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Source: Wildlife Biology, 19(3) : 317-324

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/12-121

Wildl. Biol. 19: 317-324 (2013)
DOI: 10.2981/12-121

Short communication

Gut retention time in captive brown bears *Ursus arctos*

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Knowing animals' gut retention time (GRT) for important food items is critical when using non-invasive studies based on faecal remains, e.g. when analysing nutritive quality of food, or relating diet or behaviour to movements. We analysed GRT in six captive brown bears *Ursus arctos*, after feeding on either berries (a mixture of bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea*) or animal carcasses (either reindeer *Rangifer tarandus,* European rabbit *Oryctolagus cuniculus,* domestic pig *Sus scrofa domestica,* cattle *Bos taurus* or horse *Equus ferus caballus*). Median $GRT_{50\%}$ (i.e. when 50% of all faeces containing experimental food had been defecated) was 5 hours and 47 minutes (1st and 3rd quartiles = 4 hours and 36 minutes and 7 hours and 3 minutes; N = 20) after feeding on berries and 14 hours and 30 minutes (1st and 3rd quartiles = 10 hours and 9 minutes and 16 hours and 57 minutes; N = 20) after feeding on carcasses. Median GRT_{min} (i.e. first defecation comprised of experimental food) was 3 hours and 5 minutes (1st and 3rd quartiles = 1 hour and 51 minutes and 4 hours and 12 minutes; N = 21) for berries and 8 hours and 2 minutes (1st and 3rd quartiles = 6 hours and 14 minutes and 10 hours and 44 minutes; N = 20) for carcasses. Median GRT_{max} (i.e. last defecation comprised of experimental food) was 15 hours and 27 minutes (1st and 3rd quartiles = 11 hours and 36 minutes and 17 hours and 16 minutes; N = 21) for berries and 16 hours and 16 minutes (1st and 3rd quartiles = 12 hours and 11 minutes and 17 hours and 27 minutes; N = 20) for carcasses. A carcass diet had 6 hours and 26 minutes ± 1 hour and 56 minutes (SE) longer $GRT_{50\%}$ than a berry diet (N = 39), despite low variation in food intake. Activity level, feeding time (midday/midnight), sex, age (subadult/adult), ingested amounts of food, prior food remains processed by the gut (i.e. cumulative faeces weight) and defecation rate did not influence the $GRT_{50\%}$. Our reported GRT estimates are reliable values to be used within research and management to relate diet based on faecal remains to habitat use for common and important food items used by Scandinavian brown bears.

Key words: brown bear, digestibility, food intake, gastrointestinal, gut retention time, ingestion passage, transit, Ursus arctos

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Received 26 October 2012, accepted 28 March 2013

Associate Editor: Gregory W. Thiemann

Analyses of faecal remains allow non-invasive studies of, for instance, a species' distribution, habitat use and diet (Putman 1984). Data based on faecal remains can also be related to animal movements (e.g. using GPS positions). However, these studies often require knowledge of the time for ingested food to pass through the digestive tract, hereafter called gut retention time (GRT). Therefore, knowledge of the GRT is valuable for many types of studies. Knowing the GRT allows sampling faeces within a defined time frame, thus uniting feeding patterns with spatio-temporal data of individuals. In domestic pigs *Sus* *scrofa domestica*, a short GRT is associated with increasing proportions of ingested fibre (Partanen et al. 2007). When problem carnivores are shot (e.g. because of depredation incidents), the GRT also defines the time frame during which depredated foods are expected to be found in the digestive tract of destroyed animals. The GRT has been studied for several aquatic and terrestrial carnivores (Edwards et al. 2001, Hall-Aspland et al. 2011), as well as for omnivores (Tsuji et al. 2011). In bears, Ursidae, the GRT has been studied in omnivores with mainly a vegetative diet (giant pandas *Ailuropoda melanoleuca*; Dierenfeld et al. 1982), almost exclusively carnivores (polar bears *Ursus maritimus*; Best 1985), and omnivores with relatively large variation in their diet (Asiatic black bears *Ursus thibetanus*; Koike et al. 2010, and brown bears *Ursus arctos*; Pritchard & Robbins 1990). Pritchard & Robbins (1990) estimated the GRT for hair when feeding on carcasses and (chromium-marked) clover *Trifolium repens* in North American brown bears confined in small cages.

