

GEOGRAPHICAL TRENDS IN TROPHIC CHARACTERISTICS OF MAMMAL-EATING AND BIRD-EATING RAPTORS IN EUROPE AND NORTH AMERICA

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ABSTRACT.—If dietary opportunism occurs in predators over large geographic areas, trends in the trophic characteristics of predators should be explained largely by the distribution patterns of their prey. We compiled literature information of diet for mammal-eating and bird-eating raptors (diurnal raptors [Falconiformes] and owls [Strigiformes]) in Europe and North America (299 and 300 samples, respectively) and asked: (1) Do latitudinal and longitudinal patterns occur in the food-niche breadth, number of prey taxa, and prey size within continents? (2) If so, are these patterns consistent with the intracontinental gradients in species diversity and stability (constancy in time) of birds and mammals? In both Europe and North America, latitudinal and longitudinal trends in trophic diversity of mammal-eating diurnal raptors and owls appeared to be more obvious than those of bird-eating and generalist raptors. This suggests that mammal-eating birds of prey are more opportunistic in their diet choice than are bird eaters and generalists. Within Europe, the latitudinal gradient in dietary diversity of raptors was more evident than the longitudinal gradient, whereas within North America the longitudinal gradient was more conspicuous. For both continents, these gradients were more marked in winter diets than in the breeding-season diets of raptors. These results are consistent with the known regional trends in prey assemblages: in Europe, the south-to-north gradient in diversity and stability of bird and mammal species is more marked than the west-to-east gradient, whereas in North America the number of mammal species markedly increases from east to west, but not so evidently from south to north. Received 6 September 1994, accepted 8 March 1995.

ONE OF THE MOST general patterns of animal species diversity is the increase in the number of terrestrial species from the earth's poles toward its equator (Begon et al. 1986), although a solid explanation of this latitudinal gradient has not been given (see Rohde 1992). This pattern is complicated by the variety of land forms (mountains, deserts), the proximity to the coasts, the season of the year, and the scale used when looking for patterns. The species diversity of European and North American birds generally follows this pattern (for Europe, see Järvinen and Sammalisto 1976, Järvinen 1979, Boström and Nilsson 1983; for North America, see Cook 1969, Tramer 1974, Rabenhold 1979). Among breeding birds, there is also a longitudinal gradient from east to west (Cook 1969). The numbers of quadrupedal mammal species in North America increase from north to south to a peak in diversity at 38°–40°N latitude; from that latitude south, their diversity declines (McCoy and Connor 1980, Pagel et al. 1991). In addition, the number of mammal species per unit area in-

creases from east to west within North America (Pagel et al. 1991).

Stability (constancy in time) of animal populations also varies with latitude so that southern populations are usually more stable in time than northern ones. For instance, southern and central European land-bird assemblages are relatively stable compared to northern European assemblages (Järvinen 1979), but similar trends have not been found for North American land-bird assemblages (Noon et al. 1985). Moreover, in small mammals (voles, mice and shrews) and small game (hare and grouse), large regional differences in among-year population fluctuations occur in Europe. In western and central Europe, small-mammal abundances are usually relatively stable among years, but show seasonal changes, with low densities in spring and high densities in autumn. In central and northern Fennoscandia, however, small-mammal populations fluctuate in a cyclic manner with peaks usually separated by three to five years (Hansson and Henttonen 1985, 1988, Hanski et

al. 1991, 1993). Also, small-game populations oscillate in three- to five-year cycles in central and northern Fennoscandia (Angelstam et al. 1985, Lindén 1988). However, North American voles do not appear to show obvious geographical gradients in their population dynamics; 59% of 106 years of data had annual fluctuations and 41% exhibited multiannual cycles (review in Taitt and Krebs 1985). Snowshoe hare (*Lepus americanus*) populations in the boreal forests of North America display 9- to 11-year cycles; cycles occurred as far south as Wisconsin (40°N; Stuart-Smith 1992). Hare fluctuations are largest in central Canada and decrease in all directions from that region (Bulmer 1974).

A widespread premise is that many raptors (Falconiformes and Strigiformes) are highly opportunistic in the prey they eat (e.g. Jaksić and Braker 1983, Steenhof and Kochert 1985, Marti et al. 1993, but see Korpimäki 1987). If this dietary opportunism holds over large geographic areas, examination of patterns in raptor diets should reflect and largely be explained by the distribution patterns of their prey. Raptors are convenient species for the examination of community patterns involving predator-prey interactions (Jaksić 1985). Most of their prey remains, easily obtainable from pellets and debris at nests and perches, can be identified to the species level (Marti 1987). This allows accurate estimates of the kind, number, and size of prey taken (e.g. Greene and Jaksić 1983, Jaksić 1985). Also, prey chosen by raptors is seldom influenced by the need to minimize the risk of the raptors being preyed upon (Korpimäki 1986). Additionally, many raptors eat largely birds and mammals—two groups relatively well known in terms of their distribution.

Marti et al. (1993) compiled an extensive diet database for European and American raptors (674,905 prey items for Europe and 357,448 for North America). The resulting analysis of the trophic structure of European and North American raptor communities from that database, however, did not reveal obvious intracontinental gradients in food-niche metrics despite the above-described marked intracontinental differences in species diversity and stability of prey communities (Marti et al. 1993). However, the data used for calculating regional niche metrics were collected over many seasons, many years, and at a scale that may have masked most of the effects of changing prey densities.

In this paper, we add new data to the database

of Marti et al. (1993), and focus new analyses on a finer scale. We limited our analyses on geographical trends in trophic characteristics to mammal- and bird-eating raptors of Europe and North America because more is known about the regional trends of species diversity and stability in these animals than about most other prey species. We also separated breeding-season and winter diets to dissect out possible seasonal effects. We asked: (1) Do latitudinal and longitudinal patterns occur in food-niche breadth, number of prey taxa, and prey size of mammal- and bird-eating raptors within Europe and North America? (2) If such patterns are apparent, are they consistent with the above-described intracontinental gradients in species diversity and stability of birds and mammals?

