap relate positively to body mass. We used dietary data from 18 terrestrial carnivore taxa in four families (Canidae, Mustelidae, Felidae and Ursidae; body mass 0.1–173.6 kg) in three regions in Central and Eastern Europe, i.e. deciduous forest and forest-steppe region (DFR), temperate deciduous and mixed forest region (MFR) and transitory mixed forest regions (TFR). We ranked carnivores along an axis of trophic niche (breadth and overlap), and analysed the relationship between trophic niche and body mass (or pair-wise difference in body mass). A hierarchical cluster analysis of diet composition divided carnivores into four ecological groups: wild ungulate predators; small-mammal predators; amphibians and small mammal predators and omnivores. The relationship between body mass of predators and both trophic niche breadth and trophic niche overlap were hump-shaped. The trophic niche breadth to body mass ratio was significantly lower in DFR than in TFR and trophic niche overlap was significantly higher in DFR than in MFR and TFR. The predominant food resource is small mammals whose abundance is related to local agricultural and forestry management practices. Modifications of management techniques can affect population dynamics and community composition of carnivore species, especially in the case of small-mammal predators.

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Introduction

Theoretical models (Hardin, 1960; Rosenzweig 1966) show that animals coexist in the same ecosystem through

reducing competition by partitioning of resources (e.g., food, habitat, activity time, habitat selection; Krebs 1989). In niche segregation, food is a fundamental resource for animals and its partitioning is important to understand interactions between coexisting species (Colwell & Futuyma 1971; Schoener 1974). The degree of overlap in diet represents a major interspecific relationship that affects competitive potential (Colwell & Futuyma 1971; Schoener 1974; Jones

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& Barmuta 1998; Hayward & Kerley 2008). High trophic overlap does not necessarily suggest strong interspecific exploitative competition, which depends on the abundance of food and consumers (Neale & Sacks 2001; Loveridge & Macdonald 2003; Hayward & Kerley 2008). However, narrow trophic niche breadth of one competitor and high trophic niche overlap with another may increase extinction risk within the carnivore guild (Odden, Linnell, & Andersen 2006; Hayward & Kerley 2008; Sidorovich 2011).

Coexisting carnivores can survive with high levels of trophic niche overlap if food is abundant (Colwell & Futuyma 1971; Krebs 1989; Schoener 1974). However, with increased food abundance, predator density also often increases (Hanski, Hansson, & Henttonen 1991; O'Donoghue, Boutin, Krebs, & Hofer 1997; Zalewski & Jędrzejewski 2006). This can accentuate competitive interactions between species as the increase in predator density reduces the per capita food amount. It can also potentially increase interference competition through increased encounter rates due to greater spatial and temporal overlaps, for example increased kleptoparasitism of inferior competitors (Caro & Stoner 2003; Hayward, Hofmeyr, O'Brien, & Kerley 2006). To reduce these competition costs, carnivores partition their trophic niches by utilising prey of differing sizes (Rosenzweig 1966; Dayan & Simberloff 1994; Zalewski 1996; Owen-Smith & Mills 2008), temporal and geographic segregation of the food resource (Simms 1979; Loveridge & Macdonald 2003; Merkle, Polfus, Derbridge, & Heinemeyer 2017), or utilising a greater diversity of prey species (White, Ralls, & White 1995).

Partitioning of the food niche (calculated as trophic niche overlap) can be measured by changes in trophic niche breadth or in niche position. The niche breadth of animals related to differences in morphological (e.g., body size and/or shape), behavioural, and ecological features allows for the predator community (all the predators in the system) to be divided into groups based on similar food resource use (Root 1967; Simberloff & Dayan 1991; Clements, Tambling, Hayward, & Kerley 2014). Larger carnivores generally have a broader trophic niche, as they prey on a greater variety of prey sizes (Gittleman 1985; White et al. 1995; Kitchen, Gese, & Schauster 1999; Clements et al. 2014) with smaller species having a narrow trophic niche. While the niche breadth of many groups of animals is positively correlated to body mass (e.g., Jarman 1974; Gittleman 1985; Barclay & Brigham 1991; Marti, Steenhof, Kochert, & Marks 1993; Brändle, Prinzing, Pfeifer, & Brandl 2002), this is not consistent across taxa or studies. For example, lizards exhibit a negative association (Costa, Vitt, Pianka, Mesquita, & Colli 2008), whereas marine predators showed no relation between both body size and food niche breadth (Costa 2009). The lack of consistency may result from differences in energy gained by differently-sized predators hunting for a particular prey in relation to searching and catching time (optimal foraging theory, Stephens & Krebs 1986). If large predators hunt for

small non-aggregated prey, they obtain very little per capita energy in relation to search time and body size (Carbone, Mace, Roberts, & Macdonald 1999; Carbone, Teacher, & Rowcliffe 2007). Similarly, smaller predators should hunt prey within their preferred prey weight range to achieve a higher net energy gain (Carbone et al. 2007). Furthermore, smaller predators that coexist within a predator guild risk lose larger prey items to theft by larger competitors (e.g., Caro & Stoner 2003; Hayward et al. 2006). Large predators should concentrate on hunting large prey to satisfy their energetic needs and therefore trophic niches of large predators should be narrowed in comparison to medium-sized predators. This may cause the niche breadth of predators in a community to correlate with body mass in a non-linear pattern.

