Diet of the European badgers (*Meles meles*) in urban and rural areas of Norway

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Abstract

The constant expansion of urban habitats provides new opportunities for various wildlife species, referred to as urban exploiters or adapters that allow them to thrive in new conditions. The Eurasian badger (*Meles meles*) can adapt to and exploit urban ecosystems due to its omnivorous behaviour but the species expansion into this habitat can cause conflict with humans, and there is a paucity of data

on badgers in urban habitats. The aim of our study was to explore trophic adaptations of badgers inhabiting urban and rural habitats in Norway. We examined 159 individual badgers by conducting detailed evaluation of allometric factors and trophic analyses of stomach contents. Mean body mass ($\pm$ SE) of males (9.94 ± 0.28 kg) was significantly heavier than females (9.02 ± 0.32 kg). Mean body mass of rural versus urban badgers were not significantly different. However, body mass varied between seasons with an increasing trend throughout the year from spring (7.77 ± 0.24 kg), summer (9.08 ± 0.34 kg) and autumn (11.12 ± 0.33 kg). We identified 12 unique food categories. There were no significant differences in badgers' diet with regard to sex or habitat type. However, the diet varied seasonally and was dominated by earthworms in spring, followed by insects, birds and small mammals in summer, and domestic plants (fruits and cereals) and anthropogenic food in autumn.

Keywords

Electronic supplementary material

Introduction

It has been estimated that half of the global human population resides in urban environments (McCleery et al. 2014). The expansion of urban habitats has led directly to the loss, transformation and destruction of natural habitats (Niemelä 1999; Gehrt 2010) and is an important contributor to biodiversity loss (Pimm and Raven 2000; Brooks et al.

2002; Jantz et al. 2015). Urban habitats are nevertheless suitable for a variety of generalist species, including mammals and birds. Omnivorous mammalian predators such as the red fox (*Vulpes vulpes*) (Harris 1986; Contesse et al. 2004), raccoon (*Procyon lotor*) (Graser et al. 2012) and European badger (*Meles meles*) (Huck et al. 2008b; Harris et al. 2010; Geiger et al. 2018) are typical species that have adapted to densely populated urban habitats.

A primary reason why these species are able to adapt to urban habitats is their ability to utilize anthropogenic waste such as garbage and other food materials (Bornkamm et al. 1982). Such urban food (hereafter anthropogenic food) resources can be important for many wildlife species, as they frequently contain a high calorific value (Bateman and Fleming 2012) and are permanently available (Baker and Harris 2007). Some urban carnivore populations show less inter- and intra-specific competition (Widdows and Downs 2015), aggregate in larger groups (Gilchrist and Otali 2002) and have higher survival rates, even during harsh winter conditions (Savory et al. 2014). Moreover, both urban and suburban areas can provide a mosaic of habitats including, grassland (i.e. lawns), forests, riparian and parkland that are rich in invertebrates and other food items such as fruit and berries (Bevanger et al. 1996).

The European badger is widely distributed in Europe and some parts of Asia (Proulx et al. 2016; Macdonald et al. 2017) and can inhabit urbanized habitats (Harris et al. 2010; Proulx et al. 2016). It is classified as an omnivore and an opportunistic forager (Roper 1994; Aulagnier et al. 2009). Though badgers are known as social carnivores, they are solitary feeders and have individual diet preferences (Robertson et al. 2014). Badgers use a wide variety of food resources, both locally (Harris et al. 2010) and seasonally (Byrne et al. 2012). Earthworms are considered the most common food component in Great Britain and Scandinavia where the species is considered a facultative earthworm specialist (Kruuk 1978a; Kruuk and Parish 1981; Bevanger et al. 1996). Nevertheless, in habitats that lack earthworms, other food resources dominate, including European rabbits (*Oryctolagus cuniculus*) (Martín et al. 1995), insects and fruits (Rosalino et al. 2005), highlighting the dietary flexibility of this species.

Studies of urban badger ecology including distribution, habitat selection, home range and movement patterns have mainly been conducted in Great Britain (Kruuk 1978b; Neal 1986; Huck et al. 2008a; Davison et al. 2008, 2009). Potential human-badger conflicts in urban environments have also been assessed (e.g. Delahay et al. 2009; Ward et al. 2008, 2016; Harrington et al. 2017). Although badgers are known for using food of anthropogenic origin from garbage (Iossa et al. 2010), detailed studies on urban badgers' diet are not common (Harris et al. 2010; Harrington et al. 2017). In Scandinavia, where badger populations have expanded in the last century (Bevanger and Lindström 1995), little is known concerning their trophic habits and utilisation or dependence on anthropogenic resources (Bevanger et al. 1996).

The main objective of this study was to determine the diet of European badgers based on stomach content analyses and compare diet in relation to body measurements, sex, season and habitat type (i.e. urban versus rural). We hypothesised that earthworms would be the most important food item in rural and urban habitats, and that badgers would rely on anthropogenic food items to a greater extent in urban versus rural habitats.

Study area and methods

Badger carcasses were collected from the southeast (Oppland and Østfold counties) and central regions of Norway (Nord-Trøndelang, Sør-Trøndelag, Møre og Romsdal counties; Fig. 1). Both regions were dominated by agricultural landscapes, interspersed with variable-sized patches of deciduous and coniferous forest. The badgers from central Norway, however, were mainly collected from Trondheim city, which is the third largest city in Norway with approximately 200,000 inhabitants, and thus represented typical urban/suburban habitats. Badgers obtained from southern Norway were mainly collected from roads located in typical agricultural landscapes, where no densely human-populated areas existed.

