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Diet of badgers (*Meles meles*) in central Switzerland: an analysis of stomach contents

By T. J. Roper and P. Lüps

School of Biological Sciences, University of Sussex, Brighton, UK and Naturhistorisches Museum der Burgergemeinde Berne, Berne, Switzerland

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Abstract

We investigated the contents of 217 badger stomachs from central Switzerland. Overall, faunal material constituted 55%, and vegetal material 45%, of the diet. Earthworms had a higher frequency of occurrence, were more often the only prey found in a stomach, and occurred in more months of the year, than any other food type; but they were not usually eaten in large volumes. Voles, insects and maize were eaten during most of the year but never in large volumes, while wasps, cherries, plums and oats were eaten seasonally and in large volumes. Total food intake was greatest in autumn, while the diversity of foods consumed was greatest in summer. No particular type of food was preferentially consumed at any particular time of night, nor was there a significant correlation between the number of different foods consumed and the total volume of stomach contents. Composition of the diet did not differ significantly with age, sex or degree of tooth wear of the donor animals; but total volume of stomach contents, tooth wear and age were significantly correlated with one another. Faunal foods in general, and earthworms in particular, can be regarded as staple components of the diet of badgers in this part of Switzerland. However, the most conspicuous feature of badger diet is the diversity of foods consumed, not only by the population as a whole but also by individual animals during only a few hours of foraging activity.

Introduction

Many studies of badger (*Meles meles*) diet have been undertaken, in countries including the U.K., France, Spain, Sweden, Denmark, Switzerland, Italy, Ireland, the Netherlands and the former Soviet Union (for references see Vink 1993; Lüps and Wandeler 1993). It is clear from these studies that the species consumes a wide variety of foods including both faunal and vegetal material, causing most investigators to describe badgers as "omnivorous", "generalist" or "opportunistic" foragers (see review by Roper 1994). However, there is a tendency for badger diet to be dominated by earthworms in northwestern and central Europe and by other foods, especially fruits and insects, in Mediterranean regions (Pigozzi 1987). This has led to the suggestion that badgers are in fact food specialists, with any one population preferentially selecting one or at most a few particular food types from the range that is potentially available in its particular habitat (Kruuk 1986,1989; Kruuk and Parish 1981).

The "food specialist" hypothesis can be questioned on the grounds that some studies show badgers to have a broad diet, even within a single study area (Roper 1994). A more fundamental difficulty, however, arises from the fact that almost all studies of badger diet so far published have been based on the analysis of faecal remains. Such data are likely to be incomplete, because of the difficulty of estimating the volume of food eaten on the basis of whatever fragments remain in the faeces: for example, faeces analysis tends to underestimate the importance of mammalian and avian material in the diet, and to overestimate the importance of small, frequently consumed items such as insects (e. g., Liberg 1982; Reynolds and Aebischer 1991). The problem of converting faecal remains to an estimate of volume of food consumed is particularly acute for soft-bodied invertebrates such as earthworms, whose size and number have to be deduced from fragments such as chaetae or gizzard rings (Bradbury 1977; Wroot 1985). Furthermore, faeces analysis can at best give information about the relative, as opposed to the absolute, amounts of different foods ingested (Roper 1994).

Data from stomach contents constitute a superior source of information about diet because they are more accurate and yield information about the absolute amounts of different foods eaten. Furthermore, by comparing the contents of stomachs from animals killed at different times of night, it is possible to extract information about the way in which consumption of different foods proceeds over the course of a typical foraging period (Skoog 1970; Lüps et al. 1987 b). Thus, data from stomach contents can permit inferences about the foraging tactics of individual animals as well as about the overall dietary adaptation of a population. So far, however, only four studies of badger stomach contents from western European populations have been published (Andersen 1954; Skoog 1970; Stocker and Lüps 1984; Neal 1988), and one of these (Skoog 1970) only provides information about the frequency, as opposed to the volume, of different foods consumed.

In the present study we describe the contents of 217 badger stomachs from central Switzerland. Our intention in analysing the data was (a) to provide a more accurate and detailed overall picture of badger diet from this part of Europe than has hitherto been available; (b) to address the controversy as to whether badgers are best described as food specialists or generalists; and (c) to extract information about the sequence in which different foods are eaten during a single foraging period in individual animals.

