ORIGINAL ARTICLE

Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists

You-Bing Zhou[1,2], Chris Newman[3], Wen-Ting Xu[1], Christina D. Buesching[3], Andrzej Zalewski[4], Yayoi Kaneko[5], David W. Macdonald[3] and Zong-Qiang Xie[1]*

[1]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, Beijing 100093, China,* [2]*Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences, Mengla, Yunnan 666303, China,* [3]*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney, Abingdon, Oxon OX13 5QL, UK,* [4]*Mammal Research Institute, Polish Academy of Sciences, 17–230 Białowieża, Poland,* [5]*Division of Ecosciences, Institute of Symbiotic Science and Technology, Tokyo University of Agriculture and Technology, Saiwaicho 3-5-8, Fuchu-city, Tokyo 183-8509, Japan*

ABSTRACT

Aim Studies comparing feeding habits across a genus in different geographical regions or habitats can identify factors associated with adaptive feeding behaviour, linking key ecological traits between consumers and their environment. We investigated biogeographical patterns in dietary composition and trophic diversity across the genus *Martes* in relation to geographical range and environmental variables. We hypothesized that widely distributed opportunistic *Martes* species should demonstrate adaptive variations in dietary composition and trophic diversity relative to regional geographical location (e.g. latitude, elevation), environmental variation (e.g. temperature, rainfall, snow cover and primary productivity) and concomitant variation in food supply.

Location Europe, Asia and North America.

Methods We examined the dietary habits of martens (*Martes* spp.) using original data expressed as relative frequency of occurrence, and using principal components analysis to extract the main gradients in diet composition. These were then used as response variables in regression analyses, predicted from latitude or elevation. Multiple regression analyses were performed to assess the influence of food types and environmental variables on the trophic diversity index.

Results A clear latitudinal gradient in dietary composition was observed. Small mammals were the primary food type, but were less abundant in the diet of martens at lower latitude and elevation. Vegetable matter and insects were consumed more frequently in southerly and/or lower-elevation localities. Trophic diversity was lower at higher elevation, and increased with a decline in consumption of the dominant food types, i.e. rodents, fruits and insects. Trophic diversity also increased with increasing mean temperature.

Main conclusions Biogeographical variations in feeding habits across the genus *Martes* proved to be associated with latitude, local climate (especially temperature regime) and the availability of alternative potential foods. On an extensive geographical scale, martens respond to varying food availability by adjusting their foraging strategy and thus should be considered facultative generalists. At the species level, however, different climatic variables emerged as differentially important, indicative of adaptations to local conditions. *Martes* species are opportunistic and flexible feeders, and thus their conservation requires informed management, mindful of how changes in environmental conditions might influence their varied food supply.

Keywords

Adaptive foraging, climate, fruit availability, generalist, Holarctic region, latitudinal patterns, martens, *Martes*, opportunistic feeder, trophic diversity.

*Correspondence: Zong-Qiang Xie, State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing 100093, China. E-mail: xie@ibcas.ac.cn

INTRODUCTION

The spatial and temporal abundance and distribution of food resources influences a range of life-history traits, including optimal foraging strategy, socio-spatial organization, mating system and body size over evolutionary time (Gittleman, 1986; Roff, 2002). Foraging strategies are adaptive responses to dietary constraints including food abundance and availability, diet quality (i.e. nutrient and toxin content) and energy expenditure for detecting, capturing and handling prey (Pyke *et al.*, 1977; Sundell *et al.*, 2003). Consequently, mechanisms affecting foraging behaviour are central to understanding the ecology and life-history strategies of species (Daan & Tinbergen, 1997). Many species have evolved in relatively stable environments, and thus changes to these conditions are posited to have fitness consequences as a result of selection for traits adaptable to altered conditions (Visser & Both, 2005; Parmesan, 2006; Macdonald *et al.*, 2010).

Environmental and climatic conditions affect food availability and can have an impact on dietary composition and diversity (Hill & Dunbar, 2002); by regulating primary productivity they consequently influence rates of population dynamics (see Macdonald *et al.*, 2010). In response to these dietary constraints, many species have evolved flexible strategies that enable them to exploit optimally varied food sources. Such adaptive foraging has been demonstrated for many generalist carnivores at the local scale (e.g. American martens, *Martes americana*, Ben-David *et al.*, 1997; red foxes, *Vulpes vulpes*, Kjellander & Nordström, 2003; masked palm civets, *Paguma larvata*, Zhou *et al.*, 2008a) and for several predators across extensive biogeographical scales (e.g. otters, *Lutra lutra*, Clavero *et al.*, 2003; European wildcats, *Felis silvestris*, Lozano *et al.*, 2006). Understanding the mechanisms underlying dietary strategies and their influence on other life-history traits requires a comprehensive approach. Studies comparing feeding habits across a genus in different geographical regions, or habitats, can link key ecological traits between these consumers and their environment, and thus identify factors associated with adaptation in feeding behaviour.

Members of the genus *Martes* (family Mustelidae) are medium-sized carnivores that are distributed widely over the Holarctic, although as a consequence of habitat loss, fur-trapping and human persecution, distributions are now somewhat patchy (Harrison *et al.*, 2004). They inhabit not only pristine forests but also forest–farmland mosaic landscapes, and even suburban/urban areas. This broad habitat flexibility is reflected in the plasticity of their feeding habits, where small mammals (principally rodents), fruits and insects provide primary or secondary food resources (Harrison *et al.*, 2004). This dietary plasticity makes *Martes* an exemplary model genus with which to study adaptive foraging.

Feeding habits vary across the genus *Martes* on a macro-geographical scale, and the role of regional food abundance in shaping the composition and trophic diversity of the marten diet is not well understood. The abundance and diversity of potential prey (food types) determines a predator's (consumer's) diet composition and trophic diversity in ecological time (Schoener, 1971); we thus hypothesize that widely distributed opportunistic species should demonstrate adaptive variations in dietary composition and trophic diversity relative to variation in prey communities.

While many *Martes* species are adaptable foragers (Harrison *et al.*, 2004), we explore here species vulnerabilities, potential for adaptation and the effect of environmental variables at the regional scale. We review the available literature on the diet of the genus *Martes* across the Holarctic region. Our principal objectives were: (1) to describe regional diet and feeding habits in terms of trophic diversity and niche breadth for the genus as a whole and with particular regard to the species dominating the studies in the meta-analysis [i.e. the pine marten (*Martes martes*), stone marten (*Martes foina*) and American marten (*M. americana*)]; (2) to demonstrate adaptive variations in dietary composition and trophic diversity in this genus relative to regional geographical location (e.g. latitude, elevation), environmental variation (e.g. temperature, rainfall, snow cover and a primary productivity index) and concomitant variation in food supply; and (3) to establish the role of climate, habitat productivity and food availability on shaping the dietary composition, trophic diversity and foraging ecology of martens. Furthermore, we use these comparative data to explore the resilience of *Martes* species to abrupt anthropogenic environmental changes (e.g. Melis *et al.*, 2006; Bartoń & Zalewski, 2007).