Fig. 1

Locations of badger collection in Norway, counties of Norway: Nord-Trøndelang, Sør-Trøndelang, Møre, og Romsdal, Oppland, Østfold—from North to South

places of collection

scale 1:13 000 000

Trondheim

Oslo

0   200   400
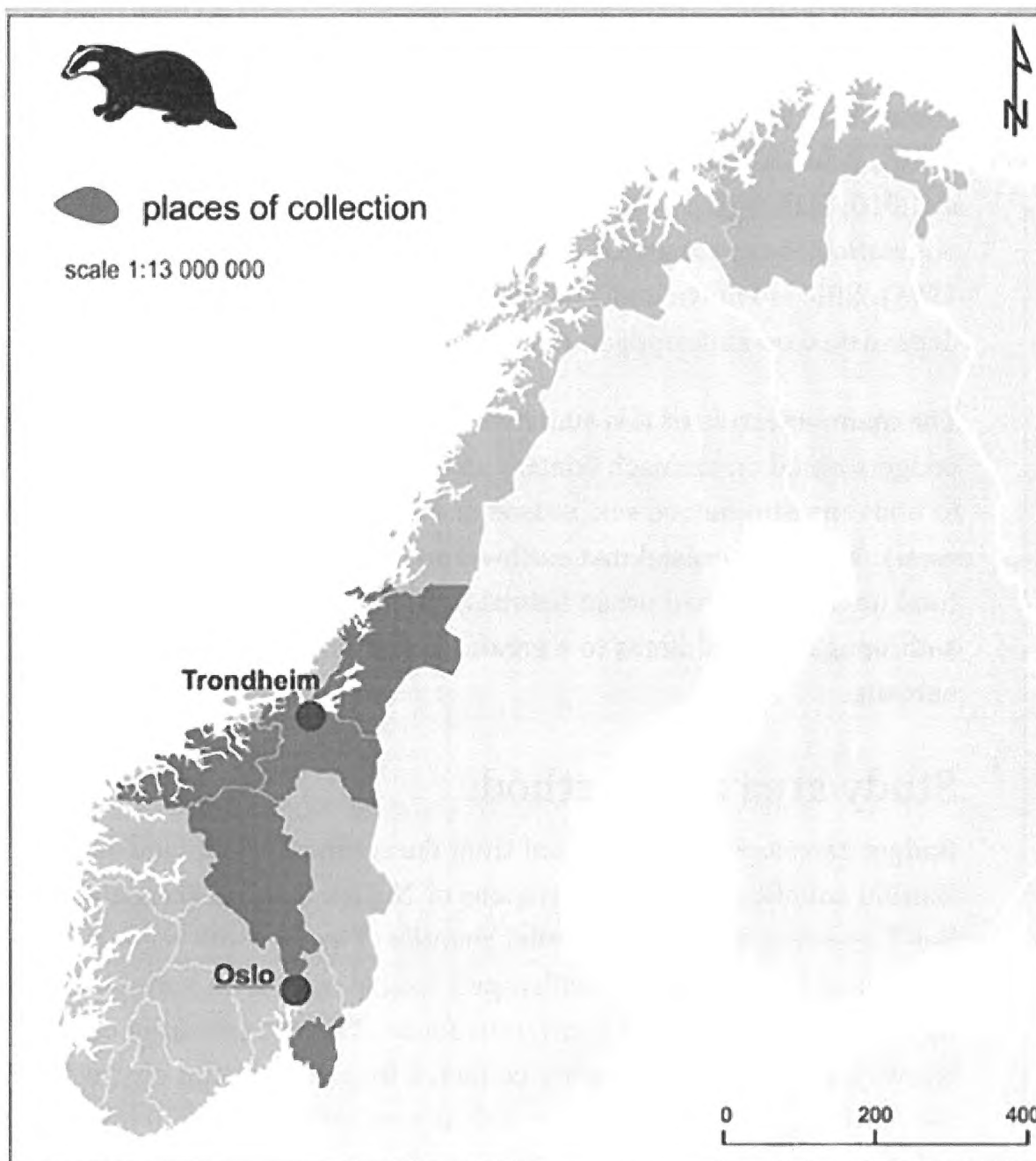
The European badger expanded its range from southern Norway to Central Norway after World War II, and apart from occupying rural areas also established populations in urban habitats (Bevanger and Lindstrøm 1995). In late 1989, the local environmental authorities in the city of Trondheim asked the Norwegian Institute for Nature Research to

initiate a research program focusing urban badgers (Bevanger et al. 1996). The initial aims of the program were related to issues on badger ecology and population dynamics; however, over time, it evolved to comprise several other aspects, including collecting roadkills. For our study, we used badgers collected between 1989 and 1999 in connection with a central Norwegian badger study (Bevanger et al. 1996), and these were mainly roadkills. Also, some specimens regarded as problem individuals when they entered urban areas and suburban gardens were caught in live traps, euthanized and used for further analyses.

For each individual badger, the date, location of collection, sex and body mass data were recorded. A thorough autopsy of each specimen was made in the laboratory at NINA (Norwegian Institute for Nature Research) and several samples were taken of tissue and organs which were frozen and left for further analyses in the freeing facilities at NINA (− 25 °C).

The collection site for each badger was divided in two habitat type categories: rural or urban. Badgers located in either rural forests or woodlands, crop fields and orchards were grouped into the rural category, while the urban areas of Trondheim and its surroundings (suburban areas) were grouped into the urban category. Badger carcasses were also grouped by season, i.e. spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). Specimens collected in winter were excluded from seasonal comparisons due to low sample size.

Stomach contents were washed with running tap water through a 0.5-mm nylon sieve and checked for macroscopic remains, placed on Petri dishes and dried overnight in the air oven (Reynolds and Aebischer 1991; Jędrzejewska and Jędrzejewski 1998). We separated bones and teeth, feathers, hair, invertebrates, fruit and seeds, other plant materials and other food items, e.g. trash. For analysing dietary samples, we used identification keys (Pucek 1981; Teerink 2003; Dove and Koch 2010), reference materials including skulls and skeletons, plant seeds as well as guard hairs, feathers and microscopic slides held at the laboratory of the Institute of Environmental Sciences, Jagiellonian University, Poland.