Material and methods

Animals and study area

Carcasses of 217 badgers (96 males, 121 females) were collected by the Berne Natural History Museum during the period 1973 to 1992, from an area of about 650 km^2 in the region Berne-Thun-Burgdorf, in the canton of Berne, Switzerland. The area consisted of 30% forest and 57% farmland, the forests containing a mixture of deciduous and coniferous species (especially beech *Fagus sylvatica*, Norway spruce *Picea abies* and silver fir *Abies alba*). Farmland was used mainly for cattle breeding and production of potatoes, other root crops and cereals (primarily maize, wheat, barley, oats and rye). Fruit trees (apple, pear, plum and cherry) were often situated near to farms and villages.

Most of the animals were killed by road or railway traffic (N = 120) or were shot to prevent damage to crops (N = 67); a minority (N = 30) were found dead from other or unknown causes. In addition to information about stomach contents, the following data were collected whenever possible: sex of the animal, cause and time of death (date and time of day), body weight and degree of tooth-wear (see Lüps 1983, 1984; Lüps and Roper 1988 for details). 160 animals were aged by counting dentine rings in the lower canines and the remainder by other methods (Lüps et al. 1987 a). Those aged 12 months or less were classed as "young", the remainder as "adult".

Analysis of stomach contents

After removal and dissection of a stomach, the contents were washed out and stored in 4% formalin. Material was subsequently analysed by washing it with water in a 1 × 1.5 mm sieve and sorting the solid remains into the following 17 "primary" prey categories: voles, other mammals, reptiles, birds (including egg shells), gastropods (slugs and snails), earthworms, wasps, bumble-bees, other insect larvae, other insect imagos, cherries, plums, strawberries, maize, oats, seeds, and grass and other types of leaves. For further analysis, these primary prey categories were combined into four "secondary" categories (invertebrates, vertebrates, fruits and cereals) and two "tertiary" categories (faunal and vegetal material).

The volume of each primary prey category was determined to the nearest 0.1 ml using a glass measuring cylinder, by recording the volume of water displaced. A given type of prey was only recorded as "present" if its volume exceeded 0.5 ml, and stomachs were classified as "empty" (i. e., none of the contents were recorded) if they contained less than 20 ml of material.

As well as recording the volume of each prey type for each stomach, we also recorded the frequency of occurrence of different prey types (i. e., the percentage of stomachs containing each prey type, regardless of volume), prey "diversity" (i. e., the number of different prey types found per stomach), and "main prey" (i. e., the most voluminous prey type found per stomach). Stomachs were collected in every month of the year but comparisons between individual months were not possible because too few stomachs containing food were available in the months December to February. Therefore, in order to examine seasonal changes in diet, the year was divided into four three-month seasons: spring (March to May), summer (June to August), autumn (September to November) and winter (December to February). Variability in intake was assessed by calculating the coefficient of variance (sd × 100/mean) for each food type across all stomachs.

One stomach (from a female, killed in September 1989) was exceptionally full: it contained 1 235 ml of material, consisting of 1 153 ml maize, 75 ml plums and 7 ml of other items (slugs, insects, carrion, grass). Since this stomach contained more than twice as much material as any other, we excluded it from the analysis in order to avoid unduly biassing the results.

Results

Empty stomachs

105 stomachs contained < 20 ml of material and were therefore classed as "empty". There were no seasonal, sex or age differences in the proportion of empty stomachs ($\chi^2 = 3.17$, df = 3; $\chi^2 = 0.85$, df = 1; $\chi^2 = 1.1$, df = 1), nor was there any relationship between the likelihood of a stomach being empty and the way in which the donor was killed ($\chi^2 = 3.21$, df = 2). Empty stomachs were therefore an unbiassed subset from the total sample, presumably deriving from animals which happened to be killed early in the night.

Effects of age and sex

Male badgers weighed significantly more than females (mean body weights = 12.62 kg and 11.23 kg respectively; Mann-Whitney test, U = 6 080, $p < 0.01$), but there was no sex difference in total volume of stomach contents, diversity of stomach contents or percentage of faunal versus vegetal material in the diet (Mann-Whitney tests, U < 3 200, $p > 0.8$). No significant effect of age (young versus adult) was found on either the diversity of stomach contents or the percentage of faunal material (Mann-Whitney tests, U < 950, $p > 0.7$). However, there were significant positive correlations between age and total volume of stomach contents (Spearman test, $r_s = 0.26$, N = 80, $p < 0.05$), age and degree of tooth wear ($r_s = 0.85$, N = 80, $p < 0.001$), and degree of tooth wear and total volume of contents ($r_s = 0.25$, N = 109, $p < 0.01$). Thus older animals had fuller stomachs at the time of death, despite the fact that their teeth were more worn.

