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ORIGINAL PAPER

Seasonal variations of the digestive tract of the Eurasian beaver *Castor fiber*

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Abstract Forage availability for wild rodents varies with season. In turn, the composition of food can affect morphometric parameters of the digestive tract. This study was performed in Eurasian beavers (*Castor fiber*) whose population was close to extinction in most Eurasian countries, but has now increased. Due to the previous low number of studies, information about the effect of forage availability on the digestive tract morphology has previously been lacking. This study was performed using beavers captured from the natural environment during three seasons of different forage availability: winter, summer and autumn. It was found that the diet of the beaver varied during the year; in winter it was dominated by woody material consisting of willow shoots, whereas in summer the diet was primarily herbs, grass and leaves. Season also affected the mass of digested contents of the digestive tract. The digestive content increased in the caecum and colon in winter and autumn, when poor-quality food dominated the beaver's diet. The results indicated that the digestive tract parameters of beavers varied based on the composition of available forage.

Keywords Digestive tract · Season · Beaver · Food preferences

Introduction

Beavers are one of the biggest rodents in the world. The genus *Castor* is represented by two species: the Eurasian beaver (*Castor fiber* Linnaeus 1758), living in Europe and Asia, and the North American beaver (*Castor canadensis* Kuhl 1820), naturally occurring in North America. Eurasian beavers originally inhabited rivers and lakes in most countries of Europe and North Asia until the middle ages. Since then, due to excessive hunting, their population has been dramatically reduced and at one time was close to extinction. At the beginning of the twentieth century, only eight relic populations survived in Europe and Asia. A number of actions were carried out, including hunting restrictions, species protection and translocation programmes to preserve this species (Nolet and Rosell 1998). As a result, the population increased to over 1.04 million individuals worldwide (Halley et al. 2012). However, *C. fiber* is still a protected species in most of the member states of the European Union (Convention on International Trade in Endangered Species of Wild Fauna and Flora and the Bern Convention on the Conservation of European Wildlife and Natural Habitats).

In Poland, beavers were close to extinction, but currently their population is estimated at over 100,000 animals (Central Statistical Office 2016). The observed increase was caused by the introduction of the Active Beaver Protection Plan (Żurowski 1979), quick adaptation of animals to newly inhabited habitats and the lack of natural enemies.

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Both species of beavers are strict herbivores. Their diet composition depends on the availability of food and shows seasonal variations (Krojerová-Prokešová et al. 2010; Severud et al. 2013). During winter, the diet of the beavers is dominated by tree shoots, mostly willow (Breck et al. 2001; Severud et al. 2013), stored in food caches (Dzięciołowski and Misiukiewicz 2002). However, twigs contain a high amount of fibre and are low in protein (Spaeth et al. 2002), and thus the winter diet is of poor quality. In summer, the diet contains a large quantity of herbs and grass (Krojerová-Prokešová et al. 2010; Severud et al. 2013) characterised by a low fibre content and higher protein content.

The digestive tract of beavers is well adapted to the digestion of plant material. However, information about the morphometry of the digestive tract is available only for North American beavers (Mortimer 1733; Morgan 1868; Rush 1927; Vispo and Hume 1995). Its structure is typical for the caecum-hindgut fermenters (Hume 1989). The stomach of the Eurasian beaver (Ziółkowska et al. 2014) as well as the North American beaver (Nasset 1953) is a unilocular, C-shaped sac with a characteristic cardiogastric gland, located along the lesser curvature near the oesophageal entrance. The small intestine is the longest part of the digestive tract of the North American beaver and can reach almost 550 cm (Vispo and Hume 1995). The large C-shaped caecum (Vispo and Hume 1995) contains fibre-digesting microorganisms (Gruninger et al. 2016) and is the main place of cellulose degradation in the digestive tract (Currier et al. 1960).

The beavers, similar to other non-hibernating rodents, must maintain a constant body temperature even during the winter time when access to plants is limited only to a low-quality diet. Covering energy needs is most important for these animals to survive. To obtain more energy from poor-quality food, small herbivorous rodents, e.g. pocket gophers (*Thomomys bottae*), prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*), increase food intake. Similar trends were observed for medium-size rodents, such as North American porcupines (*Erethizon dorsatum*), whereas such relationships did not occur in muskrat (*Ondatra zibethicus*), degu (*Octodon degus*) and Guinea pigs (*Cavia porcellus*) (Meyer et al. 2010).

