

Biogeographical patterns of the diet of Palearctic badger: Is badger an earthworm specialist predator?

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Badgers were hypothesized as an earthworm specialist predator. We reviewed spatial patterns and food habits of the Eurasian badger (*Meles spp.*) in relation to geographical variables like latitude, elevation, aspects, and environmental variables, such as temperature, snow cover depth, precipitation, primary productivity, and human influence. The relative frequencies of occurrence of food items in the diets of badgers in 19 studies across 22 localities worldwide were included in the analysis plus the data from our study on the badger diet on the Qinghai-Tibetan Plateau. Principal component analysis (PCA) was used to extract the main components of dietary composition. Multiple regression analysis was applied to reveal the relationship between trophic diversity and the main PCA factors and biogeographical variables. We found a clear latitudinal gradient in the dietary composition of badgers, which was characterized by a greater consumption of insects and reptile in southern area and a higher intake of earthworm in northern regions. Nevertheless, badgers are not an earthworm specialist predator. Furthermore, trophic diversity of badger diets was significantly positively correlated with latitude and human activity. Abundance and availability of foods appear to determine badger foraging tactics. Badgers are adept in exploiting local resources and our results confirm that badgers are generalist predators with opportunistic foraging behavior across their entire distribution range.

environmental factor, feeding ecology, generalist, latitude gradient, trophic diversity

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Carnivores are key species in ecosystems. Geographical factors affect food availability and have an impact on dietary composition and diversity of animals. For example, the diet of European otter (*Lutra lutra*) is more diverse in the southern localities than in the northern areas [1]. There are also obvious latitudinal gradients in the dietary compositions of wildcat (*Felis silvestris*) [2], martens (*Martes spp.*) [3] and red fox (*Vulpes vulpes*) [4]. Wildcats eat more rabbits in lower latitude but more rodents in higher latitude [2]. Pine martens (*Martes martes*) consume more mammals and birds in northern regions but more vegetable matter in southern regions [3]. Red fox preys on more lagomorphs and invertebrates in southern areas but eats more small mammals and fruits in northern areas. Additionally, red fox

eats more lagomorphs in lower elevation but more small mammals in higher elevation [4]. Environmental variables also play important roles in the feeding ecology of animals. For example, temperature has an obvious effect on food diversity for martens [3] and precipitation affects the prey abundance of little brown bat (*Myotis lucifugus*) [5]. For brown bears (*Ursus arctos*), their consumption of vertebrates increases as the duration of snow cover and snow depth increases, and as temperature, precipitation and primary productivity increase, their consumption of invertebrates increases accordingly [6]. Studies on the relationships between feeding habits and biogeographical variables for endangered carnivore species provide useful information on how to better protect these animals, which also help us understand the carnivore ecology and their life history strategies [7].

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The genus *Meles* is widespread across the Eurasia. Some researchers classify the taxa as a single species (*M. meles*) [8,9] whereas some researchers classify it into three species: European badger (*M. meles*), Asian badger (*M. leucurus*) and Japanese badger (*M. anakuma*) [10]. Here, we take the badgers across the Eurasia as a single species. The feeding ecology of badger has been the subject of numerous studies at many localities through out its distribution range, such as in England [11], Italy [12–20], Hungary [21], Ireland [22], Poland [23], Japan [24], Mongolia [25], Scotland [26], Spain [27–29] and Swiss [30]. Some researchers argued that badger is an earthworm specialist predator [26,31]; while other studies indicated that the badger is a generalist predator that uses resources according to its availability [19,27, 29]. Badger shows high plastic trophic diversity: rabbits, insects, and fruits are potential foods for badgers. Hence, badger is an opportunistic predator.

Roper et al. [32] reviewed the badger diet across the former Soviet Union and concluded that the badger is a generalist forager with a preference for animal foods. Goszczynski et al. [23] studied the effect of geographical factors such as latitude or habitat type on badger diets in Europe and revealed that badger mainly consume earthworm and fruits and badger diet composition had latitude gradient. However, no study has been done to explore the potential relationships between dietary composition of badgers and environmental variables such as temperature, precipitation, primary productivity and snow cover across the entire distribution range of badgers. Here, we reviewed the literatures, then described the food spectra of the badger over its entire distribution range and assessed the effect of environmental variables on badgers.