Since these findings provide no evidence that the composition of the diet (as opposed to total amount eaten) was affected by either age or sex, we combined the whole sample of stomachs for subsequent analysis.

Overall composition of the diet

Table 1 summarises the occurrence of each of the 17 primary, the 4 secondary and the 2 tertiary prey categories. The most consistently consumed primary prey was grass/leaves, which had the highest frequency of occurrence, was present in every month of the year and had the lowest coefficient of variance. There was no significant correlation between the absolute volume of grass/leaves per stomach and the volume of any other primary, secondary or tertiary prey category, contrary to what might have been expected if grass/leaves were ingested accidentally whilst foraging for other prey ($r_s < 0.25$ in all cases). Nor was the volume of grass/leaves correlated with the combined volume of all other stomach contents ($r_s = 0.20$). Nevertheless, we excluded grass/leaves from subsequent analyses since it seems unlikely that badgers derive significant nourishment from such material.

Table 1. Summary of stomach contents (N = 111).

Category	Food	Frequency of occurrence (%)	Mean vol when[1] present (ml)	Mean vol(ml)[2]	Main prey (%)[3]	Only prey (%)[4]	Months present	CV (%)
1°	Voles	27	32.5	8.8	8	2	10	235
	Other mammals	12	56.4	6.6	4	1	6	588
	Reptiles	1	3.0	0.1	0	0	1	–
	Birds	2	3.0	0.1	0	0	3	–
	Slugs/snails	20	26.6	5.3	4	0	5	395
	Earthworms	76	60.2	45.5	34	13	11	170
	Wasps	13	130.8	16.5	6	5	4	366
	Bees	1	22.0	0.2	0	0	1	–
	Insect larvae	14	1.5	0.2	0	0	8	435
	Insect imagos	49	1.1	0.5	0	0	8	167
	Cherries	21	128.9	26.7	19	2	3	266
	Plums	12	123.2	14.4	6	2	3	308
	Strawberies	2	62.0	1.1	1	0	2	–
	Maize	28	85.8	24.0	18	2	9	235
	Oats	1	110.0	1.0	0	0	1	–
	Seeds	2	3.5	0.1	0	0	1	–
	Grass/leaves	93	5.9	5.5	0	0	12	103
2°	Vertebrates	40	38.1	15.5	12	3	11	276
	Invertebrates	89	76.5	68.2	44	18	12	134
	Fruits	35	123.2	42.2	26	4	4	197
	Cereals	29	83.4	24.9	18	2	9	228
3°	Faunal	95	87.6	83.6	52	21	12	111
	Vegetal	57	118.5	67.2	48	6	11	143

[1] Includes only stomachs containing the prey in question.
[2] Includes all stomachs.
[3] Number of stomachs in which the prey in question occupied a greater volume than any other prey.
[4] Number of stomachs containing only the prey in question.

Of the remaining 16 primary prey types, earthworms had a higher frequency of occurrence and overall mean volume, were more often the main prey, were more often found as the only prey in a stomach, and occurred in more months of the year, than any other food. They also had almost the lowest coefficient of variation, though this was still high (170%) by absolute standards. However, earthworms did not have an especially high mean volume when present (mean = 60.2 ml). Thus earthworms were eaten fairly consistently, year-round, but usually only in moderate volumes. This is not because it was impossible for badgers to consume large quantities of earthworms: one stomach contained 475 ml of earthworms and another 345 ml.

Table 2. Number of stomachs containing a given number of primary prey types.

Prey types/stomach*						
1	2	3	4	5	6	$\overline{X}$
15	34	35	17	9	1	2.77

* Includes all prey present in volumes > 0.5 ml

Voles, insect larvae, insect imagos and maize were eaten in at least 8 of 12 months but did not appear in a large proportion of stomachs and did not contribute greatly to overall diet. All other foods were eaten sporadically but some of them (notably wasps, cherries, plums and oats) tended to be eaten in large amounts, given that they were consumed at all.