Regardless of the food intake by rodents, low-quality feed results in re-adaptation of the digestive system. Generally, the most common response is to increase the capacity of the digestive tract (in terms of an increase in volume and tissue as well as digesta mass) in response to a decline in diet quality (Hammond and Wunder 1991; Naya et al. 2008). However, individual species can respond in different ways, e.g. Brandt's vole (*Lasiopodomys brandtii*), after switching to a high-fibre diet, increased only the total mass of the digestive tract, whereas other parameters, such as organ size and mass, remained unchanged (Zhao and Wang 2007).

The digestive tract parameters mentioned above were affected not only by food composition but also by other factors such as temperature (Hammond and Wunder 1991; Song and Wang 2006) or length of day (Song and Wang 2006). In laboratory studies on another rodent species, *M. ochrogaster* (Hammond and Wunder 1991) exposure to cold temperature was associated with elongation of total digestive tract length and increased digesta mass as well as elongation of the small intestine, caecum and colon. Similarly, *L. brandtii* (Song and Wang 2006) increased their total digestive tract and digestive organ length and digesta mass. In the digestive tract of *L. brandtii*, elongation of the digestive tract was also observed during shorter day lengths (Song and Wang 2006).

In the natural environment, a combination of these factors, poor-quality food, low temperature, and short day, occurs in winter. However, contrary to results from laboratory studies the digestive tract of wild living animals react in a different way. In winter, *M. pennsylvanicus* and *Peromyscus leucopus* significantly increase the mass of the small intestine and caecum, whereas the length of digestive organs remained unchanged (Derting and Noakes 1995). In contrast to the above rodents, *Abrothrix andinus* increased the mass as well as length of the small intestine in winter (Bozinovic et al. 1990). The observed increase in small intestine parameters mass and/or mass occurring during winter is due to the higher energy demand (Gross et al. 1985; Hammond and Wunder 1991) and caused by an increase to the mass of absorptive tissue—mucosa (Derting and Noakes 1995). Conversely to these results, the season has no effect on the digestive tract of another species (Schwaibold and Pillay 2003).

Another reason for changes in the digestive tract morphometry is the sex of an animal. Females have greater digestive tract parameters, especially their small intestine length and mass (Derting and Hornung 2003; Schwaibold and Pillay 2003), because of their growth needs or times of lactation (Gębczyńska and Gębczyński 1971).

Information about the effect of the season on digestive tract parameters in wild rodents is limited to small rodents, e.g. the white-footed mouse (*P. leucopus*) (Derting and Hornung 2003), the root vole *Microtus oeconomus* (Gębczyńska and Gębczyński 1971), the African ice rat, *Otomys sloggetti robertsi* (Schwaibold and Pillay 2003) and the Mongolian gerbil *Meriones unguiculatus* (Liu et al. 2013). However, there is a lack of information on the effect of the season on digestive tract parameters of large wild herbivorous rodents.

The aim of our study was to elucidate the effect of season on digestive tract parameters in Eurasians beavers. We hypothesised that changes in gut length and mass will be necessary in winter, when energy demand is high and the diet of beavers is of poor quality (high dietary fibre). Morphological changes in the digestive tract may include alternations in the length and weight of the gastrointestinal tract organs and digesta, particularly an increase in caecum and colon parameters.

Materials and methods

Study animals

The experiment was performed using 36 adult beavers of both sexes (18 females and 18 males). The animals were captured in Warmia and Mazury (from 52° 83′ to 54° 36′ N, and from 17° 00′ to 22° 87′ E) over a period of 2 years (2011/2012). The animals were captured with the approval of the Regional Directorate of Environmental Protection in Olsztyn, Poland (ministerial approval: RDOS-28-OOP-6631-0007-638/09/10/pj), and the experiments were performed in accordance with the standards of the III Local Ethical Commission for Experiments on Animals at Warsaw University of Life Sciences-SGGW (Permit number 11/2010). The capture of beavers was conducted by a specialised team from the Polish Hunting Association in winter, summer and autumn. Due to the difficulties of hunting beavers in mid-winter, winter capture of beavers started in March (six females, six males)—just after mating, but before the start of the vegetative growth period of plants. Summer capture took place in July (six females, six males)—during the full growing season of plants (six females, six males). Autumn capture was carried out in November (six females, six males)—at the end of the vegetation period. The animals were caught during daytime in nets and placed in cages and transported to the laboratory of the Research Station of Ecological Agriculture and Preservation Animal Breeding of the Polish Academy of Sciences in Popielno. Immediately after delivery, beavers were weighed, and their sex was determined based on the colour of anal gland secretions (Rosell and Sun 1999). The animals were then anaesthetised by xylazine (3 mg/kg of BW; Sedazin®, Biowet Puławy, Poland) and ketamine injections (15 mg/kg of BW; Bioketan, Vetoquinol Biowet, Poland) before they were sacrificed by decapitation under full anaesthesia.