We analysed the GRT of captive Scandinavian brown bears for two common food items; berries and meat from carcasses. Meat (i.e. newborn calves of reindeer *Rangifer tarandus* and moose *Alces alces*) and berries (i.e. bilberry *Vaccinium myrtillus*, crowberry *Empetrum nigrum* and lingonberry *Vaccinium vitis-idaea*) constitute important foods for Scandinavian brown bears during spring and autumn, respectively (Dahle et al. 1998, Persson et al. 2001). Thus, although bears may have a mixed diet, they often feed on animals and berries during separate periods of the year. We compared GRT in relation to sex and age classes of bears, feeding time (midday/midnight), activity, diet (berry/carcass), weights of experimental food and supplemental food, cumulative weight of faeces and defecation rate. We hypothesised a longer GRT for a carcass than a berry diet, because Pritchard & Robbins (1990) reported higher digestibility (i.e. less material to be processed by the gut) and lower fibre content for meat than for berries.

Material and method

We studied GRT on six captive animals, three females (two subadults 2.5-year old and one adult 8.5-year old) and three males (two subadults 3.5-year old and one adult 10.5-year old) in the Orsa Bear Park, Sweden, during August of 2010. For none of the animals there were earlier reports or indications of gastrointestinal diseases. The four subadult bears were kept together in the same enclosure, whereas the two adults were kept together in a separate enclosure, both encompassing approximately 10,000 m^2. We used two individuals per experiment, and consecutive experiments were separated by a minimum of 48 hours for each individual.

During an experiment, bears were confined to an enclosure encompassing 400 m^2 for 24 hours. In order to standardise and improve the detection of experimental foods, individuals were given no food, except for ca 200 g of dog food pellets provided immediately after entering the experimental enclosure, and after four hours they were given the experimental foods. Bears were either given their experimental foods at midday (12:00) or at midnight (00:00) in order to control for last routine feeding between experiments and diel behaviour (Moe et al. 2007), which may affect gastrointestinal functions (Bron & Furness 2009). Between the experiments, bears were fed fruits (i.e. grapes *Vitis vinifera*, apples *Malus* sp. and oranges *Citrus* sp.) and bread daily at 14:00. Thus, ingestion of experimental food at midday took place ca 22 hours and midnight feeding ca 10 hours after the last routine feeding. Bears had access to carcasses (parts of domestic pig, cattle *Bos taurus* or horse *Equus ferus caballus*) within 12 hours before two experiments on carcass diet and one experiment on berry diet. Bears always had access to water and were given corn *Zea mays* weighed as fed after the experimental food had been consumed.

We mixed the experimental foods with 50-100 g plastic beads (of 5 mm in diameter), which functioned as solid markers to assist detection of experimental food items in the faeces and to confirm that faecal remains were derived from experimental foods. Experimental feeding of berries was comprised of a mixture of bilberry and lingonberry with a large proportion of the former. Experimental feeding of carcasses was comprised of meat, bones and fur from either bear-killed domestic reindeer calves, domestic rabbits *Oryctolagus cuniculus* or parts of domestic pigs, cattle or horses. All provided experimental food was consumed except larger pieces of bones or fur, which were subtracted from the weight as fed after the experiments. We only used data from experiments in which bears finished consuming the experimental food within two hours.

We video-recorded the animals during each experiment, using light-equipped cameras and recording capability within infrared wavelengths, noted start and end time of feeding, time of defecation, measured with an accuracy ± 1 second and scored an activity level every 10 minutes as active (standing/moving) or passive (laying/sitting down). After the bears had been released back into their main enclosures, all faeces were collected, labelled in order to relate each faeces to the time of defecation and bear identity (based on the video-recordings) and immediately weighed on an electronic scale. We examined faecal remains to detect the presence of markers, and we separated faeces containing experimental food item, i.e. berry or carcass, from those containing only corn. No corn defecation occurred before the first defecation containing remains of ingested experimental food, and the last defecation during experiments contained corn. The mean ± SD air temperature during the experiments was 15°C ± 4 (SD) at 12:00 and 12°C ± 3 (SD) at 00:00. Our study was approved by the Ethical Committee of Animal Research in Umeå, Sweden (permit D nr A 75-10).