MATERIALS AND METHODS

Literature compilation and data standardization

Studies quantifying dietary composition were browsed using web-based searches in Web of Science and Google Scholar with the key words '*Martes*', 'diet', 'feeding', 'food', and from our prior knowledge of the literature. In total, 163 publications covering the geographical distribution of *Martes* across the Holarctic region were examined.

Based on morphological characteristics, the extant members of the genus *Martes* had been classified previously into three subgenera and seven species: *Pekania* (*Martes pennanti*), *Charronia* (*Martes flavigula*) and *Martes* (*M. foina*, *M. martes*, *Martes zibellina*, *Martes melampus*, *M. americana*) (Anderson, 1970). But several recent studies, based on molecular data, have shown this to be incongruent with phylogeny (Koepfli *et al.*, 2008). The fisher (*M. pennanti*) and tayra (*Eira barbara*) are more closely related to the wolverine (*Gulo gulo*) than to other species formerly included in *Martes*, and thus have been reclassified with generic status as *Pekania*. In this study, we thus restrict our analyses to the five closely related species clearly included in *Martes*. Species nomenclature follows Wilson & Reeder (2005) throughout.

In an attempt to standardize the comparison of results from different species and geographical areas, we used the following criteria for inclusion in our data base: (1) the study had to cover at least one entire year; (2) dietary composition had to be

assessed by the analysis of stomach and/or faeces, and contain sufficient information with which to calculate the relative frequency of different food categories in relation to the total number of all food items; (3) sample sizes had to exceed 60 stomach and/or faecal samples; (4) all recognizable food items, and not only the dominant foods, had to be documented; and (5) geographical location and the timing and duration of the study had to be described adequately. Investigations from 59 localities across the Holarctic region met these criteria (Fig. 1 and see Appendix S1 in Supporting Information). Results from within the same study site (i.e. Jędrzejewski *et al.*, 1993; Zalewski, 2007) were pooled to avoid pseudo-replication (Hurlbert, 1984). Unfortunately, very few of the studies we included were sufficiently detailed to allow us to test Charnov's (1976) optimal foraging criteria, that is: (1) the ranks of food items (ranked by net energy gain to the consumer, or ranked in some alternative way) were not generally given, and (2) the environmental abundances of the most highly ranked food items were often not detailed. In our analyses and discussion we therefore make a subjective assessment of relative optimality informed by what data are available from the studies sampled, and thereby construct a coherent interpretive framework.

In the selected studies, variation in the derivation of analysed food material (stomach contents or faeces) was a confounding factor for inter-population comparisons (Witt, 1980; Cavallini & Volpi, 1995). Putman (1984) suggested that some food groups are under-represented in faeces compared with stomach contents due to differential digestion, which could also potentially confound the combined use of samples from different sources. However, in a broad-scale analysis for European wildcats, no significant differences in the consumption of food groups from different sources (faeces or stomach) were found (Lozano *et al.*, 2006). Amongst martens, Murakami (2003) found that, for sables (*M. zibellina*), the frequency ratio of food categories detected by stomach content analyses did not differ from the ratio detected by faecal analyses. In this review we use a two-way MANOVA with food derivation type and species as fixed factors and food groups as response variables to explore this potential source of bias. Because some of the studies used here (see Appendix S1) combined samples from different sources to characterize dietary composition, derivation of material was assigned to 'faeces' versus 'stomach and faeces'.

While the relative frequency of occurrence (RFO) is not the most comprehensive technique for assessing a carnivorous diet (Reynolds & Aebischer, 1991), RFO values are considered to be highly suitable for inter-population dietary comparisons (Clavero *et al.*, 2003; Lozano *et al.*, 2006; Moleón *et al.*, 2009). Here, seven basic food types were distinguished: carrion (large mammals too big to have been killed by a marten, mainly ungulates), other mammals, birds, herpetofauna (amphibians and reptiles), invertebrates, vegetable matter and others (secondary prey not in the previous categories, namely fish and refuse).

For all studies we calculated trophic diversity and niche breadth using, respectively, Shannon's diversity index (H') $H' = -\sum(P_i)(\log P_i)$ and Levins' index (B) $B = 1/\sum P_i^2$, where P_i gives the percentage frequency of occurrence of a given food item (after Jędrzejewski *et al.*, 1993; Zhou *et al.*, 2008a). Where possible, the proportions of fruits among vegetable matter and the proportion of rodents among mammals were also calculated. For each location, we also included latitude (to a half degree) and elevation (metres) taken from information given in the studies or from a geographical database. When samples were collected over a large area, representative mean latitudes (within a discrete range per study site of 1°) and elevations (within a discrete range per study site of < 500 m) were inferred (Lozano *et al.*, 2006).

Environmental variables

Environmental variables for each study site included in our meta-analysis were selected on the basis of their potential to
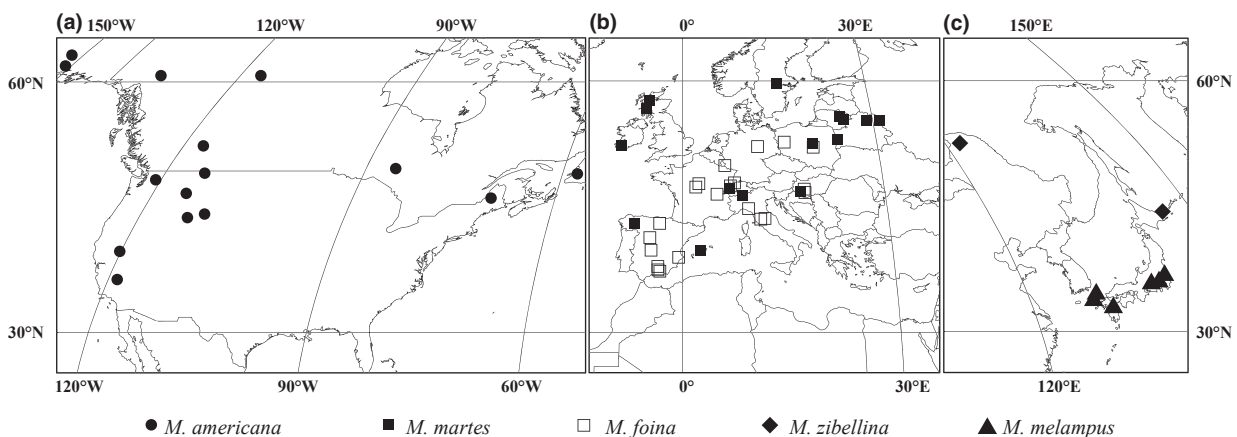

Figure 1 The 59 localities across the Holarctic region from which data were used in the analyses (for data sources see Appendices S1 & S2). (a) The American marten (*Martes americana*) in North America; (b) the pine marten (*M. martes*) and stone marten (*M. foina*) in Europe; (c) the sable (*M. zibellina*) and Japanese marten (*M. melampus*) in Asia.

influence the behavioural and foraging ecology of martens (Buskirk *et al.*, 1994; Harrison *et al.*, 2004; López-Martin, 2006). Thus, we included measures of temperature, precipitation, duration of snow cover, inferred primary productivity and degree of seasonality.