External measurements

External morphometric measurements were carried out according to the method of Richard-Hansen et al. (1999) and were performed after complete euthanasia of the beaver. External measurements included body mass, total body length (from the base of the upper jaw incisors to the end of the tail), the length of the head (from the tip of the nose to the base of the skull), chest circumference and the length and the width of the tail. The animals' ages were estimated on the basis of body mass (Rosell and Sun 1999). Only adult individuals (above 24 months of age) were used in the present study.

Internal measurements

Immediately after finishing external measurements, the entire digestive tract of the animal was removed and its sex was confirmed on the basis of internal reproductive organs. The isolated digestive tracts were carefully stripped of any connective tissues and fat, then digestive organs stomach, small intestine, caecum and colon were isolated. Calculations of stomach length were performed according to the following equation: (length of the lesser curvature + length of the greater curvature) / 2. Small intestine length was measured from the start of the duodenum to the ileocaecal junction. The caecum was measured from the proximal colon just after the junction between the caecum and the ileum and calculated according to the following equation: (length of the lesser curvature + length of the greater curvature) / 2. The length of the colon was measured from the start of the proximal colon to the start of the rectum.

The length of the digestive tract parts were measured to the nearest 1.0 cm using a measuring tape. After length measurements had been recorded, sections were weighed to the nearest 0.5 g (all weights were performed with a Radwag Model PM 10.C32 precision balance, Radom, Poland).

Stomach content analysis

Stomach contents were collected directly after weighing. Samples (100 g each) of contents were preserved in 4% formalin solutions. The analysis of food composition was performed using a botanical stomach assay according to the method described by Obidziński et al. (2013). Briefly, the preserved samples were washed in a sieve of 1-mm diameter. Subsequently, residual fractions remaining on the sieve were suspended in 50 ml of water. Three 5-ml samples of the suspension were then analysed according to the "point frame" method. The analyses were repeated three times. Collected plant particles were identified using a binocular microscope at ×25 magnification. Particles were then grouped into the following categories: shoot, pine needle, tree leaves, herbaceous plants, grasses and sedges, moss, rape, oats grain. Identified particles were dried at 60 °C for 48 h and weighed to the nearest 0.5 mg. The presence of particular types of food in the beaver stomach was calculated based on the dry mass of food and expressed as $V_{\%}$—the percentage of dry matter of a particular type of food in the sample relative to the total dry matter of the sample. Stomach contents were also analysed in terms of the presence of particular food types in individual beaver diets and expressed as (Oc)—the ratio of animals in which specific food components were found relative to all animals in the group. Chemical analyses of stomach contents were conducted in the Laboratory of Chemistry, the Kielanowski Institute of Animal Physiology and Nutrition, Polish Academy of Sciences, by AOAC methods 2005: procedure number 984.13 for crude protein determination, number 962.09 for crude fibre, procedure number 920.39 for crude fat and procedure number 942.05 for ash determination.

Statistical analyses

The results were subjected to a statistical analysis of variance for a factorial design. A Pearson correlation test was used to assess the relationship between body (mass and length), head (length and width), chest circumference and tail (length and width) values. The effect of season on food preferences was analysed using a Shapiro-Wilk test to evaluate variance and a Mann-Whitney *U* test for the comparison of percentage values. The results of the effect of the season and sex on body and digestive tract parameters were expressed as means and pooled standard error of mean values. Differences between treatments were assessed by Tukey HSD post hoc test using the Statistica 10.0 software package. The effects were considered to be significant at $p \leq 0.05$.

Results

External measurements of beavers

The itemised results of the measurements are shown in Table 1. In summary, the body weight of beavers was 19.2 ± 2.2 kg (mean ± SEM). The body length of these beavers was 113 ± 4.6 cm (mean ± SEM), of which the tail accounted for 24.5% of the total body length, whereas the head constituted 16%. The ratio of the tail length to the width was 2.1. The results of Pearson correlation analysis of body measurement (Table 2) revealed a positive correlation ($r_p = 0.85$) of body length and body mass; both parameters were also positively correlated with the length of head and tail as well as chest circumference ($r_p > 0.5$). A positive correlation also existed between head length and their width ($r_p = 0.56$), chest circumference ($r_p = 0.61$) and tail weight ($r_p = 0.53$) and length ($r_p = 0.68$). A positive correlation was also found between tail weight and length. Based on measurements, it was found that sex had no effect on any of the parameters examined, whereas elongation of the tail in summer and reduction of the head width in autumn were observed.