Food categories were firstly divided using the following main taxonomic groups: molluscs, insects, amphibians, birds, small mammals and plants. Earthworms were separated into a single food category. In stomachs with contents, earthworms were clearly distinguishable and preserved very well. In the case of empty stomachs, they were washed with water which was checked under the microscope for the presence of earthworm chaetae, but the results were negative.

Plants were separated into four groups: (1) wild plants, i.e. native wild species; (2) fruits, i.e. domestic fruit trees; (3) cereals; and (4) other plants, e.g. grass. Carrion was analysed as separate category as well as an anthropogenic food comprised of all identifiable remains such as trash, including pieces of plastic, paper, aluminium foil and food leftovers.

The diet of badgers was expressed as an absolute frequency of occurrence FO, total number of specific food items recorded in all stomachs, and as the percentage of relative frequency of occurrence of each identified food category %FO, number of stomachs containing the food category/total number of stomach samples × 100%. We calculated the trophic niche breadth using Levin's index (B) and standardized Levin's index (B_A) (Krebs 1989; Del Bove and Isotti 2001) for the all individuals, and each sex, habitat type and season:

$$B = \frac{1}{\sum p_i^2} \qquad\qquad B_A = \frac{B - 1}{N - 1}$$

where p_i is the proportion of i food category (p_i = number of occurrences of i food category/total number of occurrences of all food categories), and B is the value of Levin's index and N is the number of food categories. We determined the diet overlap between sex, habitat types and season using Pianka's index (Pianka 1974; Ciampalini and Lovari 1985; Kauhala et al. 1998).

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where O_{jk} is Pianka's measure of niche overlap index between j and k groups, p_{ij} and p_{ik} is the proportion of stomachs with i food category of group j and group k, respectively. The Pianka's index values vary between 0 (no overlap) and 1 (total overlap).

To measure the relevance of each food category for the diet, we calculated the mean dry mass proportion of each food category (xDM). Where pDM_{ip} is the proportion of dry mass of i food category in p stomach and divided by NS, the total of stomachs with food content:

$$xDM_{ip} = \frac{\sum pDM_{ip}}{NS}$$

Separate three-way analyses of variance (season × sex × habitat type), followed by Tukey's (HSD) test, were performed to reveal significant differences in the body mass (g) and stomach mass (g) of individual badger (Online resource 1a). Prior to the analysis, the distribution normality was verified using the Kolmogorov–Smirnov test. Levene's test was performed to assess the equality of variances.

The absolute FO of food categories were compared with Fisher's exact tests. Fisher's exact test was used due to the small sample size of stomachs with anthropogenic food ($n = 26$).

Detrended correspondence analysis (DCA) was applied to examine the association of badger individuals to food categories. The analysis was based on the matrix of the xDM for particular individuals. The algorithm followed Hill and Gauch (1980), with modifications according to Oxanen and Minchin (1997). Prior to DCA, food categories with a %FO lesser than 5% in the total diet were removed from the analysis (molluscs, amphibians and carrion). Permutational multivariate analysis of variance (PERMANOVA) was performed to test the differences in nutritional composition of badgers among seasons, sexes and habitat types (Anderson 2001). The analysis was based on the matrix of averaged xDM calculated for particular combinations: season × sex × habitat type (Online resource 1b). Bray-Curtis coefficient with 9999 permutations was used for each test. Next, we evaluated which food category was the most responsible for differentiating badger diet

of three considered seasons using similarity percentage (SIMPER) analysis (Clarke 1993). Subsequently, DCA was used to examine the pattern of similarities between three seasons in terms of badger nutritional composition based on the same data matrix as in PERMANOVA.

Three body mass categories for male and female badger individuals were distinguished as follows: for females, (1) up to 7.3 kg, (2) 7.3–10 kg, (3) over 10 kg; for males, (1) up to 9.1 kg, (2) 9.1–10.5 kg, (3) over 10.5 kg. Categories were set as such in order to ensure groups of similar size for analysis (Online resource 1c). Then, we used PERMANOVA to test the significance of differences in nutritional preferences between three distinguished body mass categories along with post hoc pairwise comparisons between particular categories. Next, SIMPER analysis to evaluate which food category was the most responsible for differentiating badger diet between particular body mass categories. Bray-Curtis coefficient with 9999 permutations was used for each test.

One-way analysis of variance (ANOVA) followed by Tukey's (HSD) test were performed to test the significance of differences in stomach mass (with contents) between badgers assigned to particular body mass categories for each sex separately. Student's t test were performed in order to test the significance of differences in stomach mass that had contents, between male and female badgers in each body mass category separately. Prior to analyses, the distribution normality was verified using the Kolmogorov–Smirnov test. Levene's test was performed to assess the equality of variances.

All statistical calculations were performed using PAST 3.25 (Hammer et al. 2001), Statistica 13 (StatSoft, Tulsa, OK, USA) and RStudio version 0.99.447 (RStudio Team 2015), integrated in *software* R version 3.2.0 (R Development Core Team 2015).