Data on temperature (°C) and precipitation (mm) were derived as monthly averages for the period 1950–2000, extracted from the WorldClim database (http://www.worldclim.org/current). From this data set for each study site, we calculated mean annual temperature and precipitation (T_{mean}, P_{mean}); mean temperature and precipitation of the coldest or driest and warmest or wettest 3 months across all years (T_{min}, P_{min}, T_{max}, P_{max}); and temperature and precipitation seasonality (T_{sea}, P_{sea}, i.e. the difference between mean annual maximum and minimum values). Snow cover data were derived from satellite imagery and consisted of monthly averages spanning a period from October 1978 to October 1995 at a resolution of 0.25° (see http://islscp2.sesda.com/ISLSCP2_1/html_pages/groups/snow/snow_cover_xdeg.html); the annual duration of the snow-covered period was also calculated (in days).

The productivity of the study locations was inferred from the normalized difference vegetation index (NDVI), using monthly log_{10}-transformed remotely sensed NDVI averages across the period 1982–96 at a resolution of 0.25° (see The International Satellite Land-Surface Climatology Project Initiative II, available at http://islscp2.sesda.com/ISLSCP2_1/html_pages/groups/veg/fasir_ndvi_monthly_xdeg.html.). We calculated annual mean NDVI (N_{mean}) and NDVI of the most, and least, productive three-month interval (N_{max}, N_{min}), and formulated a ratio characterizing seasonality in NDVI $[1-(N_{min}/N_{max})]$ (N_{sea}).

Statistical analyses

Data are presented as mean ± standard error, unless otherwise stated; all data were tested for normality prior to analysis. Pearson's correlation was used to estimate the relationship between trophic diversity and niche breadth with sample size. To describe the geographical variation in marten diet, Kruskal–Wallis tests were used to examine differences in the relative importance of food categories between species at a continental scale. The level of significance of multiple comparisons was assessed using Bonferroni corrections.

To gain a more complete understanding of the role of food availability in shaping the composition and trophic diversity of the marten diet, a principal components analysis (PCA) was employed for the pine marten, stone marten and American marten, which represented predominant study species within the study sample, each with a large sample size. These PCA factors were used as response variables in regression analyses with latitude and elevation as predictors. The relationship of the trophic diversity index with latitude and elevation was also examined with regression analyses.

Given the mixed sources of data for this meta-analysis, the restricted limits on parameters of interest and our parsimo-

nious analytical framework (testing the variables predicting dietary diversity), the influence of food types and environmental variables on dietary diversity was analysed using multiple regression, where H' was the dependent variable and the different types of food and environmental variables (e.g. Hill & Dunbar, 2002) were the predictors (see Revilla & Palomares, 2002; Zhou *et al.*, 2008a); multiple regression was also used to examine the influence of environmental variables on population density (e.g. Johnson *et al.*, 2002). The model was fitted with the predictors in stepwise order, according to the strength of correlation between the dependent variable and each predictor. All statistical analyses were performed using spss v.13.0.

RESULTS

We found no significant differences in the consumption of food types and trophic diversity and niche breadth values, for all species pooled, between studies deriving diet composition from different sources (e.g. undigested remains in faeces, stomach contents) ($F_{1,51} = 0.349$, $P = 0.927$). We did, however, detect significant differences across species ($F_{4,51} = 1.973$, $P = 0.004$). No significant interaction effects were detected ($F_{2,51} = 0.725$, $P = 0.744$). We were thus able to pool data from all studies for further analyses.

Overall diet

Mammals, vegetable matter and invertebrates proved to be the main food categories eaten by martens across all studies considered, representing 87.4% (SD 6.5) of consumed items. Vegetable matter comprised mostly fruits (mean ± SD, 91.8 ± 12.4%). Small rodents were the dominant component (mean ± SD, 71.2 ± 17.0%) amongst consumed mammals. Predation on birds was frequent, while carrion, herpetofauna and 'others' were rare dietary components (Table 1). Average trophic diversity and niche breadth were 1.8 (SD 0.4) and 3.0 (SD 0.9), respectively, indicating a generalist diet (see Appendix S2). Trophic diversity and niche breadth did not correlate with sample size ($R = -0.340$ to 0.165, $P > 0.2$ in all cases).

At the continental scale, studies from North America were representative of higher elevations and latitudes, whereas studies from Europe were from lower elevations, and studies located in Asia from lower latitudes (Bonferroni corrected, $P < 0.003$).

The consumption of mammals (except carrion) by martens in North American studies significantly exceeded that recorded for *Martes* species in Europe and Asia, while the consumption of vegetable matter and invertebrates showed the opposite trend (Bonferroni corrected, $P < 0.006$ in all cases). The consumption of birds was significantly higher in Europe than in Asia, and the consumption of herpetofauna was higher in Europe than in North America (Bonferroni corrected, $P < 0.05$ in all cases). Trophic diversity and niche breadth were significantly higher in Europe than in North America and Asia (Bonferroni corrected, $P < 0.05$ in all cases) (Table 1).

Table 1 Dietary composition in the genus *Martes* from the reviewed studies across the Holarctic region (see Appendices S1 & S2).