Food

Determination of food preferences based on botanical stomach content analysis indicated an effect of the season on diet composition ($p < 0.05$) (Table 3.) In winter, shoots were the main available food sources, particularly willow shoots. In summer, a change in food composition occurred corresponding to the growth of vegetation, with an increase in leaves of woody plants, grasses and sedges as well as herbaceous plants, and a simultaneous decrease of shoots. In autumn, at the end of the growing season, a decline in tree leaves, grasses and sedges and an increase of shoots as food sources were observed, although herbaceous plants were still available. The comparison of males versus females indicated that all food categories differed significantly ($p < 0.05$). The differences in food component were also apparent during the comparison of effect of season on the sex of beavers. The effect of the season on diet composition of beavers was also confirmed by chemical analysis of stomach contents. These results for dietary content (Table 4) indicated that the summer diet contained

Table 1 Characterizations of beavers captured during winter, summer and autumn

	Sex (S_x)	Season (S_n)			Description of statistic			
		Winter	Summer	Autumn	SEM	S_x	S_n	$S_x \times S_n$
Body mass (kg)	M	20.0	19.0	19.5	0.375	0.396	0.948	0.415
	F	18.0	19.5	19.1		$F = 0.741$	$F = 0.053$	
Total length (cm)	M	114.1	112.2	114.9	0.76	0.675	0.559	0.513
	F	111.2	113.8	114.3		$F = 0.180$	$F = 0.59$	
Head length (cm)	M	17.5	18.4	17.6	0.155	0.734	0.092	0.924
	F	17.6	18.2	17.5		$F = 0.120$	$F = 2.580$	
Head width (cm)	M	12.3a	12.0a	11.0b	0.171	0.278	< 0.05	0.193
	F	12.3a	13.0a	10.9b		$F = 1.221$	$F = 14.933$	
Chest (cm)	M	76.2	77.7	77.4	0.882	0.913	0.582	0.926
	F	75.7	78.9	77.3		$F = 0.012$	$F = 0.550$	
Tail length (cm)	M	27.8	27.6	26.4	0.307	0.078	< 0.05	0.343
	F	28.9a	29.4a	26.3b		$F = 3.330$	$F = 7.390$	
Tail width (cm)	M	13.02	12.53	12.57	0.183	0.128	0.195	0.196
	F	13.3	13.95	12.48		$F = 2.449$	$F = 1.727$	

Different lowercase letters indicate differences ($p < 0.05$) between season

SEM standard error of mean, S_x effect of sex ($df = 10$), S_n effect of season ($df = 15$), $S_x \times S_n$ sex season interaction effect

Table 2 Pearson correlation between body mass and body length, head (length and width), chest circumference and tail (length and width) of beavers

	Body mass (kg)	Total length (cm)	Head length (cm)	Head width (cm)	Chest circ. (cm)	Tail width (cm)	Tail length (cm)
Body mass (kg)	X	0.85	0.54	0.25	0.74	0.40	0.55
Total lengthy (cm)		X	0.53	0.21	0.61	0.45	0.56
Head length (cm)			X	0.56	0.61	0.53	0.68
Head width (cm)				X	0.21	0.73	0.63
Chest circ. (cm)					X	0.40	0.49
Tail width (cm)						X	0.79
Tail length (cm)							X

almost 60% more crude protein, 37% crude fat and 31% more crude ash compared to winter and autumn diets. In the same period, the content of crude fibre in food was about 16% lower. In contrast to stomach content analysis, the chemical analysis indicated no effect of seasons.

Digestive tract measurements

Weight measurements of the digestive tracts of beavers (Table 5) revealed that the total mass of all organs, with their contents, constituted 15% of body weight, whereas the mass of the digestive tract content amounted to 9% of body mass. After separation of the digestive tract and comparison of the digesta mass of individual organs, it was found that the largest content was in the caecum which accounted for 54% of the total mass of the digestive tract, whereas the lowest content (12%) was found in the small intestine. The mass of wet organs without the content was also compared. The results indicated that the caecum and the colon had the highest mass, as the mass of both of them accounted for almost 30% of the total mass of wet organs. The length of the gastrointestinal tract was the second parameter measured. The total length of the gastrointestinal tract of beavers was 622 cm. The small intestine was the longest part and constituted almost 63% of the total length, and the second longest was the colon that constituted almost 25% of the total length. The stomach and the caecum length did not exceed 10%.