Results

In total, 159 badgers (85 male, 74 female; 97 rural, 62 urban; 37 spring, 62 summer, 58 autumn, 2 winter) were collected. The body mass of badgers varied significantly with season (Table 1), being lowest in

spring and highest in autumn (Fig. 2). Moreover, body mass ($\pm$ SE) of males (9.94 $\pm$ 0.28 kg) was significantly higher than females (9.02 $\pm$ 0.32 kg). In regard to stomach mass, significant effects of season were found (Table 1), but it was also dependent on sex (i.e. there was a significant season $\times$ sex interaction). The stomach mass of male badgers increased from spring to autumn, whereas in female badgers, an increased stomach mass was observed in summer compared with spring and autumn (Fig. 2). Badger body mass and stomach mass did not differ between rural and urban habitat types (Table 1).
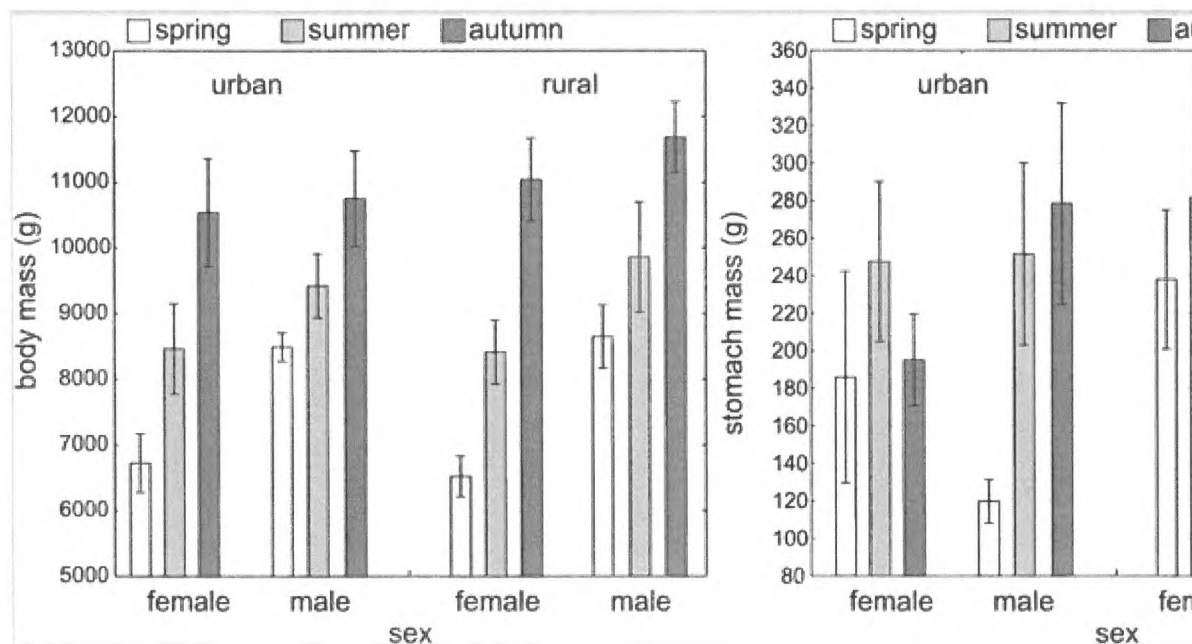
Table 1

The results of three-way ANOVA for effects of season, sex and habitat type, and their interactions, on body mass and stomach mass with content. Significant values are provided in bold letters ($p < 0.05$)

AQ3

Source	df	F	p
Body mass			
Season	**2**	**22.74**	**0.000**
Sex	**1**	**8.85**	**0.003**
Habitat type	1	0.55	0.461
Season $\times$ sex	2	1.10	0.336
Season $\times$ habitat type	2	0.30	0.745
Sex $\times$ habitat type	1	0.28	0.596
Season $\times$ sex $\times$ habitat type	2	0.00	0.998
Stomach mass before autopsy			
Season	**2**	**3.35**	**0.038**
Sex	1	0.60	0.441
Habitat type	1	0.00	0.957
Season $\times$ sex	**2**	**3.56**	**0.031**
Season $\times$ habitat type	2	0.33	0.719
Sex $\times$ habitat type	1	1.13	0.290
Season $\times$ sex $\times$ habitat type	2	0.14	0.873

Fig. 2

Body mass and stomach mass (mean ± SE) of badger individuals distinguished by season, sex and habitat type

AQ2

Twelve food categories were identified in the stomachs (Table 2). A third (33.3%) of stomachs had only a single food category present, 36.53% had two and 30.2% had three or more categories. Earthworms were the most frequent food category (%FO = 49.7%), followed by insects (%FO = 36.5), and fruits (%FO = 27.7%) (Table 2, Online resource 2).

Table 2

Diet composition of badgers, based on the analysis of 159 stomachs with fo[c] badgers. %FO, the percentage of relative frequency of occurrence (FO); mean d[i]

Food categories	Male %FO	Male xDM	Female %FO	Female xDM	Rural %FO	Rural xDM	Urban %FO	Urban xD
Earthworms	45.9	29.0	54.1	32.2	45.4	28.2	56.5	34.
Molluscs	1.2	1.2	4.1	0.1	2.1	1.1	3.2	0.1
Insects	40.0	8.8	32.4	7.3	38.1	8.5	33.9	7.5

Food categories	Male %FO	Male xDM	Female %FO	Female xDM	Rural %FO	Rural xDM	Urban %FO	Urban xDM
Wild plants	8.2	5.3	8.1	2.2	10.3	5.2	4.8	1.8
Fruits	21.2	10.3	35.1	19.1	26.8	12.9	29.0	16.7
Cereals	17.6	14.5	16.2	9.8	21.6	16.5	9.7	5.7
Other plants	14.1	5.9	14.9	6.3	13.4	5.9	16.1	6.4
Amphibians	3.5	0.5	1.4	0.1	4.1	0.5	0.0	0.0
Small mammals	15.3	5.2	23.0	10.1	18.6	8.0	19.4	6.6
Avifauna	15.3	6.2	18.9	6.1	15.5	5.1	19.4	7.9
Carrion	1.2	1.2	1.4	1.0	1.0	1.0	1.6	1.2
Anthropogenic food	16.5	12.2	16.2	5.8	11.3	7.2	24.2	12.3
Examined stomachs	85		74		97		62	

Anthropogenic food items were diverse and included items such carrots, potatoes, fish and other items of no direct dietary value but of potential hazard, e.g. string, cigarettes or plastic (Online resource 3).