The differences in body mass between sympatric carnivores allow for resource partitioning (Rosenzweig 1966; Simberloff & Dayan 1991; Loveridge & Macdonald 2003). If the relationship between body size and niche breadth is positive, smaller carnivores should be dietary specialists (monophagous predators) and larger carnivores generalists (polyphagous predators; e.g., Krebs 1989; Jędrzejewska & Jędrzejewski 1998). We expect larger predators with a broader trophic niche to have less niche overlap with specialist species as only part of the trophic niche will overlap. In long time scale, we also expect specialists to change their niche in relation to other specialist species to reduce competition. Analyses of trophic niche overlap in carnivore communities will allow us to understand interspecific interactions among carnivores and allow for the hierarchical classification of the carnivore communities in terms of trophic niche overlap. This clustering using interspecific trophic relations (pair-wise niche overlaps) should also consider grouping into ecological guilds.

Large-scale comparative analyses of food resource use by carnivore species have been carried out over several continents (123 carnivore taxa of different continents: Gittleman 1985; Africa: Caro & Stoner 2003; Owen-Smith & Mills 2008). Our aim was to analyse the relationship between body mass of 18 carnivores and their trophic niche breadth, and to test the food resource partitioning hypothesis in relation to body size in three regions with various climatic and habitat conditions in Central and Eastern Europe. We included region as predictor variable as prey abundance changed among locations, e.g., rodent abundance is lower in mixed and higher in deciduous forest (Jędrzejewski & Jędrzejewska 1996) and roe deer abundance increases with the overall productivity of vegetation cover (Melis et al. 2009). This variation may affect the trophic niche breadth of predators and trophic niche overlap. We predicted that within the terrestrial carnivore community: (1) dietary composition should separate the species into different trophic guilds; (2) trophic niche breadth should be positively related to body mass, and (3) trophic niche overlap will depend on body mass differences between carnivores.

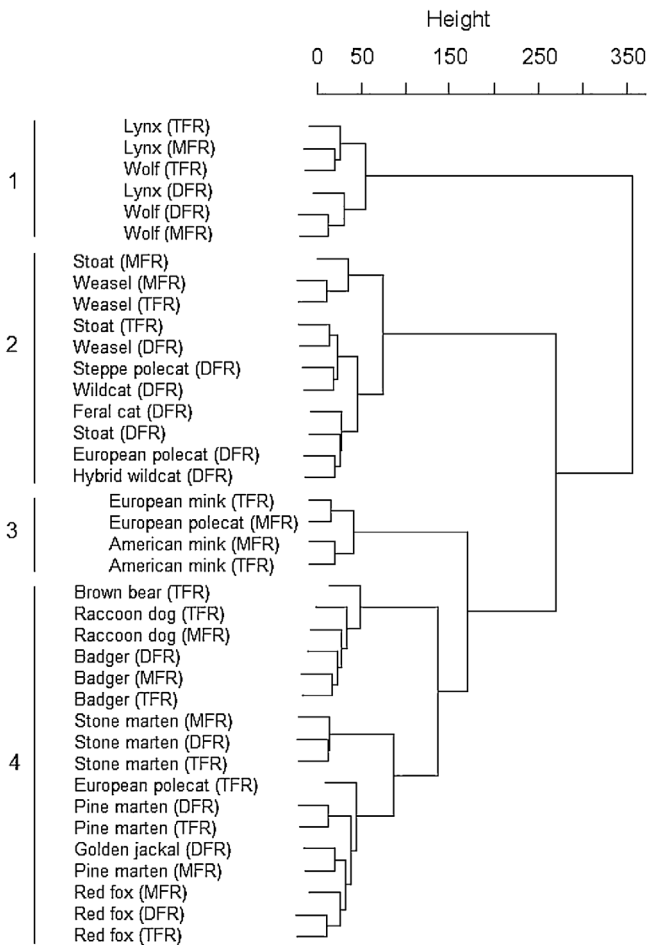


Fig. 1. Diet differences of terrestrial carnivores living in the deciduous forest and forest-steppe region (DFR), the temperate deciduous and mixed forest region (MFR) and the transitional mixed forest region (TFR). The dendrogram was conducted using cluster analysis on the basis of arcsin transformed percentage relative frequency data of 13 main food types of 18 carnivore taxa. Hierarchical cluster analysis calculated on the basis of Euclidean distances. Numbers indicate trophic guilds: (1) wild-ungulate consumers, (2) small-mammal consumers, (3) small-mammal and amphibian consumers and (4) omnivores.