Digestive tract parameters were compared in beavers captured in different seasons. The measurements of the stomach mass and length indicated that the lowest mass of the contents was found in winter. During summer, all the parameters in both sexes showed a growing trend. In autumn, the length and mass of the male stomach exhibited a decreasing trend, whereas the stomach of females demonstrated an increasing tendency. Similar to the stomach, all parameters of the female small intestine showed the same pattern, whereas the small intestines of males showed a decreasing trend in winter. In contrast to the stomach and small intestine, the mass of the caecum and its content was significantly lower during summer, with the exception of male digesta mass in winter. The digesta mass of the caecum and colon was lowest in summer, whereas their length did not vary across the year.

Table 3 The composition of the adult beaver's diet depending on the season and sex

Food category	Winter				Summer				Autumn			
	Male		Female		Male		Female		Male		Female	
	$V_{\%}$	$OC_{\%}$	$V_{\%}$	$OC_{\%}$	$V_{\%}$	$OC_{\%}$	$V_{\%}$	$OC_{\%}$	$V_{\%}$	$OC_{\%}$	$V_{\%}$	$OC_{\%}$
Shoots	99	100	82	100	26	83	34	100	69	83	74	83
Pine needle	+	17	+	17	2	17	1	17	–	–	–	–
Tree leaves		–	–	–	9	33	7	67	2	17	+	17
Blackberry leaves		–	–	–	2	33	–	–	+	33	+	17
Herbs	–	–	13	17	24	50	5	–	28	50	–	–
Grass/sedges	x	17	5	17	15	33	25	100	+	33	24	33
Moss	x	33	–	–	–	–	–	–	x	17	2	17
Oats grain		–	–	–	12	17	–	–	–	–	–	–
Rape		–	–	–	10	17	28	33	–	–	–	–

$V_{\%}$ the percentage of composition of the diet, $OC_{\%}$ percent occurrence in the diet, − lacking in the diet, *x* comprising less than 1% of the diet

Table 4 The chemical composition of the adult beaver's diet depending on the season and sex

Specification	Sex (S_x)	Season (S_n)			Description of statistic			
		Winter	Summer	Autumn	SEM	S_x	S_n	$S_x \times S_n$
Crude protein	M	10.6a	16.5b	10.8a	0.528	0.806	< 0.05	0.260
	F	9.7a	17.0 b	11.0b		$F = 0.061$	$F = 145.210$	
Crude fat	M	6.1a	8.6a	5.6b	0.205	0.278	< 0.05	0.018
	F	6.4a	7.6ab	5.7b		$F = 1.223$	$F = 59.287$	
Crude fibre	M	45.3a	35.5b	41.1c	0.713	0.181	< 0.05	0.569
	F	43.7a	35.6a	39.7b		$F = 1.88$	$F = 50.99$	
Crude ash	M	3.8a	5.4b	5.1b	0.144	0.124	< 0.05	0.016
	F	3.8a	5.6b	4.2a		$F = 2.502$	$F = 40.300$	

Different lowercase letters indicate differences ($p < 0.05$) between season (winter, summer and autumn)

SEM standard error of mean, S_x main effect of sex ($df = 10$), S_n main effect of season ($df = 15$), $S_x \times S_n$ sex season interaction effect

Table 5 The results of measurements (Measure.): mass (g) and length (cm) of beaver digestive tract organs depending on the sex (S_x) and season (S_n)