	Europe		Asia		Total				Genus
	M. martes	*M. foina*	*M. melampus*	*M. zibellina*	Europe	Asia	North America‡	H_2	*Martes*
n	15 or 14	21	6	2	36 or 35	8	15 or 14		59 or 57
Carrion	3.54 ± 1.37	1.58 ± 0.52	1.06 ± 1.06	1.91	2.40 ± 0.65	1.27 ± 0.86	0.70 ± 0.25	3.61	1.81 ± 0.43
Other mammals	31.77 ± 2.95	28.09 ± 3.44	15.08 ± 3.14	67.16	29.62 ± 2.34	28.10 ± 8.87	66.85 ± 3.59	27.45***	38.88 ± 2.95
Birds	10.91 ± 1.22	9.27 ± 1.39	5.35 ± 1.16	5.59	9.95 ± 0.95	5.41 ± 0.94	7.77 ± 0.75	6.29**	8.78 ± 0.66
Herpetofauna	3.25 ± 0.87	1.74 ± 0.75	1.99 ± 0.37	0.80	2.37 ± 0.57	1.69 ± 0.36	0.19 ± 0.18	14.41***	1.72 ± 0.37
Invertebrates	21.69 ± 2.47	20.96 ± 3.10	31.92 ± 3.12	11.59	21.26 ± 2.06	26.84 ± 4.18	9.26 ± 2.82	14.19***	18.97 ± 1.72
Vegetable matter	27.38 ± 3.75	35.17 ± 3.24	43.83 ± 4.68	12.81	31.93 ± 2.50	36.08 ± 6.13	13.29 ± 2.05	20.30***	27.75 ± 2.11
Others§	1.46 ± 0.83	3.19 ± 1.11	0.78 ± 0.35	0.16	2.47 ± 0.74	0.62 ± 0.27	1.94 ± 1.02	3.94	2.08 ± 0.52
Shannon's diversity index (*H'*)	2.08 ± 0.07	1.88 ± 0.05	1.83 ± 0.09	1.48	1.96 ± 0.04	1.74 ± 0.09	1.38 ± 0.09	23.20***	1.78 ± 0.05
Levins' index (*B*)	3.69 ± 0.19	3.17 ± 0.13	2.98 ± 0.18	2.07	3.38 ± 0.12	2.75 ± 0.21	2.07 ± 0.16	24.35***	2.96 ± 0.11
Latitude	51.52 ± 1.51	44.73 ± 1.05	34.78 ± 0.44	48.10	47.56 ± 1.04	38.11 ± 2.34	49.88 ± 2.17	11.71**	46.87 ± 1.00
Elevation (m)	263 ± 65	533 ± 85	767 ± 245	875	420 ± 60	794 ± 190	1097 ± 188	14.17***	643 ± 75

H_2, value of Kruskal–Wallis test statistic (with degrees of freedom = 2) for differences among continents, significance levels: ***$P < 0.001$; **$P < 0.05$.
‡In North America, only the American marten (*M. americana*) was included in this study.
§Others included secondary prey not in the previous categories, namely fish and refuse.

Factors affecting trophic diversity

The H' trophic diversity index revealed a significant negative correlation across the genus *Martes* only with elevation ($R^2 = 0.077$, $F_{1,57} = 4.729$, $P = 0.034$, Fig. 2a), that is, trophic diversity is lower at higher elevations. To determine the influence of prey type and environmental variables on trophic diversity, we included all food categories and environmental variables in multiple regression analyses of the factors influencing H'. From this initial model, only mammals (except carrion), vegetable matter, invertebrates and mean annual temperature (T_{mean}) were retained in the final model (Fig. 3, Table 2). While species-specific interactions with other environmental variables were shown to be important (see below) for the entire genus, the model presented in Table 2 highlights that precipitation (seasonality), snow cover and primary productivity (NDVI) did not have a major influence overall.

Per focal species, the regression analysis between the H' trophic diversity index and latitude revealed a significant positive relationship for the pine marten ($R^2 = 0.266$, $F_{1,13} = 4.718$, $P = 0.049$), a significant negative relationship for the American marten ($R^2 = 0.293$, $F_{1,13} = 5.394$, $P = 0.037$) and an indicative (but non-significant) negative relationship for the stone marten ($R^2 = 0.141$, $F_{1,19} = 3.107$, $P = 0.094$) (see Fig. 2b). Elevation showed a significant negative correlation for the pine marten ($R^2 = 0.335$, $F_{1,13} = 6.535$, $P = 0.024$, Fig. 2a). These correlations indicate a trend towards higher trophic diversity for the stone marten and American marten in the southern parts of their distribution. Pine marten diet proved to be most diverse in higher-latitude regions (Fig. 2b). Overall, trophic diversity was lowest at higher elevations. However, by chance, in our sample of study sites where pine marten diet data were collected, sites at lower latitude tended also to be at higher elevation, although not significantly so ($R_{15} = -0.473$, $P = 0.075$).

A multiple regression analysis between the trophic diversity index, food categories and environmental variables for the American marten taken alone indicated a pattern consistent with the findings for the genus as a whole. Vegetable matter, carrion and snow cover were the most important parameters explaining the biogeographical variation in pine marten dietary diversity; and mammals (except carrion), vegetable matter and precipitation seasonality (P_{sea}) most explanatory for the stone marten. Notably, primary productivity (NDVI) was not retained in the final model. Further details of species-specific trends and dietary diversity predicted by the final model are shown in Fig. 3 and Table 2.

Dietary variability

Four factors from the PCA explained 86% of the total observed variance in diet of martens (Table 3). The first factor represented an increasing frequency of carrion and herpetofauna. The second showed a gradient from diets with a high frequency of mammals (except carrion) towards diets dominated by vegetable matter. The third represented a gradient from populations with a high consumption of invertebrates to populations with a high consumption of other foods. The fourth factor described an increasing frequency of birds in the diet.

Latitude was significantly correlated with factor 2 (mammals) and factor 3 (invertebrates) ($R^2 = 0.203$, $F_{1,57} = 14.528$, $P < 0.001$, and $R^2 = 0.083$, $F_{1,57} = 5.187$, $P = 0.027$), and elevation was significantly (or on the margins of significance) correlated with factor 2 (mammals) and factor 4 (birds) ($R^2 = 0.055$, $F_{1,57} = 3.331$, $P = 0.073$, and $R^2 = 0.124$,
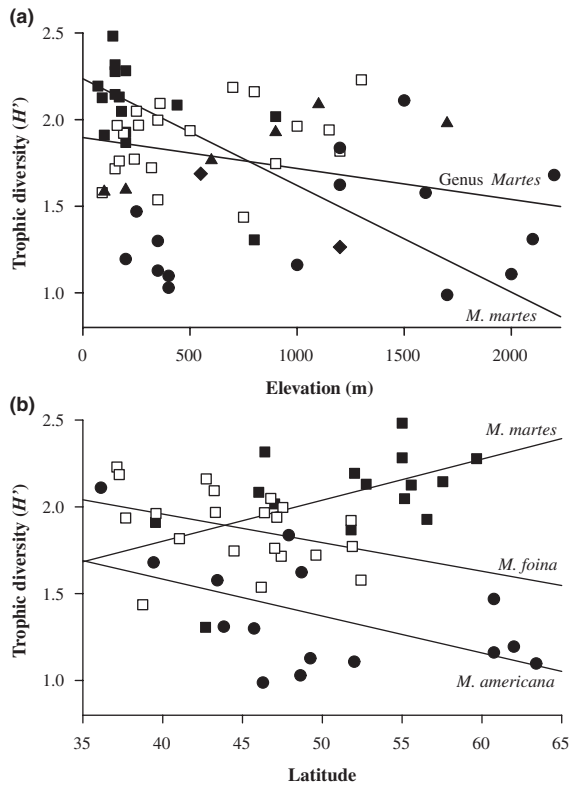
Figure 2 The relationship between the trophic diversity index (H') and (a) elevation for the entire genus *Martes* and the pine marten (*M. martes*) and (b) latitude for the pine marten, stone marten (*M. foina*) and American marten (*M. americana*). Each point represents one study site (see Fig. 1).