MATERIALS AND METHODS

Source and characteristics of data.—We searched the literature for quantitative data on food habits of falconiforms and strigiforms whose diets consisted primarily of birds and mammals. We also contacted some biologists currently engaged in raptor diet studies for permission to use their unpublished data. From these sources, we selected data sets meeting the following criteria: (1) minimum of 50 identified prey individuals; (2) vertebrate prey identified at least to genus; (3) invertebrate prey identified at least to order; (4) geographic area of data collection well defined; and (5) season(s) and year(s) of data collection stated. We excluded vultures and raptor species eating mostly prey other than mammals and birds (i.e. lizards, frogs, fishes and insects) from our analyses.

We included only those raptor species having at least five dietary studies per continent (20 species in Europe and 23 in North America). We divided these species into three categories based on their degree of food specialization (Table 1): (1) Mammal eaters are those species that feed mainly on (small) mammals and seem to be unable to shift to alternative prey when densities of their primary prey decline. (2) Bird eaters are those that use birds as their staple prey and take (small) mammals in low numbers. (3) Generalists are species that feed mainly on both (small) mammals and birds, and are able to shift their diets between these two prey classes, and sometimes even to lizards, frogs and insects (for further information of division into mammal specialists and generalists among European birds of prey, see Korpimäki 1992b).

Data for our analyses included 299 dietary samples originating in Europe from Great Britain and Iceland on the west to Poland, Slovakia and Kola Peninsula (Russia) on the east (range 17°W to 33.5°E), and from Spain and Italy on the south to Fennoscandia on the north (37°N to 71°N; Table 1, Appendix). North Amer-

TABLE 1. Raptor species included in analyses, range of geographical location, number of dietary studies, and classification of raptor species according to the degree of food specialization. Sources of diet data given in Appendix.

Raptor species	Latitude (N)	Longitude	No. studies	Feeding ^a
North America				
Northern Harrier (<i>Circus cyaneus</i>)	34–50°	65–121°W	10	g
Cooper's Hawk (<i>Accipiter cooperii</i>)	36–49°	74–123°W	8	b
Northern Goshawk (<i>A. gentilis</i>)	36–46°	74–121°W	7	b
Broad-winged Hawk (<i>Buteo platypterus</i>)	39–44°	74–96°W	7	g
Swainson's Hawk (<i>B. swainsoni</i>)	34–51°	98–120°W	8	g
Red-tailed Hawk (<i>B. jamaicensis</i>)	37–51°	74–121°W	17	m
Ferruginous Hawk (<i>B. regalis</i>)	41–51°	100–116°W	7	m
Rough-legged Hawk (<i>B. lagopus</i>)	42–69°	84–165°W	6	m
Golden Eagle (<i>Aquila chrysaetos</i>)	33–50°	106–120°W	10	g
American Kestrel (<i>Falco sparverius</i>)	41–47°	77–124°W	9	g
Merlin (<i>F. columbarius</i>)	38–63°	106–151°W	6	b
Peregrine Falcon (<i>F. peregrinus</i>)	41–69°	75–180°W	10	b
Gyr Falcon (<i>F. rusticolus</i>)	66–69°	106–165°W	5	b
Prairie Falcon (<i>F. mexicanus</i>)	41–44°	106–116°W	5	m
Barn Owl (<i>Tyto alba</i>)	19–49°	73–124°W	40	m
Great Horned Owl (<i>Bubo virginianus</i>)	24–66°	74–141°W	32	g
Snowy Owl (<i>Nyctea scandiaca</i>)	43–68°	71–167°W	8	m
Burrowing Owl (<i>Speotyto cunicularia</i>)	28–47°	82–122°W	16	g
Spotted Owl (<i>Strix occidentalis</i>)	32–48°	110–124°W	9	m
Barred Owl (<i>S. varia</i>)	40–48°	74–123°W	8	m
Long-eared Owl (<i>Asio otus</i>)	32–49°	70–124°W	34	m
Short-eared Owl (<i>A. flammeus</i>)	32–57°	47–132°W	19	m
Northern Saw-whet Owl (<i>Aegolius acadicus</i>)	39–62°	70–150°W	10	m
Europe				
Eurasian Kestrel (<i>Falco tinnunculus</i>)	38–65°	7°W–25°E	16	m
Peregrine Falcon	38–68°	7°W–26°E	15	b
Merlin	52–66°	17°W–24°E	7	b
Northern Goshawk	41–65°	5°W–25°E	19	b
Sparrowhawk (<i>Accipiter nisus</i>)	51–62°	4°W–23°E	10	b
Golden Eagle	38–67°	5°W–26°E	12	g
Common Buzzard (<i>Buteo buteo</i>)	37–65°	6°W–25°E	16	g
Marsh Harrier (<i>Circus aeruginosus</i>)	43–62°	1°W–23°E	7	g
Northern Harrier	53–62°	4°W–10°E	6	g
Short-eared Owl	47–65°	3°W–26°E	15	m
Long-eared Owl	39–63°	7°W–27°E	28	m
Barn Owl	38–57°	7°W–20°E	23	m
Tengmalm's Owl (<i>Aegolius funereus</i>)	46–66°	5–30°E	22	m
Little Owl (<i>Athene noctua</i>)	37–57°	7°W–13°E	12	g
Pygmy Owl (<i>Glaucidium passerinum</i>)	48–65°	8–28°E	14	g
Eurasian Eagle-Owl (<i>Bubo bubo</i>)	38–67°	5°W–29°E	30	g
Tawny Owl (<i>Strix aluco</i>)	41–63°	4°W–27°E	20	g
Ural Owl (<i>S. uralensis</i>)	53–65°	10–27°E	8	g
Great Grey Owl (<i>S. nebulosa</i>)	61–69°	21–34°E	9	m
Northern Hawk Owl (<i>Surnia ulula</i>)	61–71°	10–31°E	10	m

^a (m) Mammal eater; (b) bird eater; and (g) generalist.

ican data came from 300 samples in Canada, Alaska, the conterminous United States, and Mexico (47° to 180°W, 19° to 69°N; Table 1, Appendix).

Analytical techniques.—Three primary estimators of trophic characteristics were applied to the diet samples we selected: (1) The number of prey types in

diets were enumerated at two levels of discrimination. Coarse discrimination (hereafter, number of prey classes), where prey categories were taxonomic classes of prey, was used as one measure of the ability of raptors to handle diverse kinds of prey. Fine discrimination (hereafter, number of prey species), where prey

TABLE 2. Spearman rank correlations between trophic characteristics of mammal-eating, bird-eating and generalist raptors (see Table 1 for classification of species), and latitude and longitude within Europe and North America.