Data analysis

We used both start and end times of feeding to calculate GRT. GRT_{min} denotes the time elapsed before the first defecation containing experimental food with markers, and GRT_{max} denotes the time elapsed before the last defecation containing experimental food with markers, after the ingestion of experimental food. $GRT_{50\%}$ denotes the time when 50% of the cumulative weight of faecal remains of experimental food with markers had been defecated after the ingestion of experimental food. We report median values, because distributions were non-normal, and to avoid overestimating the GRT (Ormseth & Ben-David 2000).

We estimated GRT_{min}, GRT_{max} and $GRT_{50\%}$ using only faeces with confirmed presence of experimental foods and markers. However, the total amount of material processed in the gut during and after the time of ingesting the experimental food affects the available volume in the gut before the next defecation (e.g. the $GRT_{50\%}$). Thus, material processed by the gut, measured as defecation rate and cumulative weight of defecations after ingesting experimental food prior to the $GRT_{50\%}$, may affect $GRT_{50\%}$. Therefore, when calculating defecation rate and cumulative weight of defecations prior to the $GRT_{50\%}$ defecation, we included all defecations (i.e. also faecal remains of corn and not containing experimental food or markers). We used linear mixed models (LMM) to analyse $GRT_{50\%}$ in relation to the following fixed factors: sex, age class (adult/subadult), activity score (% active), feeding time (midday/midnight), diet (berry/carcass), weight of ingested experimental food, weight of ingested supplemental food (corn), cumulative weight of defecations prior to $GRT_{50\%}$ and defecation rate prior to $GRT_{50\%}$. We included an interaction term between sex and age classes to control for potential differences among these classes, because bears are sexually dimorphic (Rode et al. 2006) and body size has been suggested to influence the GRT among herbivores (Demment & Van Soest 1985). We calculated the defecation rate prior to the $GRT_{50\%}$ as the number of defecations divided by the period from midpoint of feeding (between start and end times) until the $GRT_{50\%}$ defecation occurred. We calculated $GRT_{50\%}$ using the midpoint between the start and end of feeding in our LMM. We used bear identity and experiment as random effects.

We constructed a candidate set of 14 LMMs *a priori* and selected the most parsimonious LMM based on Akaike's Information Criteria scores for small sample sizes (AIC_c) and AIC_c weights (AIC_cw; Akaike 1973, Burnham & Anderson 2002). We used the 'lme4' package (Bates & Maechler 2010) for statistical modelling and generated β and its 95% highest posterior density interval (HPD) for the fixed effects of the regression models with a Markov Chain Monte Carlo algorithm (MCMC) using 1,000 simulations, package 'LMERConvenienceFunctions' (Tremblay 2011) in R.2.14.1 (R Development Core Team 2009). We considered effects significant when the HPD 95% around β did not include 0. Outliers were controlled for by using Cleveland dotplots and multicollinearity by using variance inflation factors (Zuur et al. 2009). The number of observations (N) deviated among analyses, because the factor activity score was missing for one animal during one experiment, and weights of faeces were missing for one animal during another experiment.

Results

Gut retention times and defecation rates for berries and carcasses

Median $GRT_{50\%}$ from the midpoint time of feeding was 5 hours and 47 minutes (1st and 3rd quartiles = 4 hours and 36 minutes and 7 hours and 3 minutes; N = 20) for berry diet and 14 hours and 30 minutes (1st and 3rd quartiles = 10 hours and 9 minutes and 16 hours and 57 minutes; N = 20) for carcass diet (Fig. 1). Median GRT_{min} from the midpoint time of feeding was 3 hours and 5 minutes (1st and 3rd quar-

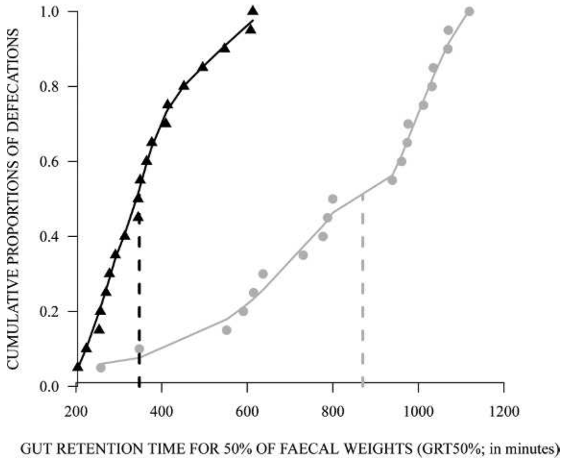

Figure 1. Cumulative proportions of defecations in relation to gut retention time when 50% of the cumulative weight of all faeces after 20 feedings of berry (▲) and 20 feedings of carcasses (•) had been defecated ($GRT_{50\%}$), for six captive Scandinavian brown bears in the Orsa Bear Park, Sweden, during 2010. Dashed vertical lines represent median $GRT_{50\%}$, and the x-axis has a minimum value of 200 minutes.