Figure 3 Linear regressions between the trophic diversity index (H') and the most important explanatory variables (overall and species-specific): mean temperature for (a) the entire genus *Martes* (solid line) and the American marten (*M. americana*) (dotted line), (b) snow cover for the pine marten (*M. martes*) and (c) precipitation seasonality index for the stone marten (*M. foina*). Statistics are provided in Table 2. Each point represents one study site (see Fig. 1).

$F_{1,57} = 8.091$, $P = 0.006$). Multiple regression analysis between PCA factors and environmental variables resulted in only T_{mean} and T_{min} being retained in the final model for factor 2 (mammals) and factor 3 (invertebrates), where factor 2 $= 0.118$ $T_{mean} -0.887$ ($R^2 = 0.410$, $F_{1,57} = 39.609$, $P < 0.001$) and factor 3 $= 0.055$ $T_{min} +0.121$ ($R^2 = 0.192$, $F_{1,57} = 11.123$, $P < 0.001$). Notably, precipitation (seasonality), snow cover and primary productivity (NDVI) were not retained in the model. This indicates that mammals (except carrion) were consumed more frequently in colder northern regions, whereas vegetable matter, invertebrate and other food were consumed more frequently in warmer southern regions. In higher-elevation areas, the consumption of vegetable matter and birds was also lower, while that of mammals (except carrion) was higher (Table 3).

Table 3 gives details of species-specific trends in PCA analyses. When these PCA factors were regressed against latitude and elevation, for the pine marten, stone marten and American marten, only PCA factor 1 was significantly (or nearly so) correlated with latitude ($R^2 = 0.364$, $F_{1,13} = 7.440$, $P = 0.017$, $R^2 = 0.170$, $F_{1,19} = 3.896$, $P = 0.063$ and $R^2 = 0.277$, $F_{1,13} = 4.977$, $P = 0.044$, respectively), and factor 3 was significantly (or on the margins of significance) correlated with elevation ($R^2 = 0.282$, $F_{1,13} = 5.098$,
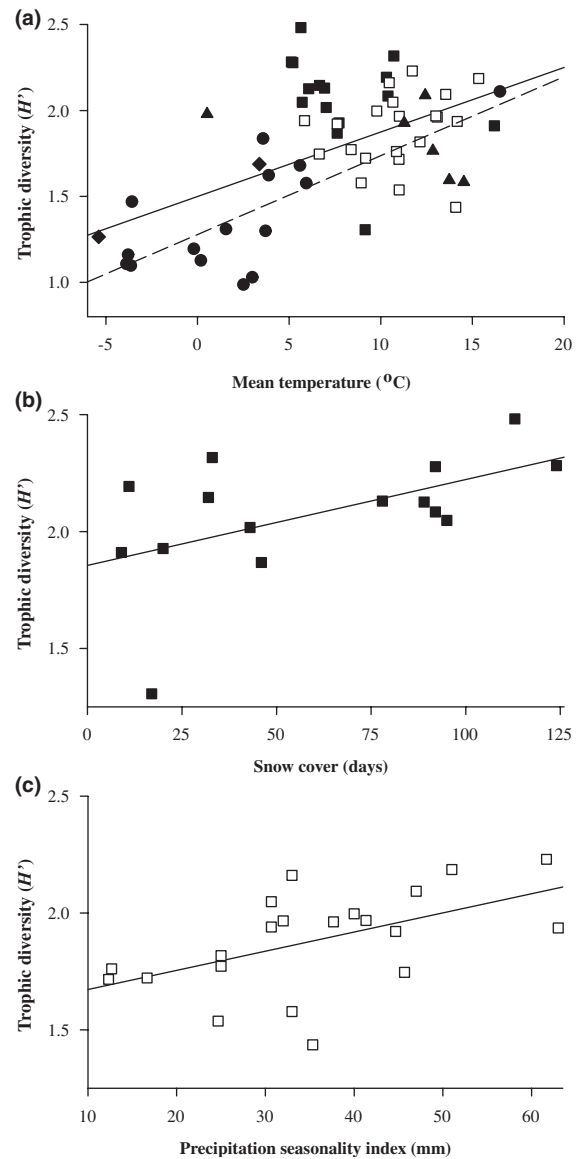
$P = 0.042$, $R^2 = 0.174$, $F_{1,19} = 4.002$, $P = 0.060$, $R^2 = 0.285$, $F_{1,13} = 5.178$, $P = 0.040$, respectively) (Table 3). Pine martens were thus observed to more frequently consume mammals (except carrion) and birds in colder northern regions, and more vegetable matter in warmer southern regions; invertebrates were consumed more frequently in lower-lying regions. By contrast, in warmer southern regions, the American marten consumed more invertebrates and herptofauna; however, the proportion of carrion in the diet was highest in lower-lying regions. The consumption of birds by stone martens was

Table 2 Final predictive models from multiple regression analyses of the entire genus *Martes*, pine marten (*M. martes*), stone marten (*M. foina*) and American marten (*M. americana*), where H' is the dependent variable and the different types of food and environmental variables listed in the Materials and Methods are the predictors.

	Final model ($H' = $)	R^2	F	P
Environmental variables				
Genus *Martes*	$1.500 + 0.038\ T_{mean}$	0.30	24.89	< 0.001***
Pine marten	$1.858 + 0.004$ snow cover	0.287	5.237	0.039*
Stone marten	$1.591 + 0.008\ P_{sea}$	0.288	7.681	0.012*
American marten	$1.477 + 0.043\ T_{mean}$	0.674	14.98	0.002**
Prey types				
Genus *Martes*	$4.097 - 0.032$ mammals (except carrion) -0.026 vegetable matter -0.020 invertebrates	0.756	45.705	< 0.001***
Pine marten	$2.308 - 0.011$ vegetable matter $+ 0.021$ carrion	0.699	13.903	< 0.001***
Stone marten	$2.318 - 0.008$ mammals (except carrion) -0.006 vegetable matter	0.358	5.026	0.018*
American marten	$4.389 - 0.038$ mammals (except carrion) -0.022 vegetable matter -0.018 invertebrates	0.939	56.383	< 0.001***

Significance levels: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

Table 3 Results from the principal components analysis (PCA) of the entire genus *Martes*, pine marten (*M. martes*), stone marten (*M. foina*) and American marten (*M. americana*) using seven food categories, and Pearson correlation values (r) of latitude and elevation with PCA factors.