Materials and methods

We compared the trophic niche of carnivore species from three regions of a temperate broadleaf and mixed forest biome in Central and Eastern Europe. These regions differ in climate and vegetation, especially forest type and mixture of deciduous and coniferous tree species. We considered: (1) temperate deciduous forests and forest-steppes (DFR) in south-western and north-eastern Hungary; (2) temperate deciduous and mixed forests (MFR) in the Białowieża Primeval Forest in north-eastern Poland; and (3) transitional mixed forests (TFR) in north-eastern and central Belarus (Supplementary Appendix A: Fig. 1).

The DFR is located in the Pannonian biogeographical region (Hungary), which is surrounded by the Carpathian

and Dinaric mountains and the Alps. The surrounding mountains have created a unique continental climate with mild winters and hot and dry summers (Varga 1995). The climate in the MFR is temperate with a transitional character between Atlantic and continental climate with clearly marked warm and cold seasons (Jędrzejewska & Jędrzejewski 1998). The TFR in Belarus is characterized by a humid continental climate with cold winters and cool, moist summers (Sidorovich 2011).

To analyse the relationship between body mass and trophic niche breadth we used published dietary data of terrestrial carnivore taxa representing four mammalian families (Canidae, Mustelidae, Felidae and Ursidae) ranging in body mass from 0.1 to 173.6 kg (see Supplementary Appendix B). We analysed carnivore populations with 14 species in DFR, 11 species in MFR and 12 species in TFR. Altogether, we analysed 18 species from the three regions (see Supplementary Appendix B for more details). The data on carnivore diet composition and body mass were obtained from the following papers, books and dissertation: Jędrzejewska and Jędrzejewski (1998), Sidorovich (1997, 2011), Lanszki (2013), Czernik, Kowalczyk, and Zalewski (2016), Wereszczuk and Zalewski (2015). As in other comparative studies of feeding habits in terrestrial carnivores (McDonald 2002; Lozano, Moleón, & Virgós 2006; Zhou et al. 2011; Széles, Purger, Molnár, & Lanszki 2018) our studies of diet composition were based on scat (faeces) analyses and a few on stomach analyses [in DFR: *Felis* sps., weasel (*Mustela nivalis*), European polecat (*M. putorius*) and steppe polecat (*M. eversmanni*)]. The different methods used in diet studies may potentially bias the results but the small proportion of studies based on stomach analysis should not affect the final result. In fact, results obtained using different method of diet analysis in the genus *Felis* did not differ significantly (Széles et al. 2018). Sources expressed results as relative frequency of occurrence (RFO) calculated as the number of occurrences of a certain food type divided by the total number of occurrences of all food types (%). We used RFO because it was available for all studies, and is highly suitable for inter-population comparisons in diet studies (e.g., McDonald 2002; Lozano et al. 2006). We used 13 food types in the calculations of our comparative analysis: 1 – small mammals (insectivores and rodents), 2 – lagomorphs and muskrat, 3 – carnivores, 4 – wild ungulates, 5 – domestic animals (and household food), 6 – birds, 7 – bird eggs, 8 – reptiles, 9 – amphibians, 10 – fish, 11 – earthworms, 12 – other invertebrates, 13 – fruits, seeds and other plant matter. Trophic niche breadth (B) was calculated in accordance with Levins (1968): $B = 1/\sum p_i^2$, where p_i is the relative frequency of occurrence of the i th food type; and standardised across food types: $B_A = (B - 1)/(n - 1)$, ranging from 0 to 1, n is the total number of the resource taxa (of the 13 food types listed above). The trophic niche overlap (O) was calculated by means of the Renkonen index (Krebs 1989): $O_{jk} = [\sum n(\text{minimum } p_{ij}, p_{ik})]100$, where O_{jk} is the percentage overlap between species j and species k ; p_{ij} and p_{ik} are the proportions of resource i in the diets of species