tiles = 1 hour and 51 minutes and 4 hours and 12 minutes; N = 21) for berry diet and 8 hours and 2 minutes (1st and 3rd quartiles = 6 hours and 14 minutes and 10 hours and 44 minutes; N = 20) for carcass diet. Median GRT_{max} from the midpoint time of feeding was 15 hours and 27 minutes (1st and 3rd quartiles = 11 hours and 36 minutes and 17 hours and 16 minutes; N = 21) for berry diet and 16 hours and 16 minutes (1st and 3rd quartiles = 12 hours and 11 minutes and 17 hours and 27 minutes; N = 20) for carcass diet. Descriptive estimates of GRT_{min}, GRT_{max} and $GRT_{50\%}$ are shown in relation to start and end points of feeding experimental foods in Table 1.

Median (1st and 3rd quartiles) defecation rate between start of feeding and last defecation of experimental food among experiments and individuals was 7.1 defecations/24 hours (6.1 and 9.4; N = 21) for berry feedings and 4.0 defecations/24 hours (1.2 and 5.4; N = 20) for carcass feedings.

Effects of diet, activity, sex, age, weights of food and faeces and defecation rate on $GRT_{50\%}$

The most parsimonious LMM included sex, age, (adult/subadult), feeding time (midday/midnight),

Table 1. Gut retention time (GRT; in hours:minutes) in six captive Scandinavian brown bears (two 2-year-old and one 8-year-old female; two 3-year-old and one 10-year-old male), after feeding on either berries or carcass (meat with bones and fur), at the Orsa Bear Park, Sweden, during 2010. GRT is combined between feeding at midday and midnight. Maximum time elapsed between start and end times of feeding was 1 hour and 39 minutes. GRT_{min} and GRT_{max} are based on 21 berry feedings and 20 carcass feedings, and $GRT_{50\%}$ is based on 20 berry feedings and 20 carcass feedings.

	Berry [a]		Carcasses [b]	
	Feeding		Feeding	
	Start	End	Start	End
GRT_{min} (First defecation)				
Median	3:09	2:38	8:21	7:39
Quartiles 1-3	2:25-4:19	1:46-4:06	6:35-11:09	5:45-10:16
Mean	3:41	3:08	9:21	8:39
SD	1:55	1:59	4:03	4:09
GRT_{max} (Last defecation)				
Median	15:38	15:17	16:41	15:56
Quartiles 1-3	12:00-17:53	11:23-16:48	12:42-17:54	11:26-17:11
Mean	14:27	13:53	14:46	14:03
SD	3:57	3:46	4:21	4:15
$GRT_{50\%}$ [c]				
Median	6:15	5:38	14:51	14:15
Quartiles 1-3	5:06-7:16	4:19-6:57	10:34-17:00	9:43-16:47
Mean	6:28	5:53	13:43	13:01
SD	2:03	2:00	4:26	4:21

[a] Mixture of bilberry and lingonberry.
[b] Either reindeer, European rabbit, domestic pig, cattle or horse.
[c] Denotes time elapsed when 50% of cumulative weight of all faeces had been defecated.

Table 2. Model selection based on AIC_c values ($w_i = AIC_c$ weights), finding the most parsimonious linear mixed model when fitting gut retention time when 50% of faeces with experimental foods had been defecated ($GRT_{50\%}$) for six captive Swedish brown bears, with bear ID and experiment as random effects, using *a priori* set of 14 candidate models. A variable on grey background represents its exclusion. A = subadult or adult, Ac = Activity score, CB = carcass or berry diet, DN = midday or midnight feeding, Dr = defecation rate, S = sex, Wc = cumulative weight of faeces , We = weight of experimental food, Ws = weight of supplemental food and * = an interaction between two factors.