	Genus *Martes* ($n = 59$)				Pine marten ($n = 15$)			Stone marten ($n = 21$)			American marten ($n = 15$)		
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Carrion	0.81	−0.04	−0.16	−0.13	0.06	0.90	−0.17	−0.06	−0.04	0.83	−0.23	0.02	0.59
Other mammals	−0.25	−0.82	−0.49	−0.10	0.89	−0.06	−0.24	0.03	−0.90	−0.20	−0.95	−0.11	0.16
Birds	−0.07	−0.07	−0.05	0.98	0.79	−0.15	−0.14	−0.07	−0.03	−0.76	0.31	−0.06	0.75
Herpetofauna	0.89	0.07	0.16	0.04	−0.09	0.93	0.04	0.72	0.02	0.42	0.78	0.23	0.30
Invertebrates	0.31	0.31	0.78	0.04	−0.21	0.02	0.88	0.74	0.59	0.07	0.85	−0.31	−0.17
Vegetable matter	−0.13	0.95	−0.12	−0.15	−0.83	−0.37	−0.41	−0.87	0.14	0.32	0.18	0.93	−0.15
Others†	−0.30	−0.13	0.79	−0.11	0.06	−0.40	0.51	0.03	0.78	−0.22	0.31	−0.64	−0.53
Eigenvalue	2.26	1.56	1.19	1.00	2.23	1.98	1.27	2.16	1.62	1.49	2.54	1.67	1.12
Explained variance (%)	32.22	22.21	16.97	14.32	31.86	28.34	18.17	30.87	23.16	21.31	36.26	23.81	15.99
r Latitude	−0.03	−0.45***	−0.29**	0.19	0.60**	0.17	0.31	−0.41*	−0.25	−0.26	−0.53**	0.06	0.11
r Elevation	−0.21	−0.24*	0.06	−0.35**	−0.30	−0.40	−0.53**	0.15	0.24	0.42*	0.26	0.00	−0.53**

Significance levels: ***$P < 0.001$; **$P < 0.05$; *$P < 0.1$.
†Others included secondary prey not in the previous categories, namely fish and refuse.

higher at higher elevations, whereas the proportion of carrion in the diet was lower.

DISCUSSION

Methodological limitations

We acknowledge that in reviewing such a variety of studies there will inevitably be variation in the type and quality of data analysed. Here we establish that sources of data derived from stomach contents and faecal analyses did not vary significantly, as also concluded from a comparable study of the diet of the European wildcat (Lozano *et al.*, 2006).

Several studies have addressed the influence of scat collection, laboratory procedures and misidentification of food remains (Reynolds & Aebischer, 1991). Yearly fluctuations of food use in wild marten populations might also lead to

estimation errors, especially for the areas where we have only 1 year of data (see Jędrzejewski *et al.*, 1993; Helldin, 1999). Nevertheless, across the entire data set, the range of local errors will be diluted heavily when compared with the large-scale range of observed dietary variation.

The time span over which these data on marten diet were collected, and the time at which the environmental variables were measured, may also be influential for our meta-analyses, as marten food habits can fluctuate temporally. Thus, in order to minimize the temporal variation at a local scale, we attempted to use averaged data for the environmental variables from as long a series as possible. When relating estimates of marten diet to various satellite-derived indices we encountered several issues that were likely to influence our results. Primary productivity, however, appears not to provide an accurate proxy for marten food supply, possibly because the availability of rodents, fruits and insects (the main marten prey) may be

limited by other factors, such as winter conditions and habitat structure (Bartoń & Zalewski, 2007).

Biogeographical variations in the diet of Holarctic martens

Here we demonstrate that small mammals, fruits and insects are the primary or secondary food categories in the diet of all marten species, generalized throughout their range. Martens have a very flexible diet that can also include birds as well as carrion (see Appendix S2, Table 1). Begon *et al.* (1996) define this kind of trophic diversity as 'generalist polyphagous feeding'. Despite dietary eclecticism, we also noted that martens will focus their foraging on a particular food category such as rodents, fruits or carrion. Such trophic tactics emphatically indicate adaptive foraging.

Interestingly, trophic diversity and niche breadth proved significantly greater in Europe than in North America and Asia, which may be explained by the lower elevation of the available European localities (Table 1).

In southern latitudes and at lower elevations, characterized by warmer and more stable climates, fruit and insects are more abundant and available for a longer proportion of the year (Rosenzweig, 1995; Chapman, 1998; Ting *et al.*, 2008). These food types are generally less important in the total biomass consumed by martens. In these regions fruits and insects were consumed as second- or third-order foods, contributing to the greater trophic diversity observed in the southern part of the range of this genus. Concomitantly, we noted that rodent consumption increased with latitude and elevation, except for pine martens, where trophic diversity was lower at southern latitudes; however, this could be an artefact of northern pine marten study sites being, on the whole, at a lower elevation than southern sites.

Mammal (mainly rodent) consumption was associated negatively with both vegetable matter (mainly fruit) consumption and general trophic diversity of the diet. A negative correlation between prey group and diet diversity has been interpreted as a good indicator of trophic specialism (Futuyma & Moreno, 1988; Lozano *et al.*, 2006). Under this construct, *Martes* would be viewed as rodent specialists, in which case the principles of optimal foraging predict that they should predate upon rodents irrespective of the availability of alternative prey (Glasser, 1982). At southern latitudes and higher elevations, however, we observed a shift from rodents to fruit, when the latter was available, contrary to any suggestion of absolute rodent specialization. Several reports indicate that in southern regions marten species eat a greater proportion of fruit (Buskirk *et al.*, 1994; López-Martin, 2006; Zhou *et al.*, 2008b). The phenology of peak fleshy fruit production and the length of the fruiting seasons show consistent differences with latitude, being longer in the tropics and shorter towards the poles (Ting *et al.*, 2008).

A similar observation has been made for other medium-sized carnivores. For example, European badgers, *Meles meles*, have been considered specialist consumers of earthworms in some study areas (Kruuk & Parish, 1981; da Silva *et al.*, 1993), but broad-scale investigations have revealed that badgers can shift their emphasis to vegetable matter when fruit or cereals are abundant (Goszczyński *et al.*, 2000); the same pattern has also been reported for broader temporal scales within a study area (Rosalino *et al.*, 2005). Wildcats also show dietary switching. Rodents are their staple prey, but when rabbits (*Oryctolagus cuniculus*) are available they will switch to optimize their energy budgets (Malo *et al.*, 2004; Lozano *et al.*, 2006). Amongst martens, Pulliainen & Ollinmäki (1996) found that pine martens decrease berry consumption with increasing snow cover, possibly because snow cover reduces access to fruit. By contrast, Helldin (1999) collected data during relatively mild winters with a general lack of snow cover. This study found that pine martens ate more berries than in most other studies in this region (Storch *et al.*, 1990). These studies also support the contention that martens prefer fruit to rodents when the former are available, arguably because of higher energetic profitability (i.e. it is easier to obtain and less costly to collect).

To summarize, across the genus we observed a facultative feeding strategy with a preference for fruit when abundant or for small mammals when they, but not fruit, are abundant. We also observe a general capacity to switch to alternative prey such as invertebrates, birds, herpetofauna, carrion and/or fishes when they are highly abundant in various habitats. These observations lead us to conclude that, as a genus, *Martes* demonstrates dietary opportunism.