We tested whether badgers are generalist predators with opportunistic foraging behavior in this study. In detail, we (i) evaluated the main food groups consumed by badgers in relation to geographical variables (latitude and elevation),

(ii) interpreted patterns in the diet of badgers from a biogeographical perspective, and (iii) tested the competing ideas that badgers are generalists or specialists across their distribution ranges.

1 Materials and methods

1.1 Review of badger diet studies

We conducted a thorough literature search in the existing databases and selected publications about badger diet that met the following criteria: (1) diet data covered at least the whole activity period of badgers in one year; (2) the sample size exceeds 60; (3) sufficient information was provided so that we could calculate the relative frequency of occurrence of food items; (4) adequate information regarding the geographical location of the study area was provided; and (5) dietary composition was accessed using stomach/scat samples. Cases in Roper and Mickevicius' review did not meet the above criteria [32]; we thus dropped the reference from the analyses. Altogether, 19 publications based on data from 22 locations were selected for this analysis (Figure 1 and Table 1) plus the results from our field study on badger diet in the Qinghai Lake basin on the Qinghai-Tibetan Plateau, China. The dietary composition of badgers in our result was obtained through scat analysis: badger faeces were soaked in water thoroughly and washed through two sieves with mesh sizes of 5 and 1 mm, respectively. Then the remaining of samples on the sieves were distinguished into the food categories (Appendix S1). Our results indicated insects were the main foods in the diet of badgers in the Qinghai Lake basin, its frequency of occurrence and relative frequency accounted 100% and 68.45%, respectively, in complementary with plateau pika (*Ochotona curzoniae*), birds, Qinghai toad-headed agamid lizard (*Phrynocephalus vlangalii*), and fruits of ephedra (*Ephedra intermedia*).

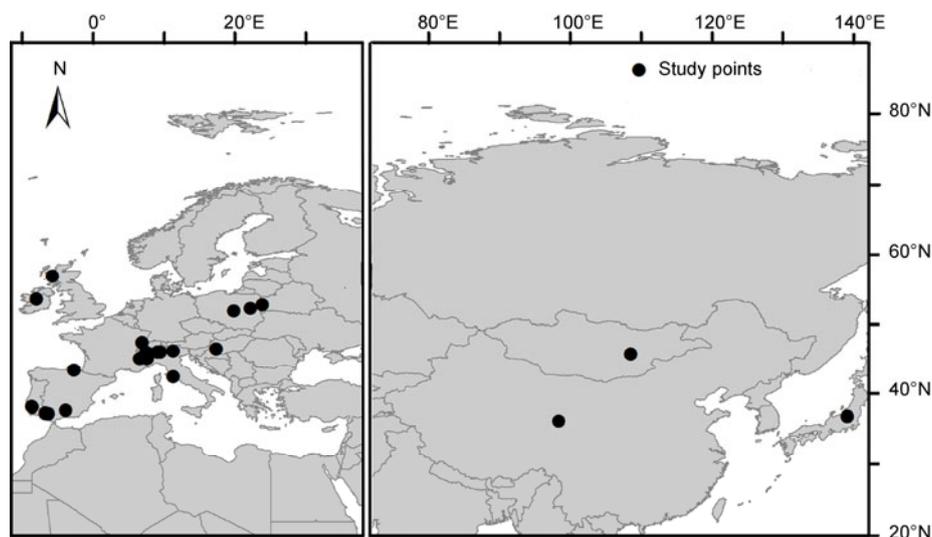


Figure 1 Localities across Eurasia from which data was obtained from publications [12–30].