Candidate models	K	AIC_c	ΔAIC_c	w_i	$w_{icum.}$
S*A+DN+Ac+**We**+**Ws**+**Wc**+Dr+CB	11	475.86	0.00	0.97	0.97
S*A+DN+Ac+**We**+Ws+Wc+Dr+CB	13	483.44	7.58	0.02	0.99
S*A+DN+Ac+We+**Ws**+Wc+Dr+CB	13	484.79	8.93	0.01	1.00
S*A+DN+Ac+We+Ws+**Wc**+Dr+CB	13	491.29	15.43	0.00	1.00
S*A+DN+Ac+We+Ws+Wc+Dr+CB	14	491.70	15.84	0.00	1.00
S*A+DN+**Ac**+We+Ws+Wc+Dr+CB	13	499.64	23.78	0.00	1.00
S*A+**DN**+Ac+We+Ws+Wc+Dr+CB	13	500.47	24.61	0.00	1.00
S*A+DN+Ac+We+Ws+Wc+**Dr**+CB	13	501.21	25.36	0.00	1.00
S*A+DN+Ac+We+Ws+Wc+Dr+CB	12	507.91	32.05	0.00	1.00
S***A**+DN+Ac+We+Ws+Wc+Dr+CB	12	508.48	32.62	0.00	1.00
S*A+**DN**+**Ac**+We+Ws+Wc+Dr+CB	12	508.85	32.99	0.00	1.00
S*A+DN+Ac+We+Ws+Wc+Dr+**CB**	13	512.01	36.15	0.00	1.00
S*A+DN+Ac+We+Ws+Wc+Dr+CB	11	515.53	39.68	0.00	1.00
Intercept model	4	560.98	85.12	0.00	1.00

activity score, prior defecation rate, diet (berry/carcass) and the interaction between sex and age class based on AIC_c ($\Delta AIC_c = 0.00$ and $AIC_cw = 0.97$; Table 2). Thus, this LMM excluded weight of experimental foods, supplemental food and prior cumulative faeces weight (see Table 2). Diet (berry or carcass) was the only fixed factor with a HPD 95% interval around β_{MCMC} that did not include 0; it had a β/SE of 3.3. A carcass diet had 6 hours and 26 minutes ± 1 hour and 56 minutes (SE) longer $GRT_{50\%}$ than berries (N = 39 feedings; Table 3). All other fixed factors in this model had HPD 95% intervals around β_{MCMC} that included 0, and β/SE ratios were ≤ 2.0; i.e. sex had $\beta/SE = 2.0$, age (adult/subadult) had $\beta/SE = 1.0$, feeding time (midday/midnight) had $\beta/SE = 0.7$, activity score had $\beta/SE = 0.5$, prior defecation rate had $\beta/SE = 0.1$ and interaction between sex and age class had $\beta/SE = 1.3$ (N = 39 feedings; see Table 3). Descriptive estimates for continuous fixed factors used in our LMM data set are shown in Table 4.

Discussion

We found no relationship between $GRT_{50\%}$ and activity levels of the animals, which were constrained within ca 400 m^2 during the experiments. Our reported median $GRT_{50\%}$ of 14 hours and 30 minutes after feeding on carcasses is similar to a

Table 3. Factors explaining gut retention time (in decimal minutes) when 50% of faeces with experimental foods had been defecated ($GRT_{50\%}$) after 39 feedings of six captive brown bears in Sweden 2010, in relation to diet of berries or carcasses, activity score, midday or midnight feeding, cumulative faeces weight, the interaction term between sex and subadult/adult and with bear ID and experiment as random effects based on the most parsimonious linear mixed model (see Table 2). Variances of random effects are < 0.0 for bear ID, 7,965.2 for experiment, and 35,474.4 for residuals. Markov Chain Monte Carlo (MCMC)-simulated β and its 95% highest posterior density interval (HPD) are given with β and standard errors (SE) based on a t-distribution.

				HPD 95%	
$\Delta AIC_c = 0.00$, w = 0.97	β	SE	β_{MCMC}	Lower	Upper
(Intercept)	299.80	168.63	313.53	-55.55	637.42
Males	257.22	128.88	272.67	-90.49	620.10
Subadults	140.65	139.00	179.66	-143.84	490.41
Midnight feeding	-57.16	76.70	-53.92	-190.30	87.81
Defecation rate	21.96	191.80	15.53	-424.67	397.61
Carcass	385.99	115.94	367.83	162.66	597.17
Activity score	-117.31	240.77	-174.57	-665.24	288.36
Males:Subadults	-194.63	149.10	-231.03	-628.17	192.94

Table 4. Descriptive estimates for fixed factors used to analyse effects on gut retention time on six captive bears after having a diet comprised of either berries (20 feedings) or carcasses (19 feedings). Bears were either given their experimental foods at midday (N = 22) or at midnight (N = 17).