Factors affecting trophic diversity: environmental variability and adaptive foraging

Over a broad geographical area, community diversity and the dietary composition of resident species are generally promoted by high prey abundance or primary productivity in habitats (Schoener, 1971; Clavero *et al.*, 2003; Lozano *et al.*, 2006; Moleón *et al.*, 2009). Contrary to our expectations, however, we found that marten diet was not related to habitat productivity (used here as a surrogate for food availability) but rather it proved to be most significantly related to mean temperature, possibly as a consequence of their varied, adaptive, opportunistic and omnivorous dietary habits.

While satellite-derived NDVI indices would afford a simple and generic index with which to model and extrapolate marten food supply (and thus provide a proxy for developing regional conservation policy: see McNaughton *et al.*, 1989; Herfindal *et al.*, 2005; Melis *et al.*, 2006), this method proved here to be inappropriate for this genus. NDVI indices of primary productivity are based on the quantity of radiation adsorbed by plants, including many dry fruit-bearing trees that do not produce fleshy fruit, and consequently do not reflect marten food supply accurately. The availability of rodents, fruit and insects (the main marten food type) is principally limited by other climatic factors that in turn determine habitat structure (Bartoń & Zalewski, 2007). Other observations also support the lack of relationship between life-history traits and

productivity. For example, the home range size of the American marten does not relate to habitat productivity (Nilsen *et al.*, 2005). Similarly, Bartoń & Zalewski (2007) found that the most important factor limiting the abundance and distribution of the red fox was winter severity (especially mean winter temperature) not habitat productivity. Moreover, marten dietary diversity also increases with the declining consumption of dominant food types (rodents, fruits and insects), also negating the influence of primary productivity.

A very striking climatic result was apparent for pine martens: snow cover was consistently the most significant coefficient in the multiple regression models, indicating that it is the most important factor affecting pine marten diet and foraging. This may be due to rodents being able to conceal themselves from marten predation more effectively under snow (Jędrzejewski *et al.*, 1993; Pulliainen & Ollinmäki, 1996; Helldin, 1999). Snow cover limits rodents' access to food resources and thus affects their survival, as well as the survival of alternative types of prey, reducing their winter abundance (Korslund & Steen, 2006). Snow cover may also increase the availability of ungulate carcasses (Selva *et al.*, 2005). Increasing snow thus makes dominant prey less available to pine martens (e.g. rodents, fruits) while simultaneously militating for greater compensatory consumption of alternative prey (e.g. carrion).

Notably, for the stone marten, seasonality of precipitation was consistently the most significant coefficient in the multiple regression models. Defined as the annual fluctuation of environmental conditions and primary productivity, seasonality is an important evolutionary pressure affecting the life history and behaviour of mammals (Boyce, 1979; Bartoń & Zalewski, 2007). We found that the dietary diversity of stone martens correlated with variation in yearly precipitation much more strongly than with the absolute precipitation itself, this variability being highest in southern Mediterranean habitats characterized by the combination of hot dry summers and cool humid winters (Blondel & Aronson, 1999; Clavero *et al.*, 2003).

As mean temperature is influential in shaping the dietary diversity of martens on a biogeographical scale, we also highlight the potential vulnerability of the genus to global climate change, especially given that this has driven many other species to shift their distributional ranges (Parmesan, 2006), phenology (Visser & Both, 2005; Cleland *et al.*, 2007) and life-history traits (Nussey *et al.*, 2005; Chamaillé-Jammes *et al.*, 2006).

In summary, our analyses reveal that biogeographical variations in feeding habits across the genus *Martes* are associated with latitude, local climate (especially temperature regime) and the availability of alternative potential foods.

At the broad geographical scale, martens respond to varying food availability by adjusting their foraging strategy and thus should be considered facultative generalist predators. These findings are comparable to those reported at the regional scale (Ben-David *et al.*, 1997; Rödel & Stubbe, 2006).

These findings reinforce the importance of understanding ecological processes across a broad scale when developing informed conservation measures for carnivores, an order that includes many rare and endangered species (Diniz-Filho *et al.*, 2009).

REFERENCES

Anderson, E. (1970) Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae). *Acta Zoologica Fennica*, **130**, 1–133.

Bartoń, K.A. & Zalewski, A. (2007) Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography*, **16**, 281–289.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: individuals, populations and communities*. Blackwell Publishing, Oxford.

Ben-David, M., Flynn, R.W. & Schell, D.M. (1997) Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia*, **111**, 280–291.

Blondel, J. & Aronson, J. (1999) *Biology and wildlife of the Mediterranean region*. Oxford University Press, Oxford.

Boyce, M.S. (1979) Seasonality and patterns of natural selection for life histories. *The American Naturalist*, **114**, 569–583.

Buskirk, S.W., Harestad, A.S., Raphael, M.G. & Powell, R. (1994) *Martens, sables, and fishers: biology and conservation*. Cornell University Press, New York.

Cavallini, P. & Volpi, T. (1995) Biases in the analysis of the diet of the red fox *Vulpes vulpes*. *Wildlife Biology*, **1**, 243–248.

Chamaillé-Jammes, S., Massot, M., Aragon, P. & Clobert, J. (2006) Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology*, **12**, 392–402.

Chapman, R.F. (1998) *The insects: structure and function*. Cambridge University Press, Cambridge.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.

Clavero, M., Prenda, J. & Delibes, M. (2003) Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats. *Journal of Biogeography*, **30**, 761–769.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, **22**, 357–365.

Daan, S. & Tinbergen, J.M. (1997) Adaptation of life histories. *Behavioural ecology: an evolutionary approach* (ed. by J.R. Krebs and N.B. Davies), pp. 311–333. Wiley-Blackwell, Oxford.

Diniz-Filho, J.A.F., Rodríguez, M., Bini, L.M., Olalla-Tarraga, M.Á., Cardillo, M., Nabout, J.C., Hortal, J. & Hawkins, B.A. (2009) Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. *Journal of Biogeography*, **36**, 2222–2236.

Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, **19**, 207–233.

Gittleman, J.L. (1986) Carnivore life-history patterns: allometric, phylogenetic, and ecological associations. *The American Naturalist*, **127**, 744–771.

Glasser, J.W. (1982) A theory of trophic strategies: the evolution of facultative specialists. *The American Naturalist*, **119**, 250–262.

Goszczyński, J., Jędrzejewska, B. & Jędrzejewski, W. (2000) Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. *Journal of Zoology (London)*, **250**, 495–505.

Harrison, D.J., Fuller, A.K. & Proulx, G. (2004) *Martens and fisher* (Martes) *in human-altered environments: an international perspective*. Springer-Verlag, New York.

Helldin, J.O. (1999) Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography*, **22**, 324–336.

Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. (2005) Prey density and environmental productivity explain variation in Eurasian lynx home-range size at two spatial scales. *Journal of Zoology (London)*, **265**, 63–71.

Hill, R.A. & Dunbar, R.I.M. (2002) Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology*, **16**, 579–593.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Jędrzejewski, W., Zalewski, A. & Jędrzejewska, B. (1993) Foraging by pine marten *Martes martes* in relation to food resources in Białowieża National Park, Poland. *Acta Theriologica*, **38**, 405–426.