Digestive organ	Measure.	S_x	S_n			Description of statistic			
			Winter	Summer	Autumn	SEM	S_x	S_n	$S_x \times S_n$
Stomach	Total mass	M	349.0a	585.2b	516.4	28.22	0.069	< 0.05	0.098
		F	451.7a	538.4	714.7b		$F = 3.551$	$F = 8.2633$	
	Digesta mass	M	188.2a	386.3b	343.2	23.94	0.572	< 0.05	0.272
		F	267.2	309.5	416.0		$F = 0.327$	$F = 4.486$	
	Wet mass	M	168.8	198.8	173.2	11.97	0.056	0.223	0.461
		F	184.6	228.9	260.4		$F = 1.628$	$F = 1.579$	
	Length	M	23.9	27.8	27.6	0.86	0.064	< 0.05	0.494
		F	25.8a	30.6	33.6b		$F = 2.8961$	$F = 5.504$	
Small intestine	Total mass	M	359.8a	558.3b	499.4b	20.49	0.348	< 0.05	0.187
		F	324.2a	617.1b	537.6b		$F = 0.908$	$F = 46.209$	
	Digesta mass	M	182.3	231.8	215.3	7.19	0.630	< 0.05	0.948
		F	185.5a	244.2b	218.8		$F = 0.237$	$F = 5.732$	
	Wet mass	M	177.5a	326.6b	284.1b	14.17	0.059	< 0.05	0.651
		F	188.7a	372.9b	318.7b		$F = 3.843$	$F = 39.9466$	
	Length	M	365.5	397.0	397.5	10.61	0.826	< 0.05	0.078
		F	312.0a	436.8b	422.7b		$F = 0.049$	$F = 8.277$	
Caecum	Total mass	M	1441.7a	1152.2b	1361.2b	39.03	0.876	< 0.05	0.001
		F	1672.0a	1037.1b	1264.7b		$F = 0.025$	$F = 46.868$	
	Digesta mass	M	1033.1a	815.4b	1017.2a	28.17	0.252	< 0.05	0.031
		F	1124.5a	709.1b	916.9c		$F = 1.363$	$F = 31.763$	
	Wet mass	M	408.6x	337.1	343.9	9.23	0.007	0.668	0.007
		F	290.4y	328.0	337.8		$F = 8.439$	$F = 0.408$	
	Length	M	48.4	48.4	42.3	0.92	0.607	0.438	0.076
		F	44.8	48.3	48.8		$F = 0.271$	$F = 0.848$	
Colon	Total mass	M	598.7	526.5a	661.1b	11.88	0.569	< 0.05	0.378
		F	547.5	558.3	638.8		$F = 0.332$	$F = 7.044$	
	Digesta mass	M	278.1a	220.9b	297.9a	8.49	0.388	< 0.05	0.396
		F	241.9a	216.5a	304.2b		$F = 0.768$	$F = 13.283$	
	Wet mass	M	320.6	305.6	363.2	11.02	0.914	0.424	0.475
		F	305.6	341.8	334.6		$F = 0.012$	$F = 0.883$	
	Length	M	166.6	166.2	170.8	3.904	0.059	0.953	0.908
		F	144.4	148.9	145.6		$F = 4.451$	$F = 2.048$	

Different lowercase letters a, b and c indicate differences ($p < 0.05$) between season (winter, summer and autumn); different lowercase letters x and y show differences ($p < 0.05$) between sexes (male and female);

SEM standard error of mean, S_x main effect of sex ($df = 10$), S_n main effect of season ($df = 15$) $S_x \times S_n$ sex season interaction effect

Discussion

Body measurements and mass

The average body mass observed here (19.2 kg) was similar to the measurements reported previously (19.3 kg) for beavers from this region (Żurowski and Kasperczyk 1986). Body mass did not differ between sexes, which was inconsistent with the observations of Żurowski and Kasperczyk (1986). However, the previous research was conducted on a larger number of individuals and the differences were only observed at a low significance level. It suggests that differences between the sexes are small, and are likely to only be seen in studies on a large group of animals. The reason for this may be due to the beaver belonging to the monogamous group of animals (Steyaert et al. 2015). In such animals, differences in size between the sexes are much lower than in polygamous species (Kleiman 1977), although they never completely disappear (Magurran and Garcia 2000). It should be also noted that body mass may also depend on the environmental conditions and vary between colonies (Smith and Jenkins 1997). The proportions of the body (e.g. the ratio of the tail length to total body length) were consistent with the data obtained by Korzeniowski et al. (2002).

Diet composition

The results confirmed earlier observations that the diet of beavers depends on the season and the food available at the time. The observed food preferences were similar to the data obtained by Krojerová-Prokešová et al. (2010), but varied from those of Simonsen (1973), who observed foraging of beavers on aquatic plants. In the present study, like that by Krojerová-Prokešová et al. (2010), there was a lack of aquatic plants in the beaver's diet, which was presumably caused by their absence in the foraging area. Another difference was a significantly higher amount of grass in the stomach contents, which was probably affected by differences in the availability of plants. Despite these dissimilarities, winter diets (Simonsen 1973; Krojerová-Prokešová et al. 2010) were dominated by shoots. This food category is collected and stored during autumn by animals inhabiting northern latitudes, and during more severe winter periods, they act as reserves or food caches (Dzięciołowski and Misiukiewicz 2002). However, it was interesting to note that atypical foods were observed in the digesta of beavers, i.e. rape and oat grains. While these might be regarded as atypical, such a supplementation of the diet with unusual food sources seems to be common for beavers (Krojerová-Prokešová et al. 2010). The chemical analysis of stomach contents of males and females indicated a lack of seasonal effect on food preferences. The reason for this could be the botanical analysis which takes into account more parameters than those for chemicals, and thus is more detailed. However, due to the small size of the group, such studies should be performed on a larger group of individuals.