As regards the secondary and tertiary prey categories, invertebrates were eaten more consistently and contributed more overall to the diet than either vertebrates, fruits or cereals. The same was true of faunal by comparison with vegetal material. However, fruits and vegetal material had the highest mean volumes when present. Overall, faunal material contributed 55% of the total provided by all stomachs, while vegetal material contributed 45%. To summarise, animal and plant material contributed approximately equally to the overall diet and both were eaten more or less year-round: but animal material tended to be eaten often and in moderate volumes, whereas plant material was eaten less often but in larger amounts.

The modal number of different primary prey types per stomach was 3 (mean = 2.7; see Tab. 2). Only 27 stomachs (24%) contained a single prey and in 13 (48%) of these the prey in question was earthworms (Tab. 1).

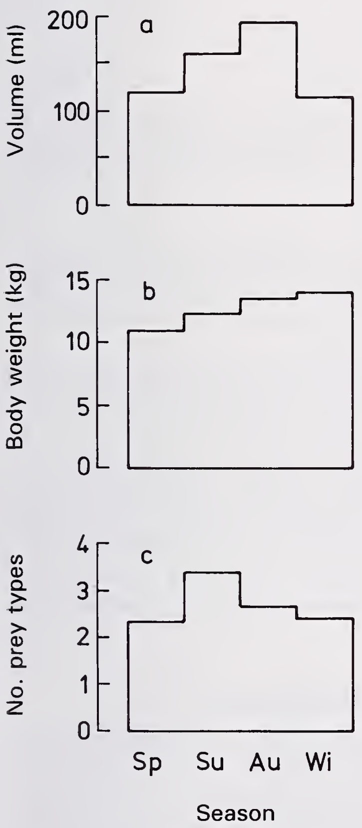

Fig. 1. Seasonal changes in (a) mean total volume of contents per stomach, (b) mean body weight and (c) mean number of primary prey types per stomach. Sp = spring (March to May); Su = summer (June to August); Au = autumn (September to November); Wi = winter (December to February).

Seasonal changes in diet

The mean total volume of stomach contents was greatest in autumn (Fig. 1 a), which was also a season in which body weight was high (Fig. 1 b). However, diversity of intake was greatest in summer (Fig. 1 c), reflecting the availability at that time of year of fruits such as plums and cherries, in addition to faunal foods, such as earthworms and voles, which were available more or less year-round.

Data on the frequency of occurrence, mean volume when present, and mean volume overall of different primary food types reveal considerable seasonal variation (Fig. 2). Only voles, earthworms and maize were eaten year-round and of these, earthworms were eaten with the highest frequency in all four seasons. Earthworms did not, however, represent an especially large volume except in spring, when they were eaten in large amounts in absolute terms (Fig. 2) and constituted 67% of the total volume ingested. Wasps, cherries, plums and mammals other than voles were eaten in only one or two seasons, and even in those seasons the frequency of

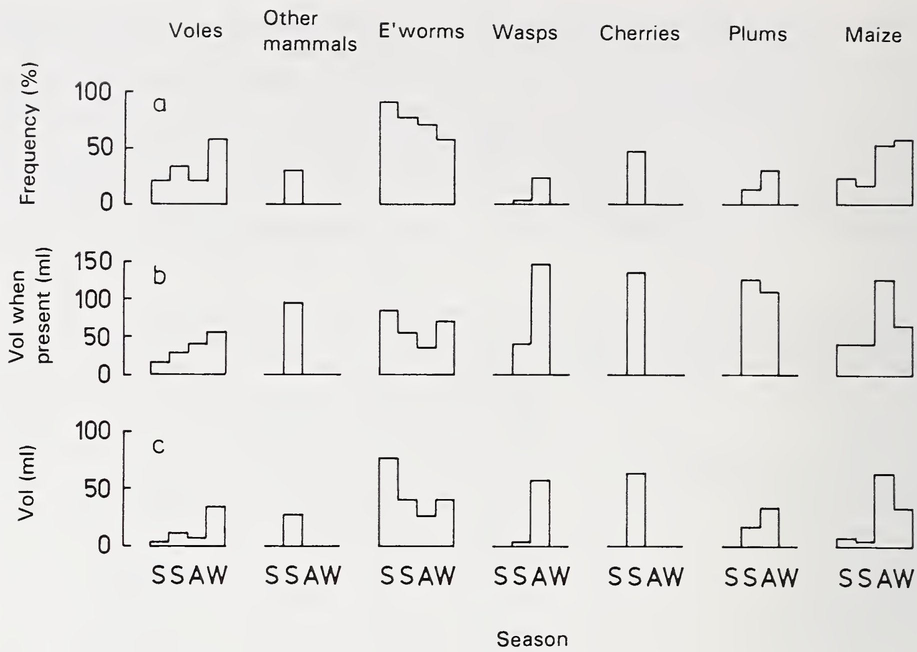

Fig. 2. Seasonal changes in the consumption of the 7 most important primary prey types. (a) Frequency of occurrence; (b) mean volume per stomach, including only stomachs that contained the prey in question; (c) mean volume per stomach, including all stomachs. SSAW: spring, summer, autumn, winter.