Diet class	No. prey		FNB _{cl}	FNB _{sp}	Mean prey mass
	Classes	Species			
Europe					
Mammal eaters (<i>n</i> = 123 studies)					
Latitude	-0.26**	-0.24**	-0.20*	-0.14	0.33***
Longitude	-0.34***	-0.29**	-0.30**	-0.24**	0.38***
Bird eaters (<i>n</i> = 51)					
Latitude	-0.12	-0.18	-0.13	0.08	0.22
Longitude	-0.04	-0.11	0.05	0.21	0.14
Generalists (<i>n</i> = 125)					
Latitude	-0.18*	0.20*	0.02	0.24**	0.03
Longitude	-0.16	0.16	-0.04	0.18	0.07
North America					
Mammal eaters (<i>n</i> = 163)					
Latitude	-0.09	-0.12	0.03	-0.14	0.08
Longitude	0.15	0.18*	0.15	0.29***	0.05
Bird eaters (<i>n</i> = 36)					
Latitude	-0.42*	-0.13	-0.30	-0.29	0.05
Longitude	-0.21	0.10	-0.34*	-0.03	0.09
Generalists (<i>n</i> = 92)					
Latitude	0.06	0.01	-0.06	-0.17	0.02
Longitude	0.22*	0.06	-0.04	-0.09	-0.09

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; two-tailed tests.

categories were species or genus for vertebrate prey and order for invertebrate prey, was employed as a means of providing higher resolution between diets.

(2) Food-niche breadth was estimated with an index that assesses both the number of prey types and their evenness in a sample ($1/\Sigma p_i^2$; Levins 1968). As in the enumeration of dietary prey types, we calculated this index at two levels. The coarse level (FNB_{cl}), where the p_i 's are the taxonomic classes of prey, provides an indication of a raptor's relative ability to handle prey providing different problems in detection, capture, and handling (Greene and Jaksic 1983). A predator with a large FNB_{cl} is able to handle many kinds of prey that present a diversity of such problems. The fine level (FNB_{sp}), where the p_i 's are species or genera for vertebrate prey and orders for invertebrate prey, permits a different evaluation of a raptor's dietary diversity independent of the factors associated with FNB_{cl}. That is, a raptor may have a narrow FNB_{cl}, but a wide FNB_{sp}, because it preys on many species within one or two prey classes.

(3) The size of prey was characterized by calculating the geometric mean mass of prey (mean prey mass) consumed in a diet sample by multiplying the log_e-transformed mean mass of each prey type by the number of that prey in the sample, summing these products, dividing by the total number of prey, and back-transforming this sum. This procedure partially com-

pensates for the skewed distribution of prey sizes in most raptor's diets and for the possibility of over or underestimating the mean mass of prey in a diet from using mean masses for each prey type. We used prey mass data if they were provided in individual studies that we selected for our analyses. For studies that did not provide such data, we used mean prey masses from Steenhof (1983), Burt and Grossenheider (1964), and Dunning (1984) for North America, and from Haensel and Walther (1966), Itämies and Korpimäki (1987), Siivonen (1974), Korpimäki (1981), Glutz von Blotzheim and Bauer (1980), and Häkkinen (1978) for Europe.

Statistical analyses were performed using the SYSTAT statistical package (Wilkinson 1989). All statistical tests were one-tailed unless otherwise noted.

RESULTS

Europe.—The number of prey classes and species, FNB_{cl} and FNB_{sp} of mammal-eating raptors were significantly negatively correlated with latitude and longitude (except FNB_{sp} and latitude). Conversely, the mean prey mass was significantly positively related to latitude and longitude (Table 2). In multiple-regression analyses, however, geographical trends in dietary

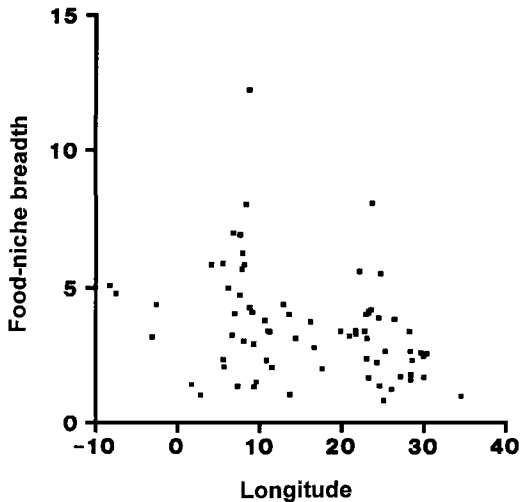


Fig. 1. Food-niche breadth at species level of discrimination of European mammal-eating raptors in breeding season plotted against longitude (e.g. $-10 = 10^{\circ}\text{W}$, $10 = 10^{\circ}\text{E}$, etc.) of study site ($r_s = -0.37$, $n = 73$, $P < 0.01$).

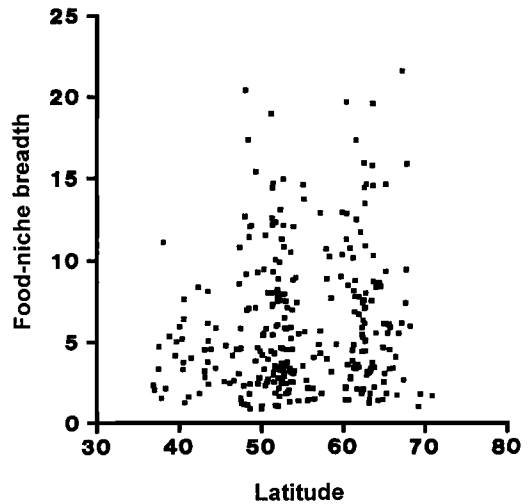


Fig. 2. Food-niche breadth at species level of discrimination of European generalist raptors plotted against latitude ($^{\circ}\text{N}$) of study site ($r_s = 0.24$, $n = 123$, $P < 0.01$).

characters of mammal-eating raptors were weak: no significant relationships were found in the data pooled from all seasons. In multiple-regression analyses using data from the breeding season only, FNB_{cl} significantly decreased toward the north ($t = 1.69$, $P = 0.043$), but not toward the east ($t = 0.42$, $P = 0.34$; model $r^2 = 0.14$). The longitudinal decline also was significant for the number of prey species ($t = 1.86$, $P = 0.034$) and FNB_{sp} ($t = 1.90$, $P = 0.031$; see also Fig. 1), whereas the latitudinal trend was not (number of prey species, $t = 0.96$, $P = 0.34$; FNB_{sp} , $t = 0.28$, $P = 0.39$; model $r^2 = 0.06$ and 0.10 , respectively).