	Ingested		Weight of prior faeces (g wet matter)	Defecation rate [a] (/hour)	Activity scores [b] (% of total)
	Experimental food (g as fed)	Supplemental food of corn (g as fed)			
Berry					
Median	5909	1810	837	0.29	51.5
Quartiles 1-3	2200-6018	950-2020	357-1248	0.18-0.60	38.3-70.3
Mean	4693	1627	813	0.36	55.6
SD	1784	643	534	0.26	21.6
Carcasses					
Median	4691	1704	265	0.16	34.5
Quartiles 1-3	4260-5425	1500-1962	0-461	0.00-0.20	30.3-38.3
Mean	4607	1682	307	0.14	33.4
SD	1004	342	300	0.14	9.8

[a] Number of defecations prior to when 50% of all faecal weight was defecated.
[b] The animal was active if standing/walking and passive if laying/sleeping, and was recorded every 10 minutes.

mean GRT for hair ingested by North American brown bears when feeding on carcass, based on amount of digested marked and unmarked hairs per defecation, 13 hours ± 2 hours (SD; Pritchard & Robbins 1990). However, Pritchard & Robbins (1990) used animals constrained within cages with a maximum dimension of 2.4 m. This suggests that GRT is not related to activity levels, and that our estimates of $GRT_{50\%}$ are reliable values to use within research (e.g. to compare diet based on faecal remains with movements) and management (e.g. for how long to expect to find ingested livestock in the gut of shot bears) for common food items used by brown bears.

We found no relation between $GRT_{50\%}$ and feeding time (midnight or midday). The main sleeping period of the bears used in this experiment was between midnight and sunrise, whereas the last routine feeding took place 22 hours before experimental feeding at midday and 10 hours before experimental feeding at midnight. This suggests that there is no effect from a circadian activity pattern on $GRT_{50\%}$ and/or effects from last ingestion before our experiments of $GRT_{50\%}$.

We provided the same amount of food during all experiments, and this may explain why we found no relationship between food intake (i.e. weight of ingested experimental or supplemental food) and $GRT_{50\%}$, as well as no relationship between cumulative faecal weights or defecation rate prior to the $GRT_{50\%}$ defecation and $GRT_{50\%}$. In the carnivorous leopard seal *Hydrurga leptonyx*, Trumble et al. (2003) reported similar GRT among experiments with different feeding frequency. However, it is possible that a larger variation in food intake would have had a larger effect on the GRT in our study, because larger food intake may shorten the GRT due to gut volume constraints. A negative correlation between food intake and GRT has been reported in omnivores, e.g. mice (McClelland et al. 1999) and herbivores (Clauss et al. 2007).

We found no differences in $GRT_{50\%}$ between subadults and adults, nor between female and male bears (i.e. groups with smaller and larger body sizes), even though foraging efficiency may decrease with increasing body size in bears (Welch et al. 1997, Rode et al. 2001). GRT does not change with body size in dogs *Canis familiaris* (Boillat et al. 2010) and primates (Lambert 1998). Steuer et al. (2011) concluded that body mass alone poorly explained differences in GRT between small and large herbivorous ungulates.

The $GRT_{50\%}$ for the carcass diet was 6 hours and 26 minutes ± 1 hour and 56 minutes (SE) longer than of berries, despite low variation in food intake. Pritchard & Robbins (1990) reported higher digestibility for carcasses (93%) than for blueberries *Vaccinium corymbosum* (64%). A higher digestibility of carcasses compared to berries results in a reduced amount of faecal remains and, hence, the gut can contain more faecal remains before the gut volume is filled and defecation occurs after feeding on carcass. Giant pandas feeding on bamboo *Phyllostachys aureosulcata*, which is rich in fibre content, have short GRT, probably because they ingest large amounts of poorly digestible food (Dierenfeld et al.