The trophic niche breadths of all badgers had similar values in different habitat types and according to sex, different values between seasons. Badger diet overlapped highly between both sexes $O_{jk} = 0.97$ and habitat type $O_{jk} = 0.96$ but had a lower overlap between seasons (Table 3).

Table 3

Badgers trophic niche breadth (B, B_A) and overlap (O_{jk}) between sexes, habitat type and season

	B	B_A	O_{jk}
All badgers	7.42	0.58	–
Male	7.29	0.57	0.97

	B	B_A	O_{jk}	
Female	7.35	0.58		
Rural	7.58	0.60	0.96	
Urban	6.87	0.59		
Spring	4.88	0.43	Spring–Summer	0.85
Summer	7.03	0.60	Spring–Autumn	0.80
Autumn	7.36	0.58	Summer–Autumn	0.88

The absolute FO of food categories did not differ statistically between sex. Anthropogenic food was the only statistical difference ($p = 0.047$) across habitat type (rural $n = 11$, %FO = 5.5%; urban $n = 15$, %FO = 11.1%). Cereals also showed a tendency to occur more frequently in the rural habitat type (rural $n = 21$, %FO = 21.6%; urban $n = 6$, %FO = 9.7%; $p = 0.054$). There were significant differences in the majority of food categories between the seasons (Table 4).

Table 4

The comparison of frequencies of badgers' food categories in relation to sex, habitat type and season. Fisher's exact test results. Bold letters indicate significant differences ($p < 0.05$)

Food categories	Sex	Habitat type	Season
Earthworms	0.342	0.195	0.082
Insects	0.409	0.616	**0.003**
Wild plants	0.999	0.253	0.065
Fruits	0.053	0.856	**0.008**
Cereals	0.836	0.054	**0.005**
Other plants	0.999	0.650	0.407
Small mammals	0.230	0.999	**0.077**
Avifauna	0.673	0.525	0.066
Anthropogenic food	0.999	**0.047**	0.962

The association of individual badgers to the identified food categories was analysed by means of DCA. The eigenvalues of axes 1 and 2 were 0.889 and 0.764, respectively. The nutritional preferences of badgers were very variable across seasons, sex and habitat type. Although no clear pattern was discernible, high insect consumption was mainly associated with the summer for both sexes in both habitat types, and large amounts of wild plants and anthropogenic food was preferred by males (Fig. 3).

Fig. 3

Detrended correspondence analysis (DCA) scatter plot of badger individuals and particular food categories along the first two axes
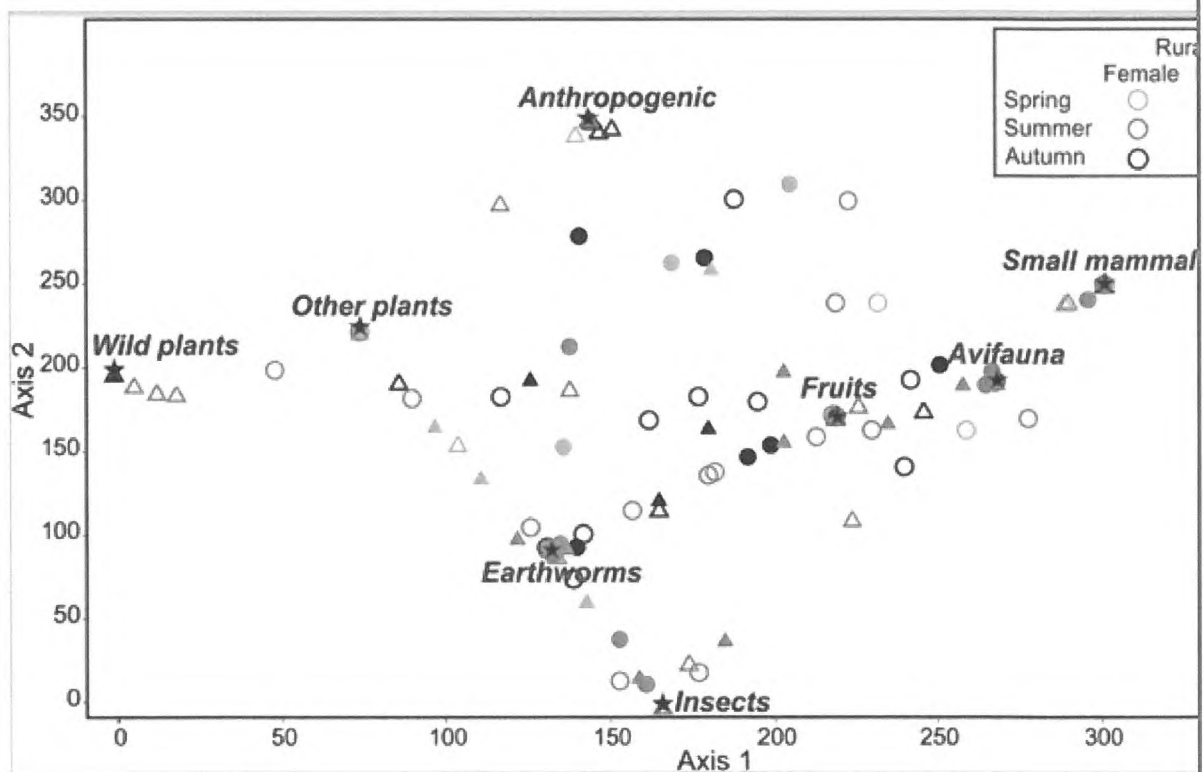
The diet of badgers differed significantly between seasons (PERMANOVA; $F = 5.404$, $p < 0.001$). Earthworms, fruits and cereals contributed greatly to differences in mean dry mass proportions of each food category in the badger diet between spring, summer and autumn seasons, constituting over 50% of the total variation (SIMPER analysis; Table 5). Earthworms and other plants had the highest contribution in spring compared with the other seasons. In summer, insects, avifauna,

small mammals and wild plants were the highest in terms of contribution to badger diet, while fruits, cereals and anthropogenic categories were more related to autumn. There were no significant differences between sexes and habitat types in terms of badger dietary preferences (PERMANOVA; $F = 0.456$, $p = 0.799$ and $F = 0.967$, $p = 0.462$, respectively). DCA ordination showed the similarities between three seasons in terms of badger dietary preferences. The seasons were clearly separated from each other along the first axis (Fig. 4).