No obvious geographical trends were found in the trophic traits of European bird-eating raptors (Table 2). In generalist species, the number of prey classes decreased, but the number of prey species and FNB_{sp} increased from south to north but not from west to east (Table 2). Multiple regression revealed that FNB_{sp} was significantly explained by latitude (Fig. 2; $t = 2.09$, $P = 0.02$), but not by longitude ($t = 0.38$, $P = 0.36$; model $r^2 = 0.05$).

The number of prey species and FNB_{sp} of European diurnal raptors increased toward the north and east, whereas the number of prey classes and FNB_{cl} decreased northward (Table 3). Mean prey mass was not significantly related

to geographical location. Multiple-regression analyses revealed that the increasing latitudinal trend in FNB_{sp} ($t = 2.54$, $P = 0.007$) and the decreasing latitudinal trend in FNB_{cl} were significant ($t = 2.23$, $P = 0.014$), whereas longitudinal trends were not (FNB_{sp} , $t = 1.03$, $P = 0.16$; FNB_{cl} , $t = 1.21$, $P = 0.12$; model $r^2 = 0.06$ and 0.12 , respectively).

In European owls, the number of prey classes and prey species declined to the north and east, and FNB_{cl} to the east (Table 3). Owls also killed larger prey items in the north and east than in the south and west. Multiple-regression analyses using the data from all seasons found that only the declining FNB_{cl} along a longitudinal gradient was significant (latitude, $t = 1.10$, $P = 0.27$; longitude, $t = 1.96$, $P = 0.026$; model $r^2 = 0.02$). Data from the breeding season produced clearer trends: the decrease in FNB_{sp} was significantly explained by longitude ($t = 1.74$, $P = 0.042$), but not by latitude ($t = 0.07$, $P = 0.48$; model $r^2 = 0.07$), and the drop in the number of prey species by longitude ($t = 1.74$, $P = 0.042$), but not by latitude ($t = 0.07$, $P = 0.48$; model $r^2 = 0.07$).

Individual European raptor species showed few significant geographical trends in the trophic estimates. The number of prey classes decreased toward the north in the Merlin (*Falco columbarius*), and toward the east in the Com-

TABLE 3. Spearman rank correlations between trophic characteristics of diurnal raptors and owls, and latitude and longitude within Europe and North America.

Diet class	No. prey		FNB _{cl}	FNB _{sp}	Mean prey mass
	Classes	Species			
Europe					
Diurnal raptors (<i>n</i> = 108 studies)					
Latitude	-0.23*	0.26**	-0.22*	0.30**	0.15
Longitude	-0.10	0.20*	-0.04	0.31**	0.18
Owls (<i>n</i> = 191)					
Latitude	-0.22**	-0.15*	-0.09	-0.03	0.25***
Longitude	-0.27***	-0.20**	-0.15*	-0.09	0.28***
North America					
Diurnal raptors (<i>n</i> = 115)					
Latitude	-0.32***	-0.01	-0.21*	-0.14	0.07
Longitude	-0.15	0.22*	-0.17	-0.02	0.22*
Owls (<i>n</i> = 176)					
Latitude	-0.05	-0.10	-0.06	-0.19*	-0.05
Longitude	0.24**	0.12	0.16*	0.26***	-0.12

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001; two-tailed tests.

mon Buzzard (*Buteo buteo*) and the Northern Hawk Owl (*Surnia ulula*), whereas the number of prey classes increased toward the north in the Northern Harrier (*Circus cyaneus*; Table 4). Northern Goshawks (*Accipiter gentilis*) and Golden Eagles (*Aquila chrysaetos*) took a larger number of prey species in the north than in the south and, in addition, Golden Eagles killed more prey species in the east than in the west. The opposite longitudinal trend was evident for the number of prey species of Eurasian Eagle-Owls (*Bubo bubo*). FNB_{cl} of the Barn Owl (*Tyto alba*) decreased with latitude and that of the Short-eared Owl (*Asio flammeus*) and the Northern Hawk Owl with longitude. FNB_{sp} of Eurasian Kestrels (*Falco tinnunculus*) and Golden Eagles increased toward the north, and also toward the east. FNB_{sp} of Tengmalm's Owls (*Aegolius funereus*) decreased toward the east. Golden Eagles and Long-eared Owls (*Asio otus*) killed larger prey items in the north than in the south, whereas the opposite was true for Eurasian Eagle-Owls. Barn Owls, Tawny Owls (*Strix aluco*), and Ural Owls (*S. uralensis*) captured smaller prey in the west than in the east, whereas Eurasian Eagle-Owls showed the opposite longitudinal trend. Using only breeding season diet or winter diet, only slightly changed the geographical trends described above. In data from the breeding season, the number of prey species of the Eurasian Kestrel significantly increased with latitude (*r_s* = 0.71, *n* = 9, *P* < 0.05) and

FNB_{sp} of the Northern Goshawk expanded with longitude (*r_s* = 0.59, *n* = 14, *P* < 0.05).

North America.—The number of prey species and FNB_{sp} of mammal-eating raptors increased with longitude (Figs. 3 and 4) but not with latitude (Table 2). Also, multiple regression of the number of prey species and FNB_{sp} on latitude and longitude revealed that the increasing trends were significantly explained by longitude (number of prey species, *t* = 2.20, *P* = 0.015;

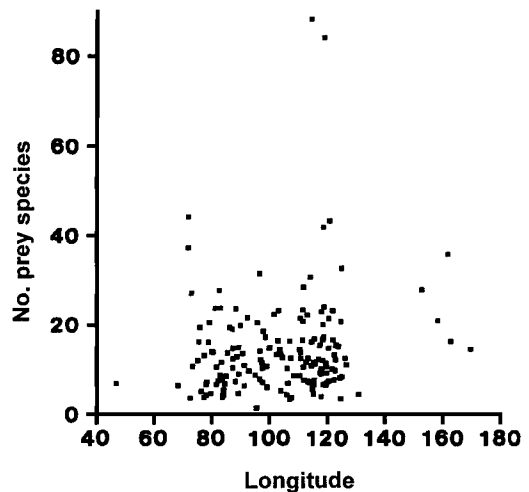


Fig. 3. Number of prey species in diet of North American mammal-eating raptors plotted against longitude (°W) of study site (*r_s* = 0.18, *n* = 163, *P* < 0.05).