1982). Partanen et al. (2007) reported a shorter GRT and lower digestibility with increasing proportions of ingested fibre for pigs that were fed the same amounts of food. In humans, ingested fibre is known to improve bowel movements and produce softer faeces (Klosterbuer et al. 2011) and fresh bilberry has been described as having a laxative function (Jaric et al. 2007). In birds, ingested seeds have been suggested to have a chemical laxative function by shortening the GRT (Murray et al. 1994). The dietary fibre content of berries is five times higher than in carcasses (Pritchard & Robbins 1990). Thus, the much shorter $GRT_{50\%}$ for berries compared to carcasses in our study may be a result of lower digestibility in combination with increased gastrointestinal activity after ingesting berries.

Berries constitute the most important food item for Scandinavian bears during hyperphagia in summer and autumn (Dahle et al. 1998). The potential median and maximum seed dispersal distances for berries, based on our $GRT_{50\%}$ and GRT_{max} for berries, are 4.2 km and 11.1 km, respectively, when combining our results with a reported median rate of movement of 0.72 km/hour by Scandinavian brown bears (Moe et al. 2007). We found that the median (1st and 3rd quartiles) defecation rate of 7.1 (6.1 and 9.4) defecations/24 hours when bears foraged on berries is similar to the 7.2 defecations/day during autumn reported by Roth (1980) in captive brown bears fed a diet of mostly plants.

Conclusions

Our results suggest that GRT estimates are reliable to use in research where GRT after berry/carcass diet of bears are required. When combined with positioning data, GRT constitutes an important tool for determining where food remains found in faeces have been consumed and where remains of consumed foods will be excreted. The GRT also constitutes an important tool for management by defining a time frame in which to expect finding particular food remains in bears, e.g. livestock remains.

Acknowledgements - we thank our reviewer M. Clauss for comments on earlier drafts. We thank the Orsa Bear Park, Grönklitt, Sweden, and their staff, for providing us the opportunity to test GRT on their bears. We are most grateful to Olle Svensson AB, a part of the Nordic Food Group, for providing wild berries for the feeding experiments and Munkplast AB for providing plastic beads to use as experimental markers. We also thank the Swedish Environmental Protection Agency for financial support. This is scientific publication number 150 from the Scandinavian Brown Bear Research Project.

References

Akaike, H. 1973: Information theory and an extension of the maximum likelihood principle. - In: Petrov, B & Caski, F. (Eds.); Proceeding of the Second International Symposium on Information Theory: 267-281.

Bates, D.M. & Maechler, M. 2010: lme4: Linear mixed-effects models using S4 classes - R package version 0.999375-37. - Available at: http://CRAN.R-project.org/package=lme4:29 (Last accessed on 27 July 2012).

Best, R.C. 1985: Digestibility of ringed seals by the polar bear. - Canadian Journal of Zoology - Revue Canadienne De Zoologie 63: 1033-1036.

Boillat, C.S., Gaschen, F.P. & Hosgood, G.L. 2010: Assessment of the relationship between body weight and gastrointestinal transit times measured by use of a wireless motility capsule system in dogs. - American Journal of Veterinary Research 71: 898-902.

Bron, R. & Furness, J.B. 2009: Rhythm of digestion: keeping time in the gastrointestinal tract. - Clinical and Experimental Pharmacology and Physiology 36: 1041-1048.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. - Springer-Verlag, New York, New York, USA, 488 pp.

Clauss, M., Streich, W.J., Schwarm, A., Ortmann, S. & Hummel, J. 2007: The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. - Oikos 116: 209-216.

Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E. & Sandegren, F. 1998: The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. - Wildlife Biology 4(3): 147-158.

Demment, M.W. & Van Soest, P.J. 1985: A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. - American Naturalist 125: 641-672.

Dierenfeld, E.S., Hintz, H.F., Robertson, J.B., Van Soest, P.J. & Oftedal, O.T. 1982: Utilization of bamboo by the giant panda. - Journal of Nutrition 112: 636-641.

Edwards, M.S., Gaffney, M. & Bray, R.E. 2001: Influence of fiber source on apparent digestibility, rate of passage and fecal consistency in small felids fed a beef-based carnivore diet. - In: Edwards, M.S., Lisi, K.J., Schlegel, M.L. & Bray, R.E. (Eds.); Fourth Nutrition Advisory Group Conference on Zoo and Wildlife Nutrition. Proceedings of the American Zoo and Aquarium Association, Walt Disney World Resort, Florida, USA 4: 71-80.