Table 1 Studies of the diet of the Eurasian badger (*Meles meles*) in this review with an indication of latitude, longitude where the study took place, year, sample size, food items and trophic diversity (H')

No.	Author	Locations	No. of samples	Earthworm (RF%)	Mammals (RF%)	Birds (RF%)	Insects (RF%)	Amphibian (RF%)	Reptiles (RF%)	Fruits (RF%)	Mollusks (RF%)	Others (RF%)	H'
1	Balestrieri (2004)	45°2'N, 7°43'E	199	44.93	6.58	3.01	18.36	11.24	0.30	10.68	4.66	0.24	1.61
2	Balestrieri (2009)	45°53'N, 7°37'E	222	44.58	2.22	0.25	20.2	11.33	0.49	20.94	0	0	1.38
3	Boesi (2002)	46°01'N, 9°09'E	118	8.04	6.92	1.79	47.99	0.67	0.22	34.38	0	0	1.23
4	Cleary (2009)	53°31'N, 7°59'W	686	43.12	1.17	0.59	41.95	5.7	0	6.29	1.17	0	1.20
5	Fedriani (1998)	37°10'N, 6°23'W	145	0	30.21	1.37	42.64	7.64	5.63	12.52	0	0	1.40
6	Del Bove (2001)	42°23'N, 11°24'E	69	0	15.50	7.50	52.50	0	0.50	14.50	9.50	0	1.35
7	Fischer (2005)	47°19'N, 6°58'W	1436	28.02	4.48	0	19.02	0	0	43.03	0	5.45	1.33
8	Gonavalski (2000)	52°43'N, 23°54'E	141	24.43	15.66	0	17.94	0	0	36.75	0	5.22	1.46
9	Gonavalski (2000)	52°13'N, 22°13'E	281	31.9	15.19	0	27.9	0	0	19.76	0	5.25	1.48
10	Gonavalski (2000)	51°48'N, 19°53'E	66	24.18	11.12	1.51	41.28	13.52	0.37	4.35	0	3.67	1.56
11	Kaneko (2006)	36°45'N, 139°15'E	82	33.55	1.94	4.52	21.29	0.65	0	35.48	2.58	0	1.41
12	Kruuk (1981)	56°53'N, 5°49'W	2159	26.37	6.49	2.41	39.98	1.49	0	19.69	0	3.57	1.49
13	Lanszki (2004)	46°24'N, 17°27'E	156	17.55	5.16	1.21	44.97	23.39	1.03	6.33	0	0.36	1.45
14	Lucherini (1995)	45°04'N, 6°39'E	76	22.44	11.21	0.93	59.82	0	0	5.6	0	0	1.09
15	Marassi (2002)	46°01'N, 9°30'E	147	20.04	6.41	1.45	29.06	0	0	41.28	1.15	0.61	1.37
16	Martin (1995)	37°07'N, 6°44'W	530	0	26.82	1.42	54.36	6.99	7.13	3.28	0	0	1.23
17	Murdoch (2010)	45°43'N, 108°39'E	116	0	14.77	3.98	63.64	0	12.5	5.11	0	0	1.11
18	Prignioni (2008)	46°07'N, 11°20'E	230	11.90	4.84	2.22	27.33	2.56	0	51.14	0	0	1.28
19	Remonti (2007)	45°38'N, 7°20'E	228	0	41.58	11.7	14.98	0	0	26.6	0	5.14	1.41
20	Zabala (2002)	43°23'N, 2°40'W	80	29.68	3.26	0	37.21	0	0	25.58	0	4.23	1.32
21	Rosalino (2005)	38°06'N, 8°36'W	282	0	1.36	0.14	66.32	0.47	0.3	31.4	0	0	0.75
22	This study (2010)	36°40'N, 100°48'E	162	0	3.34	5.41	68.45	0	13.54	8.87	0.4	0	1.04

We used the relative frequency of occurrence to access the diet of badgers. The undigested residues were distinguished into nine food categories: earthworm, birds, mammals, insects, amphibians, reptiles, fruits, mollusk and others including leaves, roots, garbage and unidentified fraction. We measured trophic diversity of badgers with Shannon-Wiener Index (H'):

$$H' = -\sum P_i \times \log(P_i), \quad (1)$$

where P_i is the relative frequency of occurrence of a given food item i .