TABLE 4. Spearman rank correlations between latitude and longitude, and trophic characteristics of European raptors.

	No. prey		FNB _{cl}	FNB _{sp}	Mean prey mass
	Classes	Species			
Eurasian Kestrel (n = 16 studies)					
Latitude	0.23	0.19	0.27	0.55*	-0.07
Longitude	0.05	-0.01	0.37	0.51*	0.22
Peregrine Falcon (n = 15)					
Latitude	0.34	-0.17	0.34	0.12	0.49
Longitude	0.19	-0.25	0.19	-0.07	0.22
Merlin (n = 7)					
Latitude	-0.80*	-0.74	-0.27	-0.22	0.22
Longitude	-0.51	-0.35	-0.58	0.22	-0.32
Northern Goshawk (n = 19)					
Latitude	-0.12	0.46*	-0.27	0.44	0.40
Longitude	0.09	0.14	-0.17	0.45	-0.15
Sparrowhawk (n = 10)					
Latitude	0.48	-0.47	0.55	0.17	0.26
Longitude	-0.06	-0.29	0.31	0.23	-0.29
Golden Eagle (n = 12)					
Latitude	0.01	0.82**	-0.21	0.65*	0.65*
Longitude	-0.03	0.71*	-0.28	0.63*	0.51
Common Buzzard (n = 16)					
Latitude	-0.48	0.07	0.07	0.33	0.18
Longitude	-0.59*	-0.04	-0.07	0.36	0.30
Marsh Harrier (n = 7)					
Latitude	0.01	0.70	-0.05	0.32	-0.16
Longitude	0.32	0.13	0.29	0.32	-0.39
Northern Harrier (n = 6)					
Latitude	0.12	0.14	0.26	-0.03	-0.03
Longitude	0.91*	0.64	0.20	0.17	-0.29
Short-eared Owl (n = 15)					
Latitude	-0.04	0.05	0.03	0.44	0.02
Longitude	-0.29	-0.26	-0.53*	-0.07	0.04
Long-eared Owl (n = 28)					
Latitude	-0.05	-0.06	-0.04	0.02	0.47*
Longitude	-0.05	-0.21	-0.29	-0.08	0.32
Barn Owl (n = 23)					
Latitude	-0.34	-0.01	-0.43*	-0.31	0.14
Longitude	-0.27	0.05	0.08	-0.35	0.65**
Tengmalm's Owl (n = 22)					
Latitude	-0.03	-0.01	0.37	-0.36	0.16
Longitude	-0.23	-0.16	0.38	-0.60**	0.04
Little Owl (n = 12)					
Latitude	0.06	0.18	0.44	-0.33	0.43
Longitude	0.44	0.44	-0.00	0.11	0.06
Pygmy Owl (n = 14)					
Latitude	0.36	-0.39	0.11	-0.41	-0.31
Longitude	0.48	-0.20	0.07	-0.25	0.21
Eurasian Eagle-Owl (n = 30)					
Latitude	-0.14	-0.18	0.11	0.10	-0.39*
Longitude	-0.12	-0.38*	-0.02	-0.12	-0.37*

TABLE 4. Continued.

	No. prey		FNB _{cl}	FNB _{sp}	Mean prey mass
	Classes	Species			
Tawny Owl (n = 20)					
Latitude	-0.03	-0.32	-0.09	0.11	0.23
Longitude	-0.26	-0.25	-0.15	0.06	0.65**
Ural Owl (n = 8)					
Latitude	-0.65	0.36	-0.16	0.12	0.28
Longitude	-0.24	0.41	0.12	0.07	0.76*
Great Grey Owl (n = 9)					
Latitude	0.42	0.06	0.34	-0.14	0.41
Longitude	-0.18	-0.62	0.16	-0.35	0.37
Northern Hawk Owl (n = 10)					
Latitude	0.04	0.21	0.08	0.25	0.33
Longitude	-0.72*	-0.28	-0.69*	-0.13	0.30

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; two-tailed tests.

FNB_{sp}, $t = 1.71$, $P = 0.045$), but not by latitude (number of prey species, $t = 0.76$, $P = 0.23$; FNB_{sp}, $t = 0.84$, $P = 0.20$; model $r^2 = 0.03$ and 0.02 , respectively). Because the species number of North American quadrupedal mammals decreases northward above 38-40°N (McCoy and Connor 1980, Pagel et al. 1991), we also removed diet data collected below 40°N, but this did not enhance latitudinal trends. Using only data from the winter produced a significant regression of FNB_{sp} on both latitude ($t = 2.16$, $P = 0.018$) and longitude ($t = 1.85$, $P = 0.036$;

model $r^2 = 0.12$); FNB_{sp} declined toward the north, but expanded toward the west (Fig. 5).

The number of prey classes of North American bird-eating raptors decreased with latitude and FNP_{cl} with longitude (Table 2). Multiple regression of the number of prey species on latitude and longitude produced significant relationships for both independent variables: the number of prey species diminished northward ($t = 1.73$, $P = 0.047$) and increased westward ($t = 1.77$, $P = 0.044$; model $r^2 = 0.11$). The number of prey classes of generalists was positively as-

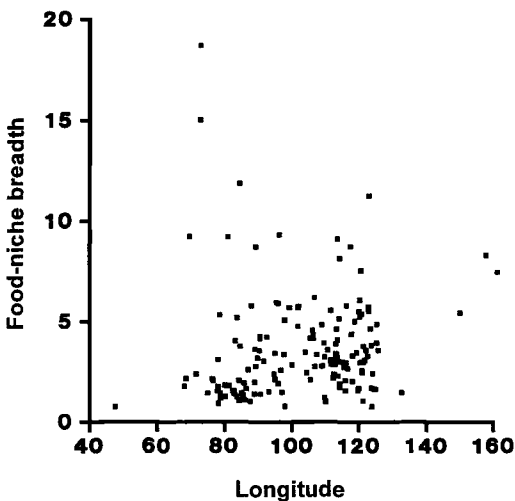


Fig. 4. Food-niche breadth at species level of discrimination of North American mammal-eating raptors plotted against longitude (°W) of study site ($r_s = 0.29$, $n = 163$, $P < 0.001$).