Hall-Aspland, S., Rogers, T., Canfield, R. & Tripovich, J. 2011: Food transit times in captive leopard seals (*Hydrurga leptonyx*). - Polar Biology 34: 95-99.

Jaric, S., Popovic, Z., Macukanovic-Jovic, M., Djurdjevic, L., Mijatovic, M., Karadzic, B., Mitrovic, M. & Pavlovic,

P. 2007: An ethnobotanical study on the usage of wild medicinal herbs from Kopaonik Mountain (Central Serbia). - Journal of Ethnopharmacology 111: 160-175.

Klosterbuer, A., Roughead, Z.F. & Slavin, J. 2011: Benefits of dietary fiber in clinical nutrition. - Nutrition in Clinical Practice 26: 625-635.

Koike, S., Masaki, T., Nemoto, Y., Kozakai, C., Yamazaki, K., Kasai, S., Nakajima, A. & Kaji, K. 2010: Estimate of the seed shadow created by the Asiatic black bear *Ursus thibetanus* and its characteristics as a seed disperser in Japanese cool-temperate forest. - Oikos 120: 280-290.

Lambert, J.E. 1998: Primate digestion: Interactions among anatomy, physiology, and feeding ecology. - Evolutionary Anthropology 7: 8-20.

McClelland, K.L., Hume, I.D. & Soran, N. 1999: Responses of the digestive tract of the omnivorous northern brown bandicoot, *Isoodon macrourus* (Marsupialia: Peramelidae), to plant- and insect-containing diets. - Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 169: 411-418.

Moe, T.F., Kindberg, J., Jansson, I. & Swenson, J.E. 2007: Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). - Canadian Journal of Zoology 85: 518-525.

Murray, K.G., Russell, S., Picone, C.M., Winnettmurray, K., Sherwood, W. & Kuhlmann, M.L. 1994: Fruit laxatives and seed passage rates in frugivores - consequences for plant reproductive success. - Ecology 75: 989-994.

Ormseth, O.A. & Ben-David, M. 2000: Ingestion of crude oil: effects on digesta retention times and nutrient uptake in captive river otters. - Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 170: 419-428.

Partanen, K., Jalava, T. & Valaja, I. 2007: Effects of a dietary organic acid mixture and of dietary fibre levels on ileal and faecal nutrient apparent digestibility, bacterial nitrogen flow, microbial metabolite concentrations and rate of passage in the digestive tract of pigs. - Animal 1: 389-401.

Persson, I.L., Wikan, S., Swenson, J.E. & Mysterud, I. 2001: The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. - Wildlife Biology 7(1): 27-37.

Pritchard, G.T. & Robbins, C.T. 1990: Digestive and metabolic efficiencies of grizzly and black bears. - Canadian Journal of Zoology - Revue Canadienne De Zoologie 68: 1645-1651.

Putman, R.J. 1984: Facts from feces. - Mammal Review 14: 79-97.

R Development Core Team 2009: R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/ (Last accessed on 19 July 2012).

Rode, K.D., Farley, S.D. & Robbins, C.T. 2006: Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. - Ecology 87: 2636-2646.

Rode, K.D., Robbins, C.T. & Shipley, L.A. 2001: Constraints on herbivory by grizzly bears. - Oecologia 128: 62-71.

Roth, H.U. 1980: Defecation rates of captive brown bears. - Ursus 4: 249-253.

Steuer, P., Südekum, K-H., Müller, D.W.H., Franz, R., Kaandorp, J., Clauss, M. & Hummel, J. 2011: Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates. - Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 160: 355-364.

Tremblay, A. 2011: A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. - Available at: http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html (Last accessed on 8 August 2012).

Trumble, S.J., Barboza, P.S. & Castellini, M.A. 2003: Digestive constraints on an aquatic carnivore: effects of feeding frequency and prey composition on harbor seals. - Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 173: 501-509.

Tsuji, Y., Shiraishi, T. & Miura, S. 2011: Gastrointestinal passage time of seeds ingested by captive Japanese martens *Martes melampus*. - Acta Theriologica 56: 353-357.

Welch, C.A., Keay, J., Kendall, K.C. & Robbins, C.T. 1997: Constraints on frugivory by bears. - Ecology 78: 1105-1119.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009: Mixed Effects Models and Extensions in Ecology with R. 1st edition. - Springer, New York, New York, USA, pp. 532-536.