Table 5

Food categories with the highest impact on differences in the badgers' diet (SIMPE highest mean dry mass proportions (xDM) for particular season are provided in bo

Food categories	Average dissimilarity	Contribution (%)	Cumulative (%)	Mean	
				Sea	
				Spring	Sum
Earthworms	12.340	24.69	24.69	**0.552**	0.271
Fruits	8.776	17.56	42.25	0.040	0.10(
Cereals	6.716	13.44	55.69	0.058	0.047
Insects	5.064	10.13	65.82	0.043	**0.158**
Anthropogenic	4.396	8.794	74.61	0.093	0.082
Avifauna	3.653	7.308	81.92	0.022	**0.109**
Small mammals	3.329	6.659	88.58	0.065	**0.117**
Other plants	3.209	6.42	95.00	**0.100**	0.05(
Wild plants	2.500	5.001	100	0.000	**0.051**

Fig. 4

Detrended correspondence analysis (DCA) scatter plot showing the association particular seasons to distinguished food categories along the first two axes. R, rural; U, urban; ♂, male; ♀, female
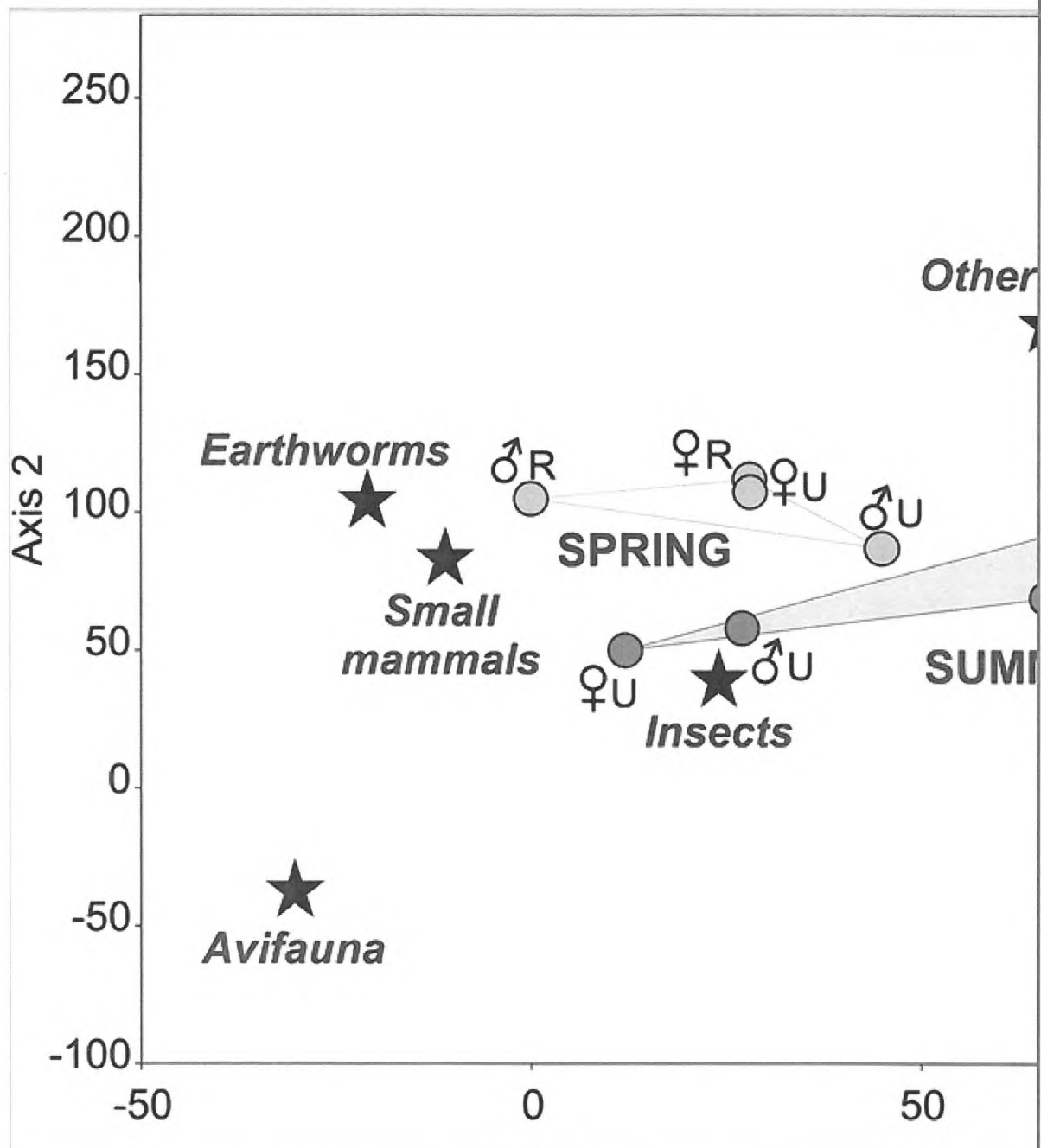
The diet of female badgers differed significantly between body mass categories (PERMANOVA; F = 1.791, p = 0.049). There were no significant differences in dietary constituents for male badgers between body mass categories (PERMANOVA; F = 1.445, p = 0.127). Pairwise comparisons for females revealed significant differences only between category '1' and '3' ($p < 0.05$). All plant categories including fruits, cereals and other plants, and insects food items were connected to the heaviest female badgers weighing over 10 kg (category '3'), whereas the lightest females (body mass category '1' up to 7.3 kg) were

associated mainly with animal diet comprised of earthworms, small mammals, birds and anthropogenic food (Table 6).