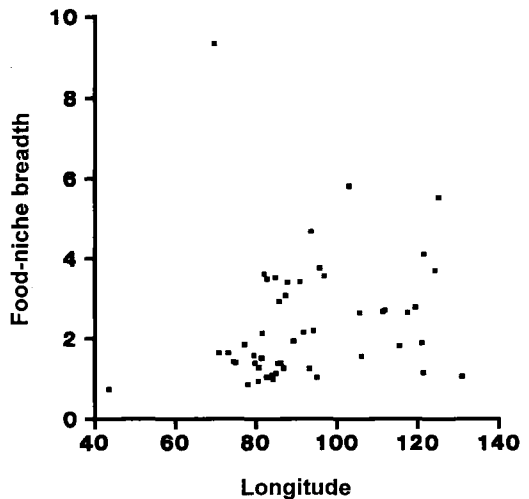


Fig. 5. Food-niche breadth at species level of discrimination of North American mammal-eating raptors in winter plotted against longitude (°W) of study site ($r_s = 0.42$, $n = 50$, $P < 0.01$).

TABLE 5. Spearman rank correlations between latitude and longitude, and trophic characteristics of North American raptors.

	No. prey		FNB _{cl}	FNB _{sp}	Mean prey mass
	Classes	Species			
Northern Harrier (n = 10)					
Latitude	0.52	-0.01	0.57	-0.22	0.15
Longitude	0.60	0.85**	0.53	0.77*	0.62
Cooper's Hawk (n = 8)					
Latitude	-0.44	-0.10	-0.02	0.20	-0.35
Longitude	0.11	0.17	-0.05	0.19	-0.60
Northern Goshawk (n = 7)					
Latitude	-0.10	0.14	0.44	0.23	-0.07
Longitude	-0.20	0.04	0.18	0.32	-0.57
Broad-winged Hawk (n = 7)					
Latitude	-0.07	-0.36	-0.27	-0.27	-0.27
Longitude	0.20	-0.41	-0.02	-0.41	-0.27
Swainson's Hawk (n = 8)					
Latitude	0.00	-0.10	-0.63	-0.81*	0.95**
Longitude	0.48	0.79*	-0.07	-0.31	0.23
Red-tailed Hawk (n = 17)					
Latitude	-0.33	-0.36	-0.01	-0.29	0.32
Longitude	0.21	0.06	0.36	-0.18	0.39
Ferruginous Hawk (n = 7)					
Latitude	-0.20	-0.25	-0.09	-0.75	-0.21
Longitude	0.19	0.29	-0.13	0.21	0.04
Rough-legged Hawk (n = 6)					
Latitude	-0.43	0.97*	0.71	0.97*	0.44
Longitude	-0.42	0.81	0.81	0.81	0.41
Golden Eagle (n = 10)					
Latitude	-0.02	0.11	0.54	-0.05	-0.29
Longitude	0.46	0.65*	0.50	0.21	0.37
American Kestrel (n = 9)					
Latitude	0.06	0.07	-0.09	-0.03	-0.09
Longitude	0.08	-0.26	-0.23	-0.28	-0.34
Merlin (n = 6)					
Latitude	-0.88*	0.46	-0.64	-0.06	-0.67
Longitude	-0.34	0.16	-0.58	0.23	-0.03
Peregrine Falcon (n = 10)					
Latitude	0.26	0.25	0.51	0.29	-0.39
Longitude	0.26	0.61	0.02	0.51	0.22
Gyr Falcon (n = 5)					
Latitude	—	-0.89	-0.22	0.22	0.22
Longitude	—	0.22	-0.22	0.22	0.22
Prairie Falcon (n = 5)					
Latitude	0.35	-0.10	-0.10	-0.80	0.10
Longitude	0.71	0.70	-0.30	0.10	0.30
Barn Owl (n = 40)					
Latitude	-0.02	-0.05	-0.31	-0.50**	-0.36*
Longitude	0.26	-0.08	-0.02	0.13	-0.33*
Great Horned Owl (n = 32)					
Latitude	0.11	0.17	-0.14	-0.20	0.02
Longitude	0.50**	-0.11	0.00	-0.11	-0.40*

TABLE 5. Continued.

	No. prey		FNB _{cl}	FNB _{sp}	Mean prey mass
	Classes	Species			
Snowy Owl (n = 8)					
Latitude	-0.06	-0.29	-0.31	-0.32	-0.26
Longitude	-0.51	0.22	-0.50	0.23	0.07
Burrowing Owl (n = 16)					
Latitude	-0.21	-0.14	-0.05	0.06	-0.14
Longitude	-0.09	-0.11	0.57*	0.50	0.37
Spotted Owl (n = 9)					
Latitude	-0.09	0.23	-0.13	0.14	0.10
Longitude	-0.14	0.33	0.13	0.30	-0.26
Barred Owl (n = 8)					
Latitude	-0.19	-0.28	-0.65	-0.32	0.73
Longitude	-0.22	-0.28	-0.65	-0.31	0.79*
Long-eared Owl (n = 34)					
Latitude	-0.11	-0.19	0.01	-0.16	0.33
Longitude	0.31	0.36*	0.12	0.59**	-0.42*
Short-eared Owl (n = 19)					
Latitude	0.02	-0.45	-0.25	-0.42	0.39
Longitude	0.35	0.10	0.40	0.26	-0.08
Northern Saw-whet Owl (n = 10)					
Latitude	0.12	0.62	0.45	0.13	-0.35
Longitude	0.44	0.69*	0.72*	0.52	-0.54

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; two-tailed tests.

sociated with longitude (Table 2). A declining trend in the FNB_{sp} of generalists was also significantly related to longitude ($t = 2.09$, $P = 0.02$), but not to latitude ($t = 0.95$, $P = 0.17$; model $r^2 = 0.06$). FNB_{sp} of generalists in winter was negatively related to both latitude ($t = 2.06$, $P = 0.025$) and longitude ($t = 3.24$, $P = 0.002$; model $r^2 = 0.39$). In eastern North America, the species diversity of birds in summer exhibits a plateau between 25° and 45°N (Tramer 1974); therefore, we analyzed the trophic characters of bird-eating and generalist raptors above 44°N, but this did not affect the results.