Digestive tract

The relative mass of the digestive tract content constituted 9% of the total body weight, whereas this value for *C. canadensis* was 13% (Vispo and Hume 1995). The data for the stomachs of both species were similar (Vispo and Hume 1995). The length of the Eurasian beaver's small intestine reaches almost 400 cm and is the longest part of the digestive tract. Its length, however, is shorter than the length of the small intestine of North American beavers, which range from 534 cm (Vispo and Hume 1995) to 629 cm (Rush 1927). The length ratio of the small intestine to the caecum and the colon was 1.9 and is lower than in *C. canadensis* (3.23) (Vispo and Hume 1995). This value, however, is much greater than 1, which is considered typical for animals in the grazer/browser rodent category (Perrin and Curtis 1980), and has been found in other herbivorous rodents, such as *Otomys angoniensis*, *O. irroratus*, (Perrin and Curtis 1980), *Microtus agrestis*, *Arvicola terrestris* (Lee and Houston 1993), *E. dorsatum* (Vispo and Hume 1995), *L. brandtii* (Song and Wang 2006) and *C. gambianus* (Byanet et al. 2015). The higher ratio suggests a classification shift of these rodents to the carnivore or omnivore category. However, the aforementioned grazer/browser category represents a small group reaching up to 5 kg (*E. dorsatum*), while this proportion is higher in big herbivorous rodents like the 40-kg capybara *Hydrochoerus hydrochaeris* (ratio of 1.6; González-Jiménez and Parra 1972), which is a grazer/browser (Barreto and Quintana 2012).

The ratio > 1 indicated that the small intestine prevails over the caecum and colon. It could result from two reasons, which are not mutually exclusive: a decreased length of caecum or an increased small intestine. The first reason could be present in small animals with a higher energetic requirement compared to larger animals (Schmidt-Nielsen 1970). The main places of energy yielding processes in rodents are the caecum and colon (Bergman 1990). This could result in enlargement of this compartment. The second reason is faster retention time of food particles by the digestive tract. The retention time for rodents which weigh below 1 kg is usually less than 20 h (Sakaguchi 2003) whereas for beavers it varied depending on food from 14 to 39 h (Doucet and Fryxell 1993). The longer retention time requires a more effective process of nutrient absorptive capacity from food occurring in the small intestine. Small rodents also commonly engage in coprophagy. In this process, a certain fraction of their own faeces are re-ingested, which allows the animal to use the end products of digestive fermentation and the microbial proteins (Hirakawa 2001, 2002). However, in the beaver, coprophagy was rarely observed (Wilsson 1971). This could suggest that digestion and absorption of nutrients from "primary food" sources are more important than from “re-ingested food” and hence required a larger surface absorption within the small intestine.

Both North American and Eurasian beavers are classified as caecum-colon fermenters based on their gut morphology (Hume 1989). The characteristic feature of this group of animals is a large C-shaped caecum, which is their primary site for microbial digestion of plant carbohydrates (Stevens and Hume 1998). The proportion of the caecum digesta mass to body mass of beavers was 4.7, and it was higher than the corresponding value for *C. canadensis* which ranged from 2.1 (Hoover and Clark 1972) to 3.1 (Vispo and Hume 1995). These values, however, are lower than in the other caecum-colon fermenter species, such as the capybara, where this proportion ranged from 7.1 (Baldizan et al. 1983) to 8.0 (Borges et al. 1996). In capybara, the digesta mass of the caecum dominated over the colon, as the ratio varied from 8.4 (Borges et al. 1996) to 10.4 (Baldizan et al. 1983). In *C. canadensis*, this proportion ranged from 0.6 (Vispo and Hume 1995) to 1.5 (Hoover and Clark 1972), whereas for *C. fiber* (this study) it was 3.6. This suggests that beavers are caecum-colon fermenters, whereas capybaras seem to be caecum fermenters according to localization of digesta mass.

Seasons

The results obtained indicate that content of fibre in food is one of the most important factors affecting digestive tract parameters which was confirmed by the results of the experiments in controlled conditions. In such experiments, an increase in length and weight of an organ (with and without contents in the total digestive tract) as well as the stomach, small intestine, colon and caecum was observed (Liu and Wang 2007). However, an increase in only the total mass of the digestive tract and organs was observed in Brandt’s voles (*L. brandtii*), as a result of more digesta mass (Zhao and Wang 2007). These results suggest that the measurements based on the total organ mass are a better comparative indicator. A similar relationship was also found in the current study when an increase in the total mass of the digestive organs was recorded without the enlargement of length and wet mass of an organ.