Table 6

Food categories with the highest impact on differences in the female badgers' diet (SIMPER analysis). The highest mean dry mass proportions (xDM) for particular body mass categories are provided in bold. 1—up to 7.3 kg; 3—more than 10 kg

Food categories	Average dissimilarity	Contribution (%)	Cumulative (%)	Mean xDM Body mass category	
				1	**3**
Earthworms	21.030	25.300	25.30	**0.369**	0.254
Fruits	16.150	19.430	44.73	0.077	**0.300**
Cereals	12.540	15.080	59.81	0.074	**0.212**
Small mammals	9.582	11.520	71.33	**0.181**	0.027
Anthropogenic	7.088	8.525	79.86	**0.129**	0.022
Insects	5.756	6.923	86.78	0.045	**0.078**
Other plants	5.611	6.749	93.53	0.055	**0.066**
Avifauna	4.222	5.078	98.61	**0.071**	0.017
Wild plants	1.159	1.394	100	0.000	**0.023**

One-way ANOVA revealed significant differences in stomach mass with content between male badgers assigned to three body mass categories (F = 4.206, $p = 0.018$; Online resource 4). The stomachs of the lightest males (category '1' up to 9.1 kg) were significantly lighter than those of the heaviest males (category '3' > 10.5 kg). Contrastingly, females did not differ significantly in terms of stomach mass between body mass categories. As regards differences between sexes in stomach mass with content, no significant differences were found in any body mass category (Student's t test, $p > 0.05$).

Discussion

In our research, road-killed badgers were used as the basis for determining diet. Hence, there is the possibility that our samples may not have been representative of the badger population as the roadkills could be biased seasonally. Badgers in Norway hibernate from late October to early April (Bevanger and Brøseth 1998). Thus, roadkills were only found during the summer months. The mortality pattern differed through the summer months among adult badgers, with males accounting for greater mortality in spring, whereas females were more common in the autumn (Bevanger et al. 1996). The explanation for this could be that females remain with their cubs until late May to early June and are restricted in movements until the cubs start to follow them in late June to early July. The male mortality may be connected to mating although the mating season seems to be prolonged from spring throughout the summer months. An increase in female mortality in late summer to early autumn would probably be connected to the fact that the females have a shorter period to rebuild the body fat reserves after the reproduction and have to be more active during late summer to autumn to prepare for winter survival (Bevanger et al. 1996). Similarly, badger road fatalities in Great Britain show a strong seasonal variation with peaks in spring (January–March) and in mid-summer (July–September). Both periods are in mating season and additionally, females search for food during lactation in summer (Davies et al. 1987; Clarke et al. 1998). In the Netherlands, the peaks of road badger fatalities were noted in March and later between August and September with slightly higher numbers of females (Dekker and Bekker 2010). In general, traffic is a considerable threat and mortality cause in badgers but observed mainly in adults (Lankester et al. 1991).

AQ4

In our study, badgers showed sexual dimorphism in their body masses, where males were heavier than females. This is similar to the results obtained by several authors (Van den Brink and Ma 1998; Abramov and Puzachenko 2005; Byrne et al. 2015). In general, European badgers tend to be the largest in temperate regions with males significantly bigger than females (Virgós et al. 2011). Female cubs grow faster than males and reach their maximum size in 16 months, whereas males continue to grow until 18 months of age. This rapid growth is due to several factors

including the impact of sex hormones and reaching puberty, intra- and inter-specific interactions and higher energy requirements of females during lactation (Sugianto et al. 2019). In contrast to males, females have high intra-sexual reproductive suppression which can directly lower body size. Larger females are more successful breeders and compete for reproduction and also have more access to resources (Yamagouchi et al. 2006). In addition, body size is affected by population density and social factors within the social group. For example, male cubs were smaller in groups with more adult males (Sugianto et al. 2019), and in female, badgers' lower body mass is related to increased group size especially in autumn (Macdonald et al. 2002). The intensity of intra-sexual competition experienced in early adulthood is more reflected later in males than females by faster mass decline in later maturity (Beirne et al. 2015).

AQ5

AQ6

In Northern Ireland, George et al. (2014) measured faecal and serum cortisol in badgers, which was related to physiological stress. It was found that there was seasonal variation in hormone levels, with spring and summer peaks corresponding to mating periods and possible nutritional stress.

Weather conditions are another important factor that may affect the body size of cubs and females especially in spring (Sugianto et al. 2019). Warmer and milder winters are positively associated with body mass of badgers and consequently higher fecundity and survival (Byrne et al. 2015). The Norwegian badgers were heavier in autumn and much lighter in the following seasons. This is related to the requirement to increase their body mass in autumn before hibernating over winter (Roper 1994; Bevanger and Brøseth 1998; Virgós et al. 2011; McClune et al. 2015). In Poland, the body mass of badgers also shows seasonal variation with the heaviest individuals found in summer, and this was related to different activity levels of the animals, which was associated directly with food availability, mainly earthworms (Kowalczyk et al. 2003). In our study, badger body mass did not differ between rural and urban areas; this could indicate that preparation for hibernation was not influenced by habitat type.