1.2 Biogeographical variables

Biogeographical variables at each site included temperature, precipitation, depth of snow cover, inferred primary productivity, elevation, aspect, latitude and longitude. Mean temperature (T_{mean}), mean precipitation (P_{mean}), mean temperature in the warm season (T_{warm}) and cold season (T_{cold}), and mean precipitation in the wet season (P_{wet}) and dry season (P_{dry}) were extracted from the WORLDCLIM database (<http://www.worldclim.org/current>) from 1955–2000 for all study areas. We used annual mean net primary productivity (NPP) from 1980–2000 as a measure of local productivity. Data on NPP were obtained from the Global Inventory Monitoring and Modeling Studies data set with a spatial

resolution of 1 km × 1 km (<http://glcf.umiaccs.umd.edu/data/gimms/>). We obtained satellite-derived data on snow cover (snow depth) from the Global Ecosystem Database V2.0 (<http://www.ngdc.noaa.gov>). Data on demography was from <http://srtm.csi.cgiar.org>, where elevation, latitude and longitude, aspects of each study site were extracted. Human influence was measured using the human influence index (HII) [33]. HII evaluates the influence of human activities on ecosystems using eight measures of human presence: population density/km² (0–10), score of railroads (8 and 0), score of major roads (8, 4 and 0), score of navigable rivers (4 and 0), score of coastlines (4 and 0), score of nighttime stable lights values (0, 3, 6 and 10), urban polygons (10 and 0) and land cover categories (10, 8, 3 and 0). The value of HII is the sum of the score of the eight factors and it ranges from 0–64, where a zero value represents no human influence and 64 represents the maximum human influence. Data on HII was obtained from the Socioeconomic Data and Applications Center with spatial resolution of 30 s (<http://sedac.ciesin.columbia.edu/wildareas/>).

1.3 Data analysis

We used Kolmogorov-Smirnov Test to check data normality and transformed data when necessary [34]. To describe the overall pattern of badger diets, we reduced the nine prey

groups into orthogonal factors using a Principal Components Analysis (PCA). Varimax Normalized Rotated Method was used to eliminate the collinearity among variables. We used Pearson Correlation Analysis to reveal the relationship between PCA factors and latitude or elevation. The PCA factors were used as dependent variables in Linear Regression Analyses while the latitude and elevation were included as predictors. Regression was also used to examine the relationship between trophic diversity index and latitude, elevation and aspect. We analyzed the influence of food categories and environmental variables on the trophic diversity index through multiple regression, where H' was the dependent variable and food category and environmental variables were predictors. All statistical analyses were performed in SPSS 16.0 (SPSS Inc., USA) and alpha was 0.05.

2 Results

2.1 Trophic diversity

Earthworm was not the main food item for badgers. Instead, insects and fruit were the main food categories consumed

by badgers across all studies (Table 1). A PCA using nine main prey items generated four orthogonal factors with eigenvalues greater than 1 accounting for more than 82% of the variance (Table 2). The first factor represented an increasing frequency of earthworms and 'other food types' and decreasing frequency of insects and reptiles. The second factor showed a gradient of diet with a high frequency of mammals and birds and low frequency of insects. The third factor represented an increasing frequency of amphibians and decreasing frequency of fruit. The fourth factor showed an increasing frequency of mollusks and decreasing frequency of birds. Latitude was significantly correlated with factor 1 (factor 1 equaled $-4.078 + 0.090 \times \text{latitude}$, $R^2 = 0.269$, $F_{21} = 7.352$, $P = 0.01$) (Figure 2(a)). Elevation and aspect were excluded from the model.

Multiple Regression Analysis between the PCA factors and environmental variables showed the variables P_{dry} and HII were retained in the final model for factor 1, where factor 1 = $-1.820 + 0.006 \times P_{\text{dry}} + 0.045 \times \text{HII}$ ($R^2 = 0.500$, $F_{21} = 9.488$, $P = 0.001$) (Figure 2(b) and (c)). T_{mean} , T_{warm} , T_{cold} , P_{mean} , P_{dry} , depth of snow cover and NPP were not retained in the model.