Johnson, D.D.P., Jetz, W. & Macdonald, D.W. (2002) Environmental correlates of badger social spacing across Europe. *Journal of Biogeography*, **29**, 411–425.

Kjellander, P. & Nordström, J. (2003) Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos*, **101**, 338–344.

Koepfli, K.P., Deer, K.A., Slater, G.J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G. & Wayne, R.K. (2008) Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographical history of a mammalian adaptive radiation. *BMC Biology*, **6**, 10.

Korslund, L. & Steen, H. (2006) Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology*, **75**, 156–166.

Kruuk, H. & Parish, T. (1981) Feeding specialization of the European badger *Meles meles* in Scotland. *Journal of Animal Ecology*, **50**, 773–788.

López-Martin, J.M. (2006) Comparison of feeding behaviour between stone marten and common genet: living in coexistence. *Martes in carnivore communities* (ed. by M. Santos-Reis, J.D.S. Birks, E.C. O'Doherty and G. Proulx), pp. 137–155. Alpha Wildlife Publications, Sherwood Park, Alberta.

Lozano, J., Moleón, M. & Virgós, E. (2006) Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. *Journal of Biogeography*, **33**, 1076–1085.

Macdonald, D.W., Newman, C., Buesching, C.D. & Nouvellet, P.M. (2010) Are badgers 'under the weather'? Direct and indirect impacts of weather variability on Eurasian badgers (*Meles meles*) population dynamics. *Global Change Biology* doi: 10.1111/j.1365-2486.2010.02208.x.

Malo, A.F., Lozano, J., Huertas, D.L. & Virgós, E. (2004) A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? *Journal of Zoology (London)*, **263**, 401–407.

McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, **341**, 142–144.

Melis, C., Szafrańska, P.A., Jędrzejewska, B. & Bartoń, K. (2006) Biogeographic variation in wild boar (*Sus scrofa*) density in Europe and western Asia. *Journal of Biogeography*, **33**, 803–811.

Moleón, M., Sánchez-Zapata, J.A., Real, J., García-Charton, J.A., Gil-Sánchez, J.M., Palma, L., Bautista, J. & Bayle, P. (2009) Large-scale spatio-temporal shifts in the diet of a predator mediated by an emerging infectious disease of its main prey. *Journal of Biogeography*, **36**, 1502–1515.

Murakami, T. (2003) Food habits of the Japanese sable *Martes zibellina brachyura* in eastern Hokkaido, Japan. *Mammal Study*, **28**, 129–134.

Nilsen, E.B., Herfindal, I. & Linnell, J.D.C. (2005) Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience*, **12**, 68–75.

Nussey, D.H., Postma, E., Gienapp, P. & Visser, M.E. (2005) Selection on heritable phenotypic plasticity in a wild bird population. *Science*, **310**, 304–306.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Pulliainen, E. & Ollinmäki, P. (1996) A long-term study of the winter food niche of the pine marten *Martes martes* in northern boreal Finland. *Acta Theriologica*, **41**, 337–352.

Putman, R.J. (1984) Facts from faeces. *Mammal Review*, **14**, 79–97.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**, 137–154.

Revilla, E. & Palomares, F. (2002) Does local feeding specialization exist in Eurasian badgers? *Canadian Journal of Zoology*, **80**, 83–93.

Reynolds, J.C. & Aebischer, N.J. (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review*, **21**, 97–122.

Rödel, H.G. & Stubbe, M. (2006) Shifts in food availability and associated shifts in space use and diet in stone marten. *Lutra*, **49**, 67–72.

Roff, D.A. (2002) *Life history evolution*. Sinauer Associates, Sunderland, MA.

Rosalino, L.M., Loureiro, F., Macdonald, D.W. & Santos-Reis, M. (2005) Dietary shifts of the badger *Meles meles* in Mediterranean woodlands: an opportunistic forager with seasonal specialisms. *Mammalian Biology*, **70**, 12–23.

Rosenzweig, M.L. (1995) *Species diversity in space and time.* Cambridge University Press, Cambridge.

Schoener, T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2**, 369–404.

Selva, N., Jędrzejewska, B., Jędrzejewski, W. & Wajrak, A. (2005) Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, **83**, 1590–1601.

da Silva, J., Woodroffe, R. & Macdonald, D.W. (1993) Habitat, food availability and group territoriality in the European badger, *Meles meles*. *Oecologia*, **95**, 558–564.

Storch, I., Lindstrom, E. & Dejounge, J. (1990) Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica*, **35**, 311–320.

Sundell, J., Eccard, J.A., Tiilikainen, R. & Ylonen, H. (2003) Predation rate, prey preference and predator switching: experiments on voles and weasels. *Oikos*, **101**, 615–623.

Ting, S., Hartley, S. & Burns, K.C. (2008) Global patterns in fruiting seasons. *Global Ecology and Biogeography*, **17**, 648–657.

Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2561–2569.

Wilson, D.E. & Reeder, D.M. (2005) *Mammal species of the world. A taxonomic and geographic reference*, 3rd edn. Johns Hopkins University Press, Baltimore, MD.

Witt, H. (1980) The diet of the red fox. Questions about method. *The red fox* (ed. by E. Zimen), pp. 65–70. Biogeographica, Vol. 18. W. Junk B.V. Publishers, The Hague.

Zalewski, A. (2007) Does size dimorphism reduce competition between sexes? The diet of male and female pine martens at local and wider geographical scales. *Acta Theriologica*, **52**, 237–250.

Zhou, Y.B., Zhang, J.S., Slade, E., Zhang, L.B., Palomares, F., Chen, J., Wang, X.M. & Zhang, S.Y. (2008a) Dietary shifts in relation to fruit availability among masked palm civets (*Paguma larvata*) in central China. *Journal of Mammalogy*, **89**, 435–447.

Zhou, Y.B., Slade, E., Newman, C., Wang, X.M. & Zhang, S.Y. (2008b) Frugivory and seed dispersal by the yellow-throated marten, *Martes flavigula*, in a subtropical forest of China. *Journal of Tropical Ecology*, **24**, 219–223.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Information about the studies across the Holarctic region used in this paper.
Appendix S2 Marten diet as described in the reviewed studies.

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BIOSKETCH

You-Bing Zhou coordinates a Chinese mustelid conservation programme. He specializes in the behavioural ecology and conservation biology of Chinese carnivores. He is also interested in the evolutionary ecology of plant–animal interactions.

Author contributions: Y.-B.Z., C.N. and Z.-Q.X. conceived the theoretical framework of this manuscript; Y.-B.Z. Y.K. and W.-T.X. collected these data; Y.-B.Z. and W.-T.X. analysed the data; Y.-B.Z. wrote the original draft. All co-authors contributed to the writing of this final version of the manuscript.

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