Male badger stomachs were lighter in spring compared with the other seasons, with stomach mass related to body mass, in that the lightest male badgers had smaller stomachs compared with the heaviest males. Female badgers had a different pattern in this study, with stomachs heavier in summer than in autumn or spring. This can be explained by the fact that in northern populations, food is mainly abundant in spring and summer, and the animals forage on available resources. Heavier stomachs of females in summer were probably associated with higher energetic demands, especially for lactating females (Davies et al. 1987; Sugianto et al. 2019). Lighter stomachs in females during autumn could reflect the period after weaning and foraging for more nutritious food, especially for smaller individuals. The lightest females (up to 7.3 kg) foraged mainly on animal derived and anthropogenic food which could help them to rebuild body reserves. At the same time, heavier females (body mass > 10 kg) foraged mainly on plant-sourced food, mainly cereals and fruits.

Badgers' diet differed between seasons, indicating that seasonality had the biggest influence on badger diet in this study. In Norway, winters are long and harsh (Bevanger and Brøseth 1998), and it is necessary for badgers to hibernate. In spring, badgers were relative earthworm specialists, while in summer and autumn, badgers had a more diverse diet. As insects were found mostly in summer, and cereals and fruits in spring, seasonality appears to be the driver of badgers' diet in Norway.

Earthworms were the most important food category for badgers in the study, having been identified in half of the stomachs (%FO = 49.7%), and with the highest xDM (30.5%). However, our results were lower than in other studies conducted on badgers at higher latitudes where the relative frequency of earthworms varied between 72.5 and 82.4% (Madsen et al. 2002; Zabala et al. 2002; Balestrieri et al. 2004; Cleary et al. 2011; Mysłajek et al. 2013). Even though badgers had a high consumption of earthworms, their diet was diverse with a total of 30 different food items recorded, and a trophic niche breadth of $B = 7.42$ across all badgers. In studies, where badgers had a high consumption of earthworms, the Levin's index varied between 2.28 and 5.01 (Madsen et al. 2002, calculated by author; Balestrieri et al. 2004, calculated by

author; Cleary et al. 2011, calculated by author; Mysłajek et al. 2013). In our study earthworms were consumed by badgers mainly in spring, which is congruent with reports for this species from a temperate climate (e.g. Kowalczyk et al. 2003; Mysłajek et al. 2013).

By using the xDM, we divided the badgers' diet into four levels: (1) earthworms (xDM = 30.5%); (2) fruits and cereals (xDM = 26.7%); (3) anthropogenic food, insects and small mammals (xDM = 24.8%); (4) all remaining categories (xDM = 18.0%). Hence, we concluded that badgers' diet was predominantly based on earthworms and agricultural (cereals) or orchard crops (fruits) (xDM = 57.2%), implying that human-altered, semi-natural habitats had a major importance in the overall diet (Byrne et al. 2015). The presence in badgers' diet of plant species from crops or fruits are also common in other ecosystems, both temperate (Shepherdson et al. 1990; Mysłajek et al. 2013; Byrne et al. 2015) and Mediterranean (Del Bove and Isotti 2001; Rosalino et al. 2005; Barea-Azcón et al. 2010; Requena-Mullor et al. 2016) regions. Also, higher consumption of cereals by badgers could be explained by an increased protein intake (Remonti et al. 2011). Cereals also had a tendency to occur more frequently in the rural habitat type. The small difference between habitats may be explained by the absence of exclusive food categories in the habitat types, which could be related to generally low urbanization levels in Trondheim city. Trondheim urban and suburban gardens had a high presence of fruit trees and bushes which were used by badgers as a common food resource (KB, personal observation), which could have led to a low difference between habitat types.

In this study, the trophic niches of male and female badgers highly overlapped, and there were no significant differences in food category occurrences in terms of sex. Between rural and urban habitats, the trophic niches also overlapped highly, and the only category which significantly distinguished both habitats was anthropogenic food. As we hypothesised, badgers in urban habitats consumed more anthropogenic food than in rural habitat type. This study has shown that anthropogenic food had a low variation in consumption across seasons ($p = 0.962$), reflecting its constant availability due to human activities, despite the general seasonality found for other food items. Together with cereals

and fruits, this food was consumed by badgers mainly in autumn which served to complement other limited resources. Anthropogenic food can be easily accessible and have a high caloric value, but garbage raiding also poses a potential hazard for badgers due to the consumption of (1) indigestible products, such as cigarette butts and plastics, as we observed in this study (Online resource 3) or (2) toxic products, e.g. chocolate (Jansson et al. 2001). Nevertheless, badgers are urban adapters (Bateman and Fleming 2012) that can dwell in urbanized areas and use supplementary food but are still largely dependent on natural resources. Badgers are considered highly adaptable in terms of foraging strategies, as they are both generalist and opportunistic feeders (Virgós et al. 2004; Byrne et al. 2015; Macdonald and Johnson 2015; Requena-Mullor et al. 2016). Our research confirms the pattern of adaptability in terms of badgers' diet in Norway.

This study did not prove that access to urban habitats significantly altered badger diet and, although anthropogenic food was utilised (especially in urban sites), it was not as a preferred alternative resource as observed for other species such as red foxes (Contesse et al. 2004; Bino et al. 2010). Continued research studies in urban habitats are important as cities continue to expand and wildlife populations exploit resources that are available. Urban habitats can also be dangerous for wildlife species, creating conservation problems and conflicts (Bjerke et al. 2003; Ward et al. 2016) that will need careful management. As badgers dwell in cities, the species can be an appropriate model organism to study mitigations and conservation techniques for the increasing challenges that exist between wildlife and urban development.

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Compliance with ethical standards

The collection of the material and analyses within the research submitted to the journal were conducted along with the current legislative regulations obligatory in Norway that do not require additional ethical clearance.

Conflict of interest   The authors declare that they have no conflict of interest.

Electronic supplementary material

ESM 1   **ESM 2**   **ESM 3**   **ESM 4**

(PDF 296 kb)(PDF 138 kb)(PDF 292 kb)(PDF 288 kb)

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AQ7

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