Table 2 Principal Component Analysis (PCA) of Eurasian badger diet expressed as relative frequency of occurrence, and Pearson correlation values (r) of latitude and elevation with PCA factors

Variables	Relative frequency of occurrence ^{a)}			
	Factor 1	Factor 2	Factor 3	Factor 4
Earthworm	0.70	-0.53	0.26	-0.02
Mammals	-0.03	0.93	0.08	-0.10
Birds	-0.09	0.73	-0.13	0.53
Insects	-0.92	-0.12	0.08	0.03
Amphibian	0.12	-0.14	0.88*	-0.02
Reptiles	-0.81	0.23	0.11	-0.12
Fruits	0.43	-0.16	-0.79	-0.07
Mollusks	0.08	0.05	0.02	0.94
Others	0.59	0.37	-0.21	-0.47
Eigenvalue	2.54	1.91	1.56	1.41
Variance explained (%)	28.23	21.23	17.29	15.63
r_{latitude}	0.52*	-0.09	0.10	-0.26
$r_{\text{elevation}}$	-0.29	0.03	-0.26	0.01

a) *, $P < 0.05$.

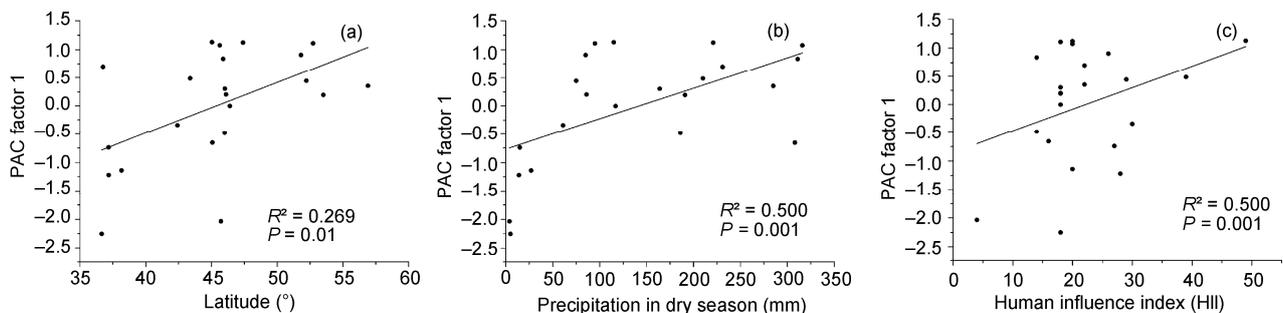


Figure 2 Relationship between PCA factor 1 and (a) latitude, (b) precipitation in dry season and (c) human influence index (HII) for the Eurasian badger.

2.2 Factors affecting trophic diversity

Multiple Regression Analysis between the H' trophic diversity index and food categories indicated H' was negatively correlated with insects and fruits ($R^2 = 0.702$, $F_{21} = 22.362$, $P = 0.000$) (Figure 3). The analysis through multiple regression of H' and geographical variables such as latitude, elevation and aspect revealed there was a significant positive correlation of H' with latitude ($R^2 = 0.199$, $F_{21} = 4.97$, $P = 0.037$) (Figure 4). A Multiple Regression Analysis between H' and environmental variables indicated that the HII was positively correlated with H' ($R^2 = 0.204$, $F_{21} = 5.118$, $P = 0.035$) (Figure 4).

3 Discussion

Eurasian badgers have a flexible diet: fruits, annelids, mollusks, insects, amphibians, reptiles, birds and mammals are all potential preys for badgers. Only in England, badger mainly preys on earthworms [11]. While in most of other localities, insects, mammals and fruits are the main food categories in the badger diet [14,23–25]. The geographical distribution of badger prey may be partly explained by differences in the availability of food resources [35]. In arid areas at low latitude, insects and reptiles are more abundant whereas earthworms are richer in humid areas at high latitudes. Thus, earthworms were eaten by badgers more frequently in humid and high latitude areas [14,21,26] whereas insects and reptiles were predated on in arid areas at low latitudes [25,28,29]. Other carnivore species also display