consumption was in all cases less than 50%. However when they were eaten, these foods tended to be eaten in large quantities. Cherries were the most voluminous food overall in summer (38% of total intake), maize in autumn (35%) and earthworms in winter (36%).

There were striking differences in the seasonal pattern of intake of faunal and vegetal foods (Fig. 3). Faunal material occurred in virtually every stomach in all four seasons and the absolute volume consumed showed relatively little seasonal variation. Vegetal foods, by contrast, never appeared in more than 75% of stomachs in any one season, and only contributed significantly to the diet in summer and autumn. In the latter seasons, however, they formed a slightly higher proportion of the diet overall than did faunal material.

Pattern of consumption within a single feeding period

In order to make deductions about the pattern of consumption of different foods from hour to hour in individual animals, using data from stomach contents, it was necessary to know when the donor animals ceased feeding. In 52 animals for which the relevant data were available, the volume of total stomach contents was positively correlated with time of death, which ranged from 1800 to 0600 h ($r_s = 0.64$, $p < 0.001$). The volume of total stomach contents could therefore be used as an indication of time of death in cases where the latter was not known.

It follows that if badgers preferentially consume a particular type of food early in the night, this food should be disproportionately evident in stomachs whose total contents are relatively small. To test this prediction, we plotted the percentage by volume of each primary, secondary and tertiary food category against total stomach contents, for all stomachs containing both faunal and vegetal material. (We included only stomachs containing

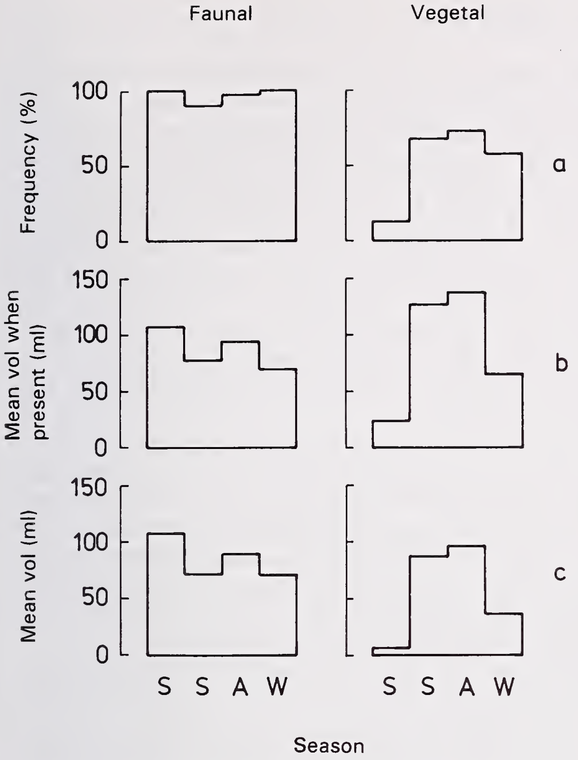

Fig. 3. Seasonal changes in the consumption of faunal and vegetal material. Conventions as in Fig. 2.

both faunal and vegetal material because only in these cases could we be sure that a range of different foods was available on the night when the animal was killed.) None of the correlations was significant ($r_s < 0.1$). Furthermore, data from stomachs whose total contents were <100 ml, and which therefore derived from animals killed very early in the night, showed no evidence of a bias towards any particular food category. Thus, there was no evidence that any one type of food was preferentially eaten at any particular stage in an individual's nocturnal foraging period.

To test whether there was an increase in the diversity of stomach contents as a function of time spent feeding, we correlated diversity (i.e., number of different prey types per stomach) with total stomach contents for all stomachs (Fig. 4). The result was not significant ($r_s = 0.168$, N = 111). Diversity in stomachs containing <100 ml of total contents ranged from 1 to 5 (mean = 2.62), while in stomachs containing <50 ml it ranged from 1 to 4 (mean = 2.4). Thus, even stomachs collected very early in the night usually contained more than one food type.