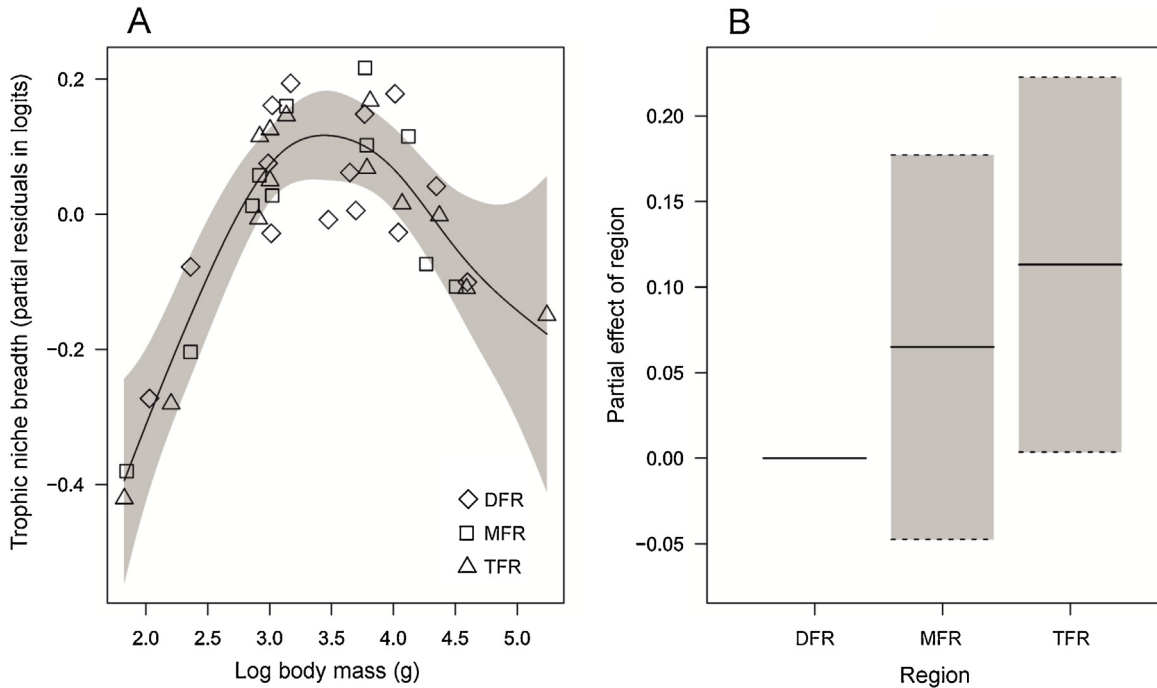


Fig. 2. Effects of carnivore body mass (A) and region (B) on the trophic niche breadth estimated by the generalized additive mixed model (GAMM). Solid lines represent the estimated smooth function and shading denotes 95% confidence intervals. The y-axis presents the partial residuals of the model after removing the effects of the other covariates. The slope of zero indicates a constant influence of the covariates on trophic niche breadth. DFR — deciduous forest and forest-steppe region, MFR — temperate deciduous and mixed forest region, TFR — transitional mixed forest region.

j and species k (the minimum means that the smaller value should be used).

We calculated mean RFO values for 13 prey types from the diet of 18 carnivore species from the three regions (Supplementary Appendix B). We used the diet composition values to calculate percent trophic niche overlap (O) among all possible species pairs ($n = 153$ combinations).

We used hierarchical cluster analysis [with Ward as cluster method and Euclidean distance (E_d) as interval of measure] to compare diet composition (arcsin transformed RFO values of 13 main food types) among 18 carnivore taxa from the three regions presented in Supplementary Appendix B. The dendrogram was created with the R package used ('rcomdr' library, R Core Team 2017).

We used Generalized Additive Mixed Models (GAMM) to test the non-linear relationship between trophic niche breadth and carnivore body mass. Trophic niche breadth (response variable) was related to the predictor variable body mass and region, through GAMM using Gaussian distribution and identity link function. We did not use phylogenetic contrast in our analysis because this technique is known to perform poorly when the relationship between traits is non-linear (Quader, Isvaran, Hale, Miner, & Seavy 2004). Instead we log-transformed our data which removed the effects of the relationship between body size and location in the phylogeny,

in accordance with the suggestion of Freckleton (2000). The additive model estimates a non-parametric function and has the benefit of avoiding prior assumptions about the shape of the function. It also provides a flexible and effective technique for modelling linear and nonlinear data and including the model random factors (Wood 2006). As the number of analysed samples was different for each predator, and sample size may bias the trophic niche breadth, we used number of samples as a random factor. In analyses of niche overlap variation we used the body mass difference between carnivores and region as response variable but we were unable to add sample size as a random factor, as it should be a sum of the sample size from both species and this will not reflect the bias of small sample size in one species. Consequently, in this analysis we used Generalized Additive Models (GAM) with log-transformed values before modelling and we used Gaussian distribution and identity link function. We ran the GAMM and GAM models using thin plate regression splines as the smooth function with the 'mgcv' library (Wood 2001) in the R statistical software (R Core Team 2017). From both models we re-calculated predicted values using function 'predict' incorporated in 'mgcv' library (Wood 2001) and we plotted that figures presenting variation of the trophic niche breadth and overlap in response to the body mass in three regions (Supplementary Appendix C: Fig. 2).

Table 1. The numerical outputs (parametric coefficients and approximate significance of smooth terms) of the GAMM model for food niche breadth.

Variables	Parametric coefficients				
	Estimate	SE	t-Value	P-Value	
Intercept	0.37579	0.03739	10.049	<0.0001	
DFR vs. MFR	0.06493	0.05614	1.157	0.2561	
DFR vs. TFR	0.11310	0.05477	2.065	0.0472	
MFR vs. TFR	0.04816	0.05750	0.838	0.4086	
Approximate significance of smooth terms					
	Estimate	df	Ref df	F	P-Value
S (Body mass)	3.407		3.407	11.29	<0.0001

Ref df — estimated degree of freedom for reference. DFR — deciduous forest and forest steppe region, MFR — temperate deciduous and mixed forest region, TFR — transitional mixed forest region.