The number of prey classes of North American diurnal raptors was larger in the south than in the north, and the number of prey species was larger in the west than in the east (Table 3). FNB_{cl} correlated significantly negatively with latitude and mean prey mass positively with longitude. The geographic trends in the number of prey species and mean prey mass also held in multiple-regression analyses: the relationships were explained by longitude (number of prey species, $t = 2.36$, $P = 0.01$; mean prey

mass, $t = 2.57$, $P = 0.006$), but not by latitude (number of prey species, $t = 1.08$, $P = 0.14$; mean prey mass, $t = 1.66$, $P = 0.05$; model $r^2 = 0.05$ and 0.06 , respectively).

The number of prey classes, FNB_{cl}, and FNB_{sp} of North American owls were larger in the west than in the east (Table 3). FNB_{sp} also declined toward the north. Multiple-regression analysis showed that latitude explained the decreasing trend of FNB_{sp} better ($t = 1.98$, $P = 0.025$) than longitude explained the increasing trend ($t = 1.57$, $P = 0.059$; model $r^2 = 0.03$, $n = 176$). The number of prey species was significantly negatively associated with latitude for the winter diet data ($t = 2.19$, $P = 0.017$), but not with longitude ($t = 1.16$, $P = 0.13$; model $r^2 = 0.10$, $n = 48$).

Few North American raptor species showed significant geographical trends in the trophic estimates. The number of prey species decreased toward the north in the Merlin, and increased toward the east in the Great Horned Owl (*Bubo virginianus*; Table 5). The number of prey species increased with latitude in the

Rough-legged Hawk (*Buteo lagopus*) and with longitude in the Northern Harrier, Swainson's Hawk (*B. swainsoni*), Golden Eagle, Long-eared Owl, and Northern Saw-whet Owl (*Aegolius acadicus*). FNB_{cl} of Burrowing Owls (*Speotyto cunicularia*) and Northern Saw-whet Owls increased toward the west. FNB_{sp} of the Swainson's Hawk and the Barn Owl declined, and that of the Rough-legged Hawk increased northward. FNB_{sp} of the Northern Harrier and the Long-eared Owl increased westward. Swainson's Hawks took larger prey in the north than in the south, whereas the opposite was true for the Barn Owl. Barn Owls, Great Horned Owls and Long-eared Owls killed smaller prey, and Barred Owls (*Strix varia*) larger prey in the west than in the east.

When we restricted the species-level analyses to breeding-season or winter diet data only, the geographical trends described above changed somewhat. The number of prey species in the Peregrine Falcon's breeding-season diet increased with longitude ($r_s = 0.69$, $n = 9$, $P < 0.05$). For winter diets, the number of prey classes and species, FNB_{cl} , FNB_{sp} and mean prey mass of Short-eared Owls decreased northward ($r_s = -0.53$, -0.65 , -0.59 , -0.53 , respectively; $n = 15$, all $P < 0.05$), whereas mean prey mass increased northward ($r_s = 0.66$, $n = 15$, $P < 0.05$). The number of prey classes ($r_s = -0.52$, $P < 0.05$), the number of prey species ($r_s = -0.74$, $P < 0.01$), FNB_{cl} ($r_s = -0.53$, $P < 0.05$), FNB_{sp} ($r_s = -0.89$, $P < 0.001$) and mean prey mass ($r_s = 0.58$, $P < 0.05$) of Long-eared Owls showed similar relationships, but FNB_{sp} ($r_s = 0.53$, $P < 0.05$) was also positively and mean prey mass ($r_s = -0.59$, $P < 0.05$) negatively correlated with longitude ($n = 17$ in each case).

DISCUSSION

Intra-European trends.—The number of prey species and food niche breadth of European mammal-eating raptors declined northward and eastward, whereas the corresponding trophic estimates of generalist raptors increased northward. The decreasing latitudinal trend found for mammal-eating raptors coincides with the fact that populations of small mammals and small game become more cyclic northward (see Introduction). During population peaks, raptors concentrate their feeding on these abundant food supplies, but when rodent populations crash, raptors disperse over long distances to search for areas of vole abundance (e.g. Kor-

pimäki and Norrdahl 1991, Korpimäki 1992a,b). This response probably reduces their dietary diversity. In the south, abundant rodent supplies do not exist, and raptors have to capture all the available small- and medium-sized mammals (Goszczyński 1977, Erlinge et al. 1983, Korpimäki 1992b), thus creating wider dietary diversity. Generalist raptors, instead, take large numbers of small rodents in years when they are abundant, but stay in the same areas and shift to alternative food sources when rodent populations crash (e.g. Saurola 1987, Korpimäki et al. 1990, Korpimäki 1992b). This may induce an increasing latitudinal trend in their food niche estimates. The prey size of mammal-eating raptors increased northward, possibly because the body size of warm-blooded animals is larger in colder climates (Bergmann 1847, but also see Erlinge 1987). There were no obvious geographic gradients in the dietary estimates of bird-eating raptors, an observation that does not parallel the declining species diversity pattern of birds toward the north in Europe.

In the number of prey classes, diurnal raptors and owls showed analogous geographical patterns in dietary diversity. The decreasing latitudinal trend is probably attributable to the declining number of cold-blooded animals in the same direction. At the species level, however, the trophic diversity of diurnal raptors and owls showed different south-to-north trends. The reasons may be the same that were proposed to explain the different trends in mammal-eating and generalist raptors (see above). Owls took larger prey items in the north and east than in the south and west, but diurnal raptors did not. One reason may be that owls eat mainly mammals, and the body size of mammals increases toward the north (see above).