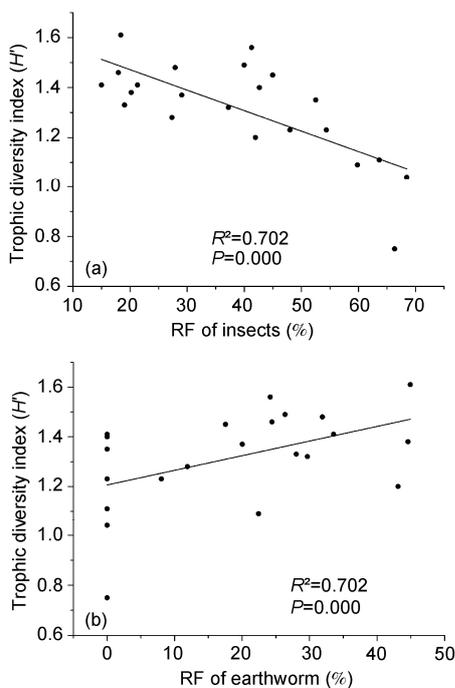


Figure 3 Relationship between trophic diversity index (H') and (a) insects and (b) earthworms for the Eurasian badger.

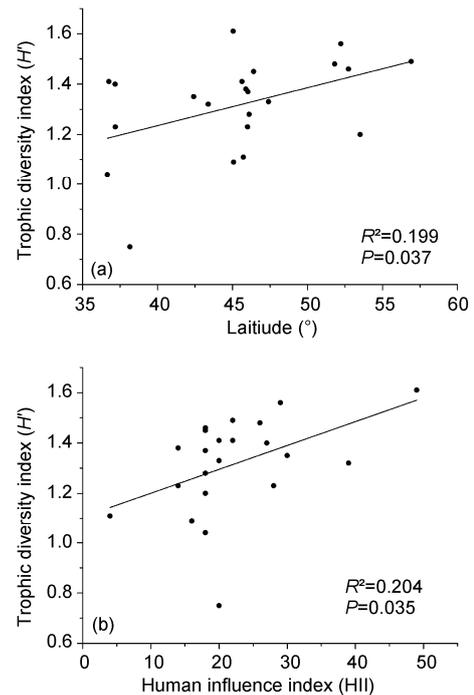


Figure 4 Relationship between trophic diversity index (H') and (a) latitude and (b) human influence index (HII) for the Eurasian badger.

lanalogic flexibility and the characteristic of switching of main food items across their spatial distribution. For example, wildcats mainly eat rodents at northern latitudes but prey on rabbits at southern latitudes [2]. The same pattern of rabbit intake has been shown for red fox [4]. Martens shift from preying on mammals to eating fruit when fruit is abundant [3].

Our results indicate that badgers are generalist foragers across their distribution, according to the definition by Hanski [36]. Badgers should not be considered earthworm specialist predator because earthworms are the principal prey of badgers only at several localities. It is clear that badgers often exploit local resources because reptiles, mammals, insects and fruits are consumed by badgers at an unexpectedly high frequency when these prey are abundant locally. For instance, fruits (mainly olives, pears and figs) are principal food for badgers in the cork oak woodland in Portugal [27]. Badger mainly consumes insects in arid area of Mongolia [25]. Lagomorphs, insects and fruit are main food items in Doñana National Park in Spain [28].

Over a broad geographical area, trophic diversity in wild animal is usually affected by latitude. Researches on the trophic ecology of several species support the prediction of a decreasing trophic diversity at higher latitude. The diversity of the Montagu's harrier (*Circus pygargus*) diet decreased from south to north in northern hemisphere [37]. Diets of wildcats also show similar patterns [2]. However, badger diets show an opposite trend. The lower trophic diversity in badger diets was found at more southern latitudes. Goszczynski et al. [23] also found in Europe

badger food niche was broadest in temperate zone and was narrow at south latitude. Zhou et al. revealed the marten has higher trophic diversity and niche breadth at south latitude because insects are not the main prey of martens, but insects are the principal prey items for badgers especially in southern area [3]. Therefore, it is not surprising that trophic diversity of badgers shows an opposite trend to that of other carnivores.