Results

Trophic guilds

The hierarchical cluster analysis of diet compositions identified four main trophic groups (Fig. 1). Wolf (*Canis lupus*) and lynx (*Lynx lynx*) represented the wild ungulate consumer guild. Differences between the diet composition of wolves and the other taxa were the highest (mean Euclidean distance, $E_d = 68.6$). Most *Mustela* species, i.e. stoat (*M. erminea*), weasel (*M. nivalis*), steppe polecat (*M. eversmanni*), European polecat (*M. putorius*) examined in the DFR, and all *Felis* species, i.e. wildcat (*F. silvestris silvestris*), feral domestic cat (*F. silvestris f. catus*) and hybrid wildcat (*F. s. catus* × *silvestris*) formed the small-mammal predator guild. European mink (*M. lutreola*), American mink (*Neovison vison*) and European polecat (examined in the MFR) represented the small-mammal and amphibian predator guild. The remaining carnivore species formed the omnivore guild (Fig. 1). Differences in the diet composition between the omnivorous pine marten (*Martes martes*) or red fox (*Vulpes vulpes*) and the other taxa was the lowest ($E_d = 41.6–42.0$).

Relationship between body size and trophic niche

The trophic niche breadth (B) varied from 1.3 (weasel) to 4.6 (stone marten, *Martes foina*) in DFR, from 1.2 (weasel) to 5.9 (raccoon dog, *Nyctereutes procyonoides*) in MFR and from 1.1 (weasel) to 5.3 (raccoon dog) in TFR. The proportion of variance explained by the GAMM model with two variables (body mass and region) equalled 50% (Table 1). The results indicated a non-linear response of the trophic niche breadth to body mass of the carnivore (edf = 3.407), with a broader trophic niche in medium-sized predators (peak at

Table 2. The numerical outputs (parametric coefficients and approximate significance of smooth terms) of the GAM model for food niche overlap between carnivores from three regions.

Variables	Parametric coefficients				
	Estimate	SE	t-Value	P-Value	
Intercept	1.47834	0.02853	51.825	<0.0001	
DFR vs. MFR	−0.22598	0.04163	−5.429	<0.0001	
DFR vs. TFR	−0.18777	0.03933	−4.775	<0.0001	
MFR vs. TFR	0.03820	0.04416	0.865	0.3880	
Approximate significance of smooth terms					
	Estimate	df	Ref df	F	P-Value
S (Body mass)	2.442		2.811	42.39	<0.0001

Ref df — estimated degree of freedom for reference. DFR — deciduous forest and forest steppe region, MFR — temperate deciduous and mixed forest region, TFR — transitional mixed forest region.

about 2.5 kg) and lower in both smallest and largest predators (Fig. 2A). The mean predicted trophic niche breadth values calculated from the GAMM models increased from 1.328 in small carnivores (body mass = 0.1 kg) to 3.562 in intermediate carnivores (BM = 2.5 kg) and decreased to 1.834 in the biggest carnivores (BM = 160.0 kg) (Fig. 2, Supplementary Appendix C: Fig. 2). The ratio between niche breadth and body mass of carnivores increased from south to north, by approximately 0.11 response ratio units from the DFR to TFR (Table 1, Fig. 2B). However, the only significant difference obtained was between the DFR and TFR regions, the predicted trophic niche breadth in carnivores with a body mass of 2.5 kg increased from 3.107 in DFR to 4.032 in TFR (Table 1, Supplementary Appendix C: Fig. 2).

Trophic niche overlap (O) among the carnivore species varied from 4.6% to 88.9% and was related to pair-wise differences in the body mass of carnivores and region (Fig. 3). The GAM models analysed the trophic niche overlap variation explained 45% of the deviance and 44% of the variance (Table 2). The magnitudes of the effects of body mass difference between carnivores was large ($P < 0.001$). The trophic niche overlap predicted from the model varied from 62% in carnivores with 0.01 kg difference in body mass to 12% in carnivores with 160.0 kg difference in body mass (Fig. 3, Supplementary Appendix C: Fig. 2). The percentage trophic niche overlap of some species pairs (golden jackal, *Canis aureus*, with stoat, weasel, steppe polecat, red fox and feral domestic cat; wolf with lynx; wildcat with hybrid wildcat and steppe polecat) were higher than trophic niche overlap of smaller and larger carnivores (Fig. 3, Supplementary Appendix C: Fig. 2). The ratio between niche overlap and body mass difference was significantly higher in DFR than MFR and TFR, by approximately 0.20 response ratio units (Fig. 3, Table 2).