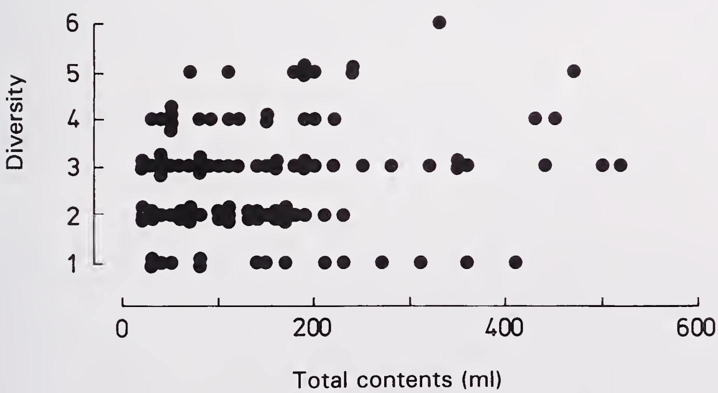

Fig. 4. Relationship between diversity (the number of primary prey types per stomach) and the total volume of food in the stomach.

Discussion

In common with almost all previous studies of badger diet (see reviews by Neal and Cheeseman 1991; Lüps and Wandeler 1993; Roper 1994), our results confirm that badgers eat a wide range of foods even within a relatively restricted geographical area. Specific foods that contributed to the diet, in descending order of overall volume consumed, were earthworms, cherries, maize, wasps, plums, voles, other mammals, slugs and snails, strawberries, oats, bumble-bees, unidentified insects (both larvae and imagos), reptiles, birds and seeds. There were no sex or age differences in the composition of the diet; but there was substantial individual and seasonal variability in the consumption of all food types, with the volume of no single food having a coefficient of variation of less than 150%. Overall, faunal and vegetal foods contributed about equally to the diet in terms of total volume consumed. However, faunal foods occurred in a substantially higher proportion of stomachs than did vegetal foods, and the total amount of faunal material eaten was subject to relatively little seasonal variation.

Small amounts of grass and leaves were also found in a large majority of stomachs but it seems unlikely that these yield any nutritional benefit, given the structure of the badger gut (Stark et al. 1987). Furthermore, grass and leaves recovered from stomachs showed no signs of having been digested. It is generally assumed that badgers ingest such material accidentally whilst grubbing for other prey in or on the surface of the ground (e. g., Neal 1986), but we found no correlation between the volume of grass and leaves present in stomachs and either the total volume of all other prey or the volume of any other single prey type. Thus, the consumption of grass and leaves remains unexplained.

To what extent do our results support the idea that badgers are food specialists (Kruuk 1986, 1989; Kruuk and Parish 1981)? The "food specialist" hypothesis predicts, first and foremost, that one or at most a few of the foods that are available in a particular location should predominate in the diet. This was the case in Kruuk's study areas in Oxfordshire and Scotland, where earthworms accounted for about 50% by volume of all foods eaten (Kruuk and Parish 1981; see also Neal 1988 for a similar finding); and also in two study areas in Italy, where diet was dominated by fruits and/or insects (Kruuk and de Kock 1981; Ciampalini and Lovari 1985). But several other studies of badger diet in the U.K. and Scandinavia have not shown any single type of food to be especially important (Andersen 1954; Harris 1982; Skinner and Skinner 1988; Shepherdson et al. 1990). Our results show that earthworms were the most frequently eaten food overall, were eaten in more months of the year than any other food and contributed the largest volume overall of any food. Earthworms were also most often the "main prey" (i. e., the most voluminous food in any one stomach) and, in stomachs containing only one type of food, that food was more often earthworms than anything else. On the other hand, earthworms were rarely eaten in very large quantities and they did not often constitute the only food consumed. More importantly, they only constituted 30% of the diet overall, in terms of volume. Thus while earthworms could reasonably be described as a staple food, eaten consistently in moderate amounts, they did not dominate the diet to the extent implied by the "food specialist" hypothesis.