Primary productivity is often correlated with species and dietary diversity. Bird species richness increases with higher primary productivity [38]. Primary productivity is also an important variable for predicting distribution of herbivores and carnivores. Mongolian gazelles (*Procapra gutturosa*) preferred habitat with intermediate primary productivity [39]. Primary productivity also affects the body mass of roe deer (*Capreolus capreolus*) in low primary productivity area [40]. The consumption of fruit is significantly correlated with primary productivity in brown bears [6]. However, our results indicate that primary productivity does not affect dietary composition in badgers. A similar result was found in dietary diversity of martens [3]. Zhou et al. [3] found martens only utilize trees bearing fleshy fruits; primary productivity does not truly reflect diet composition of martens. Badger mainly predate on animals whereas the fruits in badger diet are seasonal and complementary. Thus, no relationship is found between badger diet and primary productivity.

Our result also reveals that the trophic diversity of badgers is positively related to the intensity of human influence. Human activities lead to wildlife habitat fragmentation and transformation [41]. Researchers have revealed the abundance of species decreases as human activity increases [42,43]. Species diversity and abundance vary distinctly between different habitats, especially for insects [44]. The feeding habitats of badger are more heterogeneous in area under high human influence. When badgers forage during active period, badgers have to cover several different types of habitat patches and capture different categories of foods to sustain themselves every time. This may be the reason for discovering high trophic diversity of badgers in areas of high human influence. Another reason is that badgers have more chances to utilize fruits from gardens. Consuming fruits could lead to higher trophic diversity of martens [3].

In Eurasia, the food spectrum of badgers includes invertebrate, vertebrate, and vegetables; they even adopt to explore the feeding opportunities in human society. Badgers are efficient at exploiting local resources and their trophic diversities have latitude gradients. Therefore, badgers are generalist predators with opportunistic foraging behavior.

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Appendix

S1 The methods and results of badger diet in Qinghai-Tibetan Plateau, China

Methods: Data in China was from our own fieldwork. From October 2008 to October 2010, the study was conducted in the Qinghai Lake Basin (36°39'N, 100°49'E) on the Qinghai-Tibetan Plateau. We collected scats of badgers in typical latrine once a week throughout the whole study period. Badger-like scats found on the ground were discarded, so as were old or visibly weathered scats. Collection from a latrine is considered as one sample during a collection. Scat samples were stored individually in labeled polyethylene bags at –12°C before analysis. Prior to analysis, scats were thawed, oven dried at 50°C for 48 h, and then weighed. They were soaked in water and thoroughly washed through two sieves with mesh sizes of 5 mm and 1 mm respectively. The residue of undigested remains was put into a large shallow tray, and allocated to one of following categories: mammals, birds, reptiles, insects, fruits and other vegetation materials. Rinse water was discarded because there was no earthworm found in badger habitat according to our field survey. We also inspected samples under microscope to observe whether there are any remains of earthworms.

Results: We analyzed 162 scats in total, which contained insects, mammals, birds, reptiles, fruits and mollusk. There were average 3.91 items per scat. Insects occurred most frequently, its frequency of occurrence (FO) and relative frequency (RF) were 100% and 68.45%, respectively. We identified insects eaten by badger were mainly from three orders: Coleoptera, Orthoptera and Hymenoptera respectively. Mammal remains were mainly plateau pika (*Ochotona curzoniae*); its FO and RF were 11.73% and 3.95%, respectively. Bird remains occurred in scats included mostly bones, feather fragments, bills and egg. Birds' FO and RF in scats were 17.90% and 6.30%, respectively. Reptile found in faeces was Qinghai toad-headed agamid lizard (*Phrynocephalus vlangalii*). Its FO and RF were 39.51% and 13.31%, respectively. The FO and RF of fruits of (*Ephedra intermedia*) in badger diet were 25.9% and 8.87%, respectively. No earthworm was found in the scats of badgers.