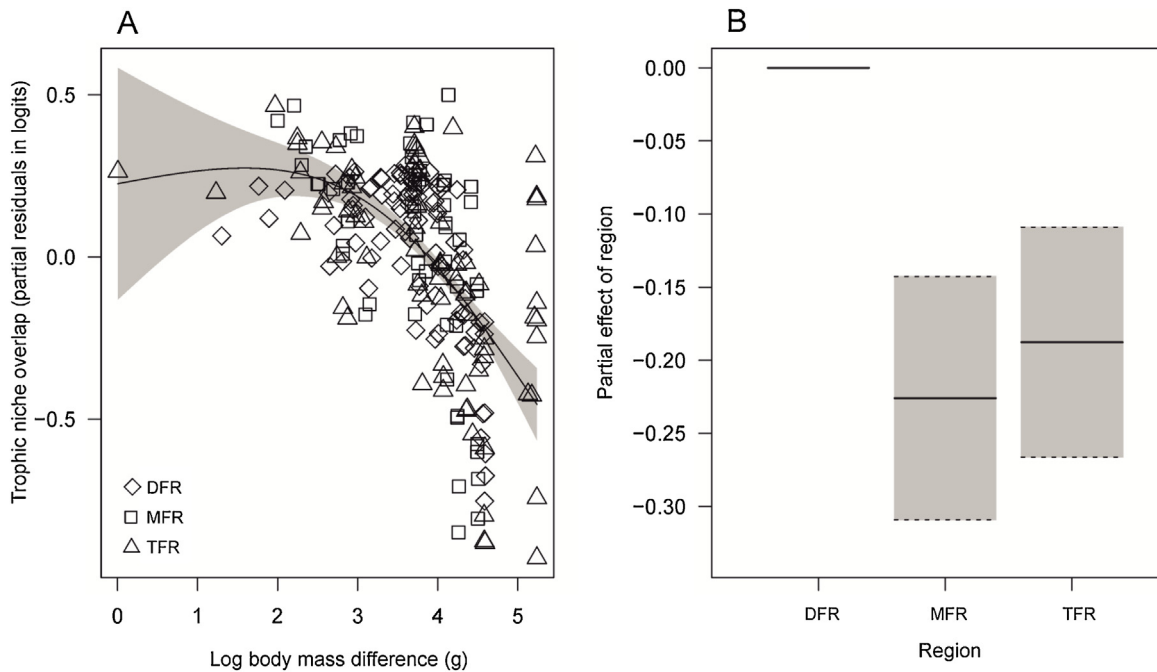


Fig. 3. Effects of carnivore body mass (A) and region (B) on the trophic niche overlap estimated by the generalized additive model (GAM). Solid lines represent the estimated smooth function and shading denotes 95% confidence interval. The y-axis presents the partial residuals of the model after removing the effects of the other covariates. The slope of zero indicates a constant influence of the covariates on the trophic niche overlap. DFR — deciduous forest and forest-steppe region, MFR — temperate deciduous and mixed forest region, TFR — transitional mixed forest region.

Discussion

In our study, eighteen terrestrial carnivores were divided into trophic guilds as defined by the resource partitioning hypothesis (Hardin 1960; Rosenzweig 1966). This grouping was supported by analyses of both trophic niche breadth and trophic niche overlap. Our data showed that resource partitioning based on trophic niche breadth and overlap depended on carnivore body mass. Trophic niche breadth increased with increasing body size (mass) but medium-sized predators with a body mass of about 2.5 kg had the highest trophic niche breadth thereafter trophic niche breadth decreased with increasing body mass.

Trophic guilds

Carnivore species which preyed on wild ungulates or small mammals only were specialists (or less generalistic); species in the transitional group consumed two food types relatively frequently; and species, which were included the omnivore group, were generalists as they consumed various types of food relatively frequently. The classification of the species into trophic groups was similar among regions. The European polecat was the only species, which was classified into three different guilds, depending on study region. Nine out of 18 carnivore species were classified into small-mammal or small-mammal and amphibian consumer groups. This indicates the high importance of small mammals, mainly rodents

for the carnivore species belonging to these groups, as it was found in carnivore communities from other regions in Europe (Jędrzejewska & Jędrzejewski 1998; Hanski, Henttonen, Korpimäki, Oksanen, & Turchin 2001; McDonald 2002).

Previous studies have demonstrated the uncertainty of the classification into generalist vs. specialist classification (e.g., Roper 1994), as we found in the case of the European polecat. Our study suggests that there is a continuous gradient from specialists to generalists and grouping species into groups is equivalent to discretizing a continuous gradient. Additionally, food partitioning and preference can vary with changes in prey abundance (Hanski et al. 2001; Randa, Cooper, Meserve, & Yunger 2009; Katano, Doi, Eriksson, & Hillebrand 2015) and/or habitat type and intensity of habitat management (Jędrzejewska & Jędrzejewski 1998; Crooks & Soulé, 1999; Lanszki, Heltai, & Szabó 2006), and in different geographic sites (McDonald 2002).