European raptors fell into the following categories with respect to the geographical trends in trophic diversity: (1) at the class level, decreasing trends northward (Merlin and Barn Owl) or eastward (Common Buzzard, Short-eared Owl, and Northern Hawk Owl); (2) at the class level, increasing trend toward the east (Northern Harrier); (3) at the species level, decreasing trends eastward (Eurasian Eagle-Owl and Tengmalm's Owl); (4) at the species level, increasing trends toward the north (Eurasian Kestrel), or toward both north and east (Northern Goshawk and Golden Eagle); and (5) no consistent geographical trend—the remaining species. Our results deviate somewhat from those obtained by Marti et al. (1993), who com-

pared the trophic diversity of European raptors in five assemblages. In the present study, we used the exact geographical locations of the study sites unlike the large geographical regions used by Marti et al. (1993; Mediterranean area, western Europe, eastern Europe, central Fennoscandia, and northern Fennoscandia). Our species-level analysis removed what had appeared to be an increasing latitudinal trend in FNB_{sp} for the Merlin, the Sparrowhawk, the Common Buzzard, and the Tawny Owl, as well as a decreasing FNB_{sp} for the Ural Owl and Pygmy Owl (Marti et al. 1993). Our new analysis revealed different trends for the Northern Goshawk and the Golden Eagle.

Trends within North America.—The number of prey species and FNB_{sp} of mammal-eating raptors increased from east to west, which is consistent with the increasing number of mammals per unit area farther west (Pagel et al. 1991). In winter, FNB_{sp} also declined from south to north, in agreement with the decreasing number of North American quadrupedal mammals above 38–40°N (McCoy and Connor 1980, Pagel et al. 1991).

In bird-eating raptors, the number of prey species diminished northward and increased westward, which parallels the geographical trends in the number of bird species (see Introduction). FNB_{sp} of generalist raptors decreased from east to west and, in winter, also from south to north. The latitudinal trend is consistent with that in the species diversity of birds, especially in that of wintering birds, whereas the longitudinal trend is opposite to that in the bird species diversity.

The number of prey species of diurnal raptors was larger in the west than in the east. The same trend also held for the number of prey species and FNB_{sp} of owls, but FNB_{sp} also decreased from south to north. In winter, the number of prey species of owls was negatively associated with latitude but not with longitude. These trends are in agreement with those in the species diversity of mammals and birds.

North American raptors can be categorized into the following groups with respect to the geographical trends in trophic diversity: (1) at the class level, decreasing trends toward the north (Merlin, Long-eared Owl, Short-eared Owl; only in winter data for the two owl species) or east (Northern Saw-whet Owl and Burrowing Owl); (2) at the class level, increasing trend toward the east (Great Horned Owl); (3) at the species level, declining trends toward the

north (Swainson's Hawk, Barn Owl, Long-eared Owl, and Short-eared Owl; only in winter data for last two owl species) or east (Northern Harrier and Long-eared Owl); (4) at the species level, increasing trends toward the north (Rough-legged Hawk), or east (Golden Eagle, Swainson's Hawk, Northern Harrier, Northern Saw-whet Owl, Long-eared Owl, and Peregrine Falcon; only in breeding-season data); and (5) no consistent geographical trend—the remaining species.

Our results for North America deviated somewhat from those reported by Marti et al. (1993), who compared the trophic diversity of North American raptors in five regions (Alaska-Canada, western North America, midcentral North America, eastcentral North America and southeastern United States). The more precise geographic locations of study sites used in the present analysis did not confirm the increasing latitudinal trend in FNB_{sp} of the Short-eared Owl nor the opposite trend in FNB_{sp} of the Merlin and the Peregrine Falcon. In addition, the increasing trend of FNB_{sp} from east to west for the Cooper's Hawk, Northern Goshawk, Red-tailed Hawk, Ferruginous Hawk, Peregrine Falcon, Prairie Falcon, Barn Owl, Great Horned Owl, Snowy Owl, Barred Owl, and Short-eared Owl, and the declining of FNB_{sp} of the Broad-winged Hawk and American Kestrel were not found at the finer geographic resolution used in this study.

CONCLUDING REMARKS

If dietary opportunism of predators holds over large geographic areas, trends of raptor trophic characteristics should be explained largely by the distribution patterns of their prey. In both Europe and North America, latitudinal and longitudinal trends in trophic diversity of mammal-eating diurnal raptors and owls were more obvious than those of bird-eating and generalist raptors. This suggests that mammal-eating raptors are more opportunistic in their diet choice than bird eaters and generalists. Also, a widespread premise is that raptors feeding mainly on mammals, especially on small rodents, are opportunistic predators and show high dietary overlaps (e.g. Jaksic and Braker 1983, Marks and Marti 1984, Steenhof and Kochert 1985; but see Nilsson 1984, Korpimäki 1987) because they usually concentrate predation on one or two abundant prey species. In contrast, bird-eating raptors typically show low dietary overlap and

clear morphological separation (e.g. Opdam 1975, Reynolds and Meslow 1984, Schoener 1984). However, geographic trends in trophic diversity of both European and North American mammal-eating raptors were usually not very evident, because in multiple-regression analyses the geographical location of the study site only explained a small part (maximum < 15%) of the variation in trophic characteristics. This suggests that diet composition of those species cannot be interpreted in terms of simple opportunistic foraging without implicating other explaining factors, such as interspecific competition, which may alter the diet composition at the individual level among species pairs undergoing competition (e.g. Korpimäki 1987).

Within Europe, the latitudinal gradient in dietary diversity of raptors was more evident than the longitudinal gradient, whereas within North America, the longitudinal gradient appeared more conspicuous. In both continents, these gradients were more marked in winter diets than in the breeding season diets of raptors. These results are consistent with the known regional trends in prey assemblages: in Europe, a south-to-north gradient in diversity and stability of bird and mammal communities appears to be more marked than a west-to-east gradient, whereas in North America, the number of mammal species markedly increases from east to west but not so evidently from south to north (Pagel et al. 1991). In winter, most northern birds migrate to the south and many mammals live below the snow, which decreases their availability to aerial predators. This further ameliorates the latitudinal gradient in dietary diversity of raptors in winter.

Our analyses revealed different intracontinental trends in trophic characters than those found by Marti et al. (1993). Among the raptor species occupying both continents, only the Merlin and Short-eared Owl showed significant geographical trends in trophic diversity at the class level and the Golden Eagle at the species level both within Europe and North America. Although we controlled the biases possibly due to different seasons of sampling food data, the trophic characteristics of individual species studied showed weak geographical patterns. Obviously, raptor species perceive food resources variously in different localities and respond to these resources differently even in nearby areas. Therefore, diet composition of a given raptor species cannot be extrapolated to even a neighboring area.

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APPENDIX. Sources of the diet data.

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