The term "food specialist" has also been used to refer to two other perceived features of badger diet, namely that (i) intake of one particular food is immune from seasonal variation, and (ii) this food is preferred over other foods (Kruuk 1986, 1989). As regards the former point, Kruuk and collaborators found that in Scotland, badgers maintained a fairly constant year-round intake of earthworms, despite variation in earthworm availability (Kruuk and Parish 1981; Kruuk 1989). However, since the study in question was based on faeces analysis, it could only provide information about the relative, and not the absolute, intake of different foods at different times of year (Roper 1994). Contrary to Kruuk's results, we found that earthworms were virtually absent from the diet in January and February, when the main foods eaten were voles and maize. Furthermore, the absolute amount of earthworms consumed was not noticeably less variable than that of other foods, either comparing variance in intake across the whole sample of stomachs or comparing the mean volume consumed across seasons. In summer, for example, cherries were a more important food than earthworms in terms of the average volume consumed, while in autumn the same was true of both wasps and maize. We did find relatively little seasonal variation in the total amount of faunal material eaten, but this result is not shared by other studies of badger diet (e.g., Pigozzi 1987). To conclude, there is no compelling evidence, either from our results or from other literature on badger diet, that badgers forage in such a way as to sustain a constant level of intake, either of earthworms or of any other particular dietary component.

Since badgers have not been subjected to food-choice experiments, any claims made about their dietary preferences are bound to be speculative. However, it could be argued that if badgers seek out one particular food in preference to others, this food should be especially predominant in the diet early in the night. We found no evidence to support this idea: there was no overall correlation between the percentage of any single food in the stomach and the total volume of contents, and no suggestion that relatively empty stomachs, which can be assumed to have resulted from animals killed early in the night, were especially likely to contain any particular food. Furthermore, there was no correlation between the total number of food types in a stomach and the total volume of its contents, showing that the diversity of foods eaten did not significantly increase as a function of time spent foraging. Even stomachs containing as little as 50 ml in toto could contain as many as four different types of food. Thus it seems that badgers normally consume several different prey types within a few hours of the start of their activity period.

To conclude, by far the most striking feature of badger diet is the diversity of foods consumed, not only when considering the species as a whole but also considering single stomachs whose contents represent the results of a few hours of foraging activity by one animal. The simplest and most convincing hypothesis to account for these data is the traditional one (e.g., Neal 1948; Andersen 1954; Skoog 1970) that badgers are opportunistic food generalists. Their foraging behaviour is such that they both encounter and consume a variety of foods, rather than concentrating on a single one.

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Zusammenfassung

Nahrung von Dachsen (Meles meles L.) in der Zentralschweiz: Eine Analyse von Mageninhalten

Untersucht wurden die Mageninhalte von 217 Dachsen in der Zentralschweiz. Insgesamt bestand die Nahrung zu 55% aus Tiermaterial und zu 45% aus Pflanzenmaterial. Regenwürmer waren häufiger und in mehr Monaten in der Nahrung vertreten und waren öfter die einzige Futterart im Magen, als alle anderen Nahrungstypen, aber sie wurden für gewöhnlich nicht in großen Mengen gefressen. Spitzmäuse, Insekten und Mais wurden die meiste Zeit des Jahres gefressen, aber nie in großen Mengen; während Wespen, Kirschen, Pflaumen und Hafer nur in den entsprechenden Jahreszeiten und dann in großen Mengen gefressen wurden. Die gesamte Nahrungsmenge im Magen war im Herbst am größten, während der Reichtum an verschiedenen Nahrungsarten im Sommer am größten war. Keine Nahrungsart wurde bevorzugt zu einer bestimmten Zeit in der Nacht gefressen. Es wurde auch keine Korrelation

zwischen der Anzahl verschiedener Nahrungsarten und dem gesamten Volumen an Mageninhalt gefunden. Die Zusammensetzung der Nahrung unterschied sich nicht signifikant zwischen Dachsen verschiedenen Alters, Geschlechts oder Zahnabnutzung; aber das Gesamtvolumen des Mageninhalts, Zahnabnutzung und Alter waren jeweils signifikant korreliert miteinander.

Tiermaterial allgemein und Regenwürmer im besonderen können als konstanter Bestandteil der Nahrung von Dachsen in diesem Teil der Schweiz betrachtet werden. Aber der auffallendste Aspekt der Dachsnahrung war die Diversität an Nahrungsarten, die gefressen wurde, nicht nur von der Dachspopulation als Gesamtes, sondern ebenfalls von individuellen Dachsen innerhalb nur weniger Stunden der Nahrungsaufnahme.

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Authors' addresses: Dr. Timothy J. Roper, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK; Dr. Peter Lüps, Naturhistorisches Museum der Burgergemeinde Berne, Bernastrasse 15, CH-3005 Berne, Switzerland.

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