Trophic niche breadth

Many studies suggest that small predators are limited to smaller size classes of prey but in some cases small predators may hunt in a group for larger prey; e.g., yellow throated marten *Martes flavigula* (Woo, Choi, Lim, & Park 2017). Larger predators utilize both larger and smaller prey (Gittleman 1985; Barclay & Brigham 1991; Marti et al. 1993), therefore niche breadth should increase with body

mass of predator. However, the smaller prey are too costly to catch in relation to energy gain for very large predators (Carbone et al. 1999; Hayward & Kerley 2008; Hayward, Jędrzejewski, & Jędrzejewska 2012), and hence they should also reduce their niche breadth and hunt on large prey. Indeed, in our study, the relationship between niche breadth and body mass is not linear but hump-shaped as the trophic niche breadth was smaller in small and large carnivores. The observed hump-shape is general for carnivore communities in all three regions, and there was a tendency of increasing trophic niche breadth from southern to northern study regions. This relationship may be linked to the distribution and abundance of various prey classes (Jędrzejewska & Jędrzejewski 1998; Lanszki et al. 2006; Sidorovich 2011) and higher energetic needs of larger predators (Gittleman & Harvey 1982; Carbone et al. 1999). Our data also suggest that a more profitable way for large predators is to capture large prey (ungulates) rather than to search for many small prey items (insects), which may not satisfy the daily energetic needs of these predators (e.g., Hayward et al. 2012; Lyngdoh et al. 2014). When the abundance of large prey decreased and predators switched to smaller prey, their body mass also decreased (Zalewski & Bartoszewicz 2012; Hayward et al. 2016). Therefore, large predators focus on large prey, resulting in a narrow trophic niche.

The general pattern from our study shows that the smallest and largest species used a narrow proportion of food types, but each species from these groups used different types (low trophic niche overlap with higher body mass differences). In contrast, medium-sized predators utilized various food types in smaller proportions from each type (broad trophic niche), which probably allows coexistence. The data also suggest that medium-sized predators might have some adaptation to utilise various proportions of particular food types, for example, various age classes from particular rodent species (Zalewski 1996). This is another way allowing them to coexist in sympatry.

The hump-shape relationship between trophic niche breadth and body mass contradicts previous results from larger scale studies showing increased food niche breadth with body size of many taxa (Rosenzweig 1968; Jarman 1974; Gittleman 1985; Barclay & Brigham 1991; Marti et al. 1993; Novotny & Basset 1999; Brändle et al. 2002). In birds, small species have a narrower trophic niche and larger species tend to have a broader trophic niche (Brändle et al. 2002). In contrast, for lizards a negative relationship was reported (Costa et al. 2008), whereas marine predators showed no relationship between body size and trophic niche breadth (Costa 2009). This contradicts the results of our study and other research, and may have results to the type of diet e.g., herbivorous vs. carnivorous. In herbivorous insects, a positive relationship between body size and trophic niche breadth was reported (Novotny & Basset 1999). Alternatively, it may relate to the availability of different food types for different taxa. The inconsistent pattern in relationship between body size and trophic niche breadth among taxonomic group (mammals,

birds, reptile and insects) may also be a consequence of different physiology (e.g., ectotherm vs. endotherm), locomotion performance or foraging strategies across taxonomic groups. Finally, variation of food categories grouping may affect differences between the studies. In our study, we used functional food type group categories similar to those used in other studies of carnivore diet (McDonald 2002; Lozano et al. 2006; Zhou et al. 2011; Széles et al. 2018).

Trophic niche overlap

Trophic niche overlap decreased non-linearly with increasing pair-wise difference in body mass between predators. Numerous carnivores may occur sympatrically partly due to variation in body size, which affects the differences in trophic niche overlap (Jędrzejewska & Jędrzejewski 1998; Lanszki et al. 2006; Sidorovich 2011). Our analysis suggests a pattern of trophic niche partitioning in predator communities in three regions in Central and Eastern Europe (broader trophic niche in the northernmost region of our study but with lower overlap). Smaller-sized mammals, compared to larger-sized species, may be more vulnerable to local food constraint, especially due to smaller home range size (King 1990). On the other hand, small-sized mustelids, like stoats (especially females) and weasels, can hunt rodents in their underground burrows, which may increase the hunting success of these species (King 1990). Therefore, they can share food resources with medium-sized predators in spite of a high trophic overlap (Jędrzejewska & Jędrzejewski 1998) by having a unique access to prey. Similarly, differences in daily activity patterns between carnivore species can result in food resource partitioning (Gittleman 1985; Marti et al. 1993; Monterroso, Rebelo, Alves, & Ferreras 2016).