In natural conditions, during summer, the diet of *C. fiber* was composed of high-quality food and contained a large amount of leaves and grasses, with a lower crude fibre content. In winter and autumn, the diet was of low quality, and the content of crude fibre in food was about 16% higher. The reason for this was probably the high percentage of small shoots with a diameter of up to 3 cm (Janiszewski et al. 2006) that contained high percentages of crude fibre (Scotter 1972). However, in the natural environment factors other than fibre content in food can also have an effect on digestive tract parameters: e.g. temperature and day length (Song and Wang 2006). The factors could also have affected the results in the current studies because they were performed in summer (long day, low fibre, warm temperature, etc.) and winter (short day, high fibre, cold temperature).

In beavers, season has no effect on total digestive tract parameters such as length, as well as wet and dry digesta mass. These findings were similar to the results obtained in studies on other wild rodents, *O. sloggetti robertsi* (Schwaibold and Pillay 2003) or the prairie vole *M. ochrogaster* (Voltura 1997). However, differences were found in digestive parameters of particular organs. There was a decline in the total mass and stomach length in winter. This observation was consistent with the results in the study by MacPherson et al. (1988) on seasonal and habitat variations in the diet of pine voles (*M. pinetorum*). However, the results obtained were contradictory with the study conducted by Hammond (1993) on *M. ochrogaster*, who found a higher mass in the stomach in winter due to the increasing intake of poor forage quality.

Based on previous studies of rodents *O. sloggetti robertsi* (Schwaibold and Pillay 2003) and *P. leucopus* (Derting and Hornung 2003), it was expected that deterioration of food and low temperatures in winter would have no effect on the length of the small intestine but would increase their mass with digesta (Derting and Hornung 2003). The results of the current studies on beavers indicated, however, that in winter there is a decrease of both parameters. In females, there was a tendency for a higher digesta mass and length than was observed in males. This suggests that activity in summer and autumn requires more energy than thermoregulation in winter. During spring, summer and autumn, beavers spend more time on dam building and foraging, whereas in winter when the lake is covered with ice they spend most of the time in their dens (Nolet and Rosell 1994). In Warmia and Mazury, the area from which the beavers originated, the average time when the lake is covered with ice ranges from 110 to 125 days. In such conditions, beavers spend most of the time in their den. In the beavers’ den, the temperature oscillates from 0.8 to 1.6 °C, whereas outside it fluctuates from − 6.8 to − 21.0 °C (Stephenson 1969). Under these conditions, the energy needed for thermoregulation is comparatively reduced. A similar mechanism of reducing energy demand was postulated for *M. lochrogaster* by Wunder (1992).

In the present study, the mass of the caecum and colon contents increased, whereas other parameters—the length and weight of the organ—remained unchanged. These results were similar to those obtained by Derting and Hornung (2003), who found an increase of caecum mass and length. The observed increase in the size of the digestive organs was due to a higher content of fibre in the diet, as was reported in *M. ochrogaster* (Hammond and Wunder 1991; Young Owl and Batzli 1998), *Clethrionomys glareolus* and *M. agrestis* (Lee and Houston 1993), *M. pennsylvanicus* (Young Owl and Batzli 1998), *L. brandtii* (Song and Wang 2006) and *M. unguiculatus* (Liu and Wang 2007), as well as due to the decreasing environmental temperature in *M. ochrogaster*

(Hammond and Wunder 1991; Hammond and Wunder 1995), *Dicrostonyx groenlandicus* (Hammond and Wunder 1995) and *L. brandtii* (Song and Wang 2006). In contrast to these results, Lee and Houston (1993) found no change in gut morphology due to diet quality in their study on *A. terrestris.*

According to a previous publication (Schwaibold and Pillay 2003), we expected that in summer the length of small intestine of females would be significantly longer compared to those of males; however, differences were not significant. We also expected differences between a reproductive and non-reproductive female. An experiment on *L. brandtii* indicated that reproductive females possess a longer digestive tract than do non-reproductive females (Lou et al. 2015). A similar dependence may be expected in the case of beavers; however, the studies should be conducted on a larger number of individuals.

As hypothesised, the beaver as a wild-living animal showed an adaptation of its digestive tract to a poor-quality diet by means such as elongation of the caecum and colon which is common for herbivorous rodents (Derting and Hornung 2003; Schwaibold and Pillay 2003). However, in this study in winter beavers were observed to have a decrease in parameters of the small intestine. This suggests similarity to those found in *M. lochrogaster* (Wunder 1992) with higher energy needs in summer/autumn for times of activity (dam building) than for thermoregulation in winter.

The current research focusses on morphological adaptation to diet; such information is essential and important, as it provides fundamental basic knowledge. The relationship between season, diet and digestive tract is complex. To understand this interaction more fully, future investigations including enzymatic activity, microbial diversity and physical characteristic of the digestive tract contents should be undertaken.

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