Knowledge of interspecific trophic relations among closely related species is important in management and conservation of the carnivore community. For example, very high overlap values (76–83%) within *Felis*, including hybrid wildcat and feral domestic cat, may lead to negative competitive effects on native populations of wildcat (Biró, Lanszki, Szemethy, Heltai, & Randi 2005). There is a low risk of competition between lynx and wildcat in Hungary because of low lynx density and low (29%) trophic niche overlap with wildcat. However, during times of low food abundance or higher density of lynx population, the lynx may suppress the wildcat and other smaller-sized carnivores (Odden et al. 2006; Sidorovich 2011). Similarly, within Canidae, relatively low (<40%) dietary overlap between wolf and medium-sized canids indicates that there should be less competition between wolf and these species. Among canids this may have an effect on occurrence, population size, feeding habits, hunting strategies (solitary, pair or group hunting) and social structure of smaller species. It was observed that when a top predator was eradicated from an area, mesocarnivore release may occur (Crooks & Soulé 1999). However, wolf and golden jackal do not seem to coexist in the same areas, although their ranges

partly overlap in Europe (Kryštufek, Murariu, & Kurtonur 1997). In some cases, this may be due to aggressive behaviour of wolves towards jackals. Their coexistence has not been demonstrated in the DFR studied, which may be due to the limited range of wolf occurrence. Despite the high trophic overlap (75%) between red fox and golden jackal (Lanszki et al. 2006), both species occur sympatrically. During years or seasons of food shortage, these species use different resources, with the smaller and solitary red fox shifting to less profitable food types (e.g., plants). The trophic niche overlap values between the omnivorous brown bear (*Ursus arctos*) and other carnivore species were generally low. Only with other omnivores, i.e. raccoon dog and pine marten, was the trophic overlap higher (>50%). Among them, the competition for food (e.g., plants and invertebrates) may be small. Studies indicate that several carnivores are also able to coexist feeding on similar food resources, when other niche dimensions (e.g., time, space) separate these species (Wereszczuk & Zalewski 2015; Monterroso et al. 2016). Activity in different time of the day reduced chances of interference competition through encounters, although exploitative competition would still be high between closely competing carnivore species.

Differences between regions

The trophic niche breadth increased from south to north, however, only the difference between DFR and TFR was significant. The highest niche breadth may relate to lower food abundance in the north and predators may need to compensate for lower abundance of their main prey by hunting for alternative prey. For example, rodent abundance is related to net productivity of the ground vegetation and rodent abundance is lower in deciduous than in coniferous forest regions (Jędrzejewski & Jędrzejewska 1996). With a decrease in rodent abundance the carnivores need to travel for longer distances per day (Zalewski, Jędrzejewski, & Jędrzejewska 2004) and therefore utilised larger home ranges (e.g., Jędrzejewska & Jędrzejewski 1998; Zalewski & Jędrzejewski 2006), and generally the density of carnivores in northern Europe is lower (Zalewski & Jędrzejewski 2006; Bartoń & Zalewski 2007). Lower niche breadth in the southern region suggests that carnivores there are more specialised on a particular prey type. However, overall trophic niche overlap was the highest in DFR compared with the other two regions. This may imply that in the south more carnivores consumed more often the same group of prey. Indeed, there are more species included in the rodent consumer group from DRF than from the other regions. However, our comparison between regions should be treated with caution as we compared only three sites in Europe.

Overall, our analyses may be biased by a few factors, mainly temporal variation of prey abundance. Rodent abundance especially varied greatly among years (Jędrzejewski & Jędrzejewska 1996; Hanski et al. 2001), which may alter the trophic guilds, niche breadth and niche overlap among pred-

tors in each region. However, most of the studies of predator diets used in our analyses were conducted for few years (3–5 years) and covered years of high and low food abundances. A question, which can be analysed in future studies, is how trophic guilds, niche breadth of predators and niche overlap change in years of high and low abundance of food (especially in the case of small-mammal consumers). Generally, prey abundance (especially rodents) often drives the local density of predators (King 1990; Jędrzejewski, Jędrzejewska, & Szymura 1995; Zalewski & Jędrzejewski 2006; Byrom et al. 2014). Food abundance is related to habitat productivity but also to local agricultural and forestry management practices (e.g., King 1983; Jędrzejewski & Jędrzejewska 1996; Gehring & Swihart 2003; Báldi & Faragó 2007; Melis et al. 2009). Modifications of management techniques can affect the trophic niche and trophic niche overlap which consequently may affect population dynamics and community composition of carnivore species, especially in the case of small-mammal consumers.

Conclusion

This study included almost all terrestrial carnivore species from Central and Eastern Europe and the calculated values of trophic niche breadth of carnivores and the values of trophic niche overlap show potential competitive interactions which are mediated by the body size of predators (Caro & Stoner 2003; Jones & Barmuta 1998). Competition between carnivores is important in shaping species community composition (MacArthur & Levins 1967) and our results suggest that body mass and body mass differences between carnivores are two of the factors shaping trophic niche breadth and trophic niche overlap. The trophic niche breadth tends to increase from the south towards the north of Europe within our study sites, which may imply higher competition in the north, but the overlap was lower, which suggests a wider spectrum of food types in predator diets. Knowledge of potential competition, such as trophic niche overlap among terrestrial carnivores, can be a starting point for a more detailed study of food resource partitioning among carnivore populations, which should consider prey density, habitat change and presence of competitors. Understanding factors that influence carnivore community structures could improve species conservation, reveal the causes of population changes, and provide the basis of sustainable population management.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.baae.2019.06.004>.

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