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Feeding adaptation of alimentary tract length in arboreal squirrels

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Abstract. The Jarman-Bell Principle among ungulates explains that larger species feeding on high-fiber foods have developed fermentation chamber such as rumen than smaller species feeding on low-fiber foods. Among arboreal squirrels, it seems that larger *Petaurista* species feed on high-fiber leaves and smaller species feed on low-fiber fruits and seeds. Therefore, relative length of the cecum may be positively correlated with body mass which is associated with tendency of folivory. To test this hypothesis, we examined body mass, head-body length, and the alimentary tract lengths (small intestine, cecum, colon, large intestine, and total intestine) of 13 arboreal squirrel species ($n = 19$) from six genera. Spearman rank correlation analysis showed that larger folivorous *Petaurista* had a longer fermentation chamber. Smaller granivorous squirrels might have longer small intestine. These differences in alimentary tract morphology of arboreal squirrels could reflect feeding adaptation.

Key words: fermentation chamber, folivory, granivory, Jarman-Bell Principle, *Petaurista*.

In mammals, morphological characteristics of alimentary tract seem correlated with food habits and body mass. Development of different parts of alimentary tract generally reflects adaptations to different foods (Bruerton and Perrin 1991), even though structure of alimentary tract is essentially homogeneous among different orders (Chivers and Hladik 1980). In particular, herbivorous mammals have fermentation chambers in their foregut and/or hindgut to digest high-fiber diets (Feldhamer et al. 2015). Furthermore, larger herbivorous mammals feed on a large quantity of high-fiber foods and smaller ones feed on low-fiber foods (Cork 1994), as mass-specific metabolic rate (rate of oxygen consumption per gram of body mass) generally decreases as body size increases (Feldhamer et al. 2015). This variation in ungulate species is explained by the Jarman-Bell Principle: large-sized species feeding on high-fiber foods such as grass have more developed fermentation chambers (e.g., rumen) than small-sized species feeding on low-fiber foods such as forbs, flowers, and fruits (Bell 1970; Jarman 1974; Hofmann 1989). Jarman-Bell Principle applies not only to ungulates, but also to primates (Gaulin 1979), although this principle is still controversial (McArthur 2014; Steuer et al. 2014). Folivorous primate species tend to be larger than insectivorous ones (Gaulin 1979; Kay and Simons 1980; Cork 1996). The subfamily Colobinae, which is the most

folivorous of arboreal primates, has a highly specialized, complex stomach (Gaulin 1979; Cork 1996).

Arboreal squirrels (Rodentia: Sciuridae) are distributed in all continents except both polar regions and the Australian Continent (e.g., Tamura 2011). These squirrels feed mainly on plant materials such as leaves, buds, fruits, seeds, and fungi. Their feeding habits seem to be associated with body size: larger species feed on high-fiber foods such as leaves, and smaller ones feed on low-fiber foods such as fruits and seeds. In North America, two marginally sympatric flying squirrel species essentially use different resources (Weigl 1978). The smaller southern flying squirrel (*Glaucomys volans*) feeds on fruits, seeds, and nuts (Harlow and Doyle 1990), whereas the larger northern flying squirrel (*G. sabrinus*) feeds on fungi and lichen (e.g., Weigl 1978; Mitchell 2001; Wheatley 2007), although for both species, diet composition and diversity vary depending on forest type, ecological community, and season (Smith 2007). Comparative study of diets between two sympatric flying squirrel species in northern Pakistan shows that the larger red giant flying squirrel (*Petaurista petaurista albiventer*) is more folivorous than the smaller Kashmir flying squirrel (*Eoglaucomys fimbriatus*) (Shafique et al. 2006). Similarly, Muul and Liat (1978) compared feeding habits of 11 flying squirrel species from seven genera (*Aeromys*,

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Hylopetes, *Iomys*, *Petaurillus*, *Petaurista*, *Petinomys*, and *Pteromyscus*) on the Malay Peninsula and found that larger species tended to include more foliage in their diet than smaller species.

Alimentary tract length of arboreal mammals increases with degree of folivory (Eisenberg 1978; Chivers and Hladik 1980; Cork 1996). Most rodents are cecal fermenters (Hume 1989). Herbivorous rodents have a longer cecum than omnivores (Lovegrove 2010). Giant flying squirrels *Petaurista* also have a long cecum that has been related to their high levels of folivory (Miyao 1972; Muul and Liat 1978). The Indian giant squirrel (*Ratufa indica*), which subsists entirely on a diet of leaves and bark when its preferred fruit are unavailable, has an enlarged cecum to help consumption of high-fiber foods (Borges 1998, 2008).

In this study, we focus on the relationship between alimentary tract length, food habits, and body mass in arboreal squirrels. Similar to ungulates and primates, we expect that larger arboreal squirrels have a longer cecum, because of their high-fiber diets. Therefore, we hypothesize that relative cecum length of larger *Petaurista* species is longer than those of smaller other arboreal squirrels.

Materials and methods

We examined 19 materials from a total of 13 arboreal squirrel species: *Callosciurus erythraeus*, *C. notatus*, *C. prevostii*, *G. volans*, *Petaurista alborufus*, *Pe. grandis*, *Pe. leucogenys*, *Pe. petaurista*, *Pteromys volans*, *Sciurus lis*, *S. vulgaris*, *S. stramineus*, and *Tamiasciurus hudsonicus* (Table 1). These materials were either the result of traffic

death, obtained commercially from pet stores in Japan, or provided from zoos. All materials were adults and have been deposited in the Laboratory of Wildlife Biology, Obihiro University of Agriculture and Veterinary Medicine, Japan. Body mass (BM) and head-body length (HB) were measured. We, however, could not measure HB of *C. notatus* and *C. prevosti*, because their whole-body materials were lost during preservation. Therefore, we estimated their HB by transforming the equation for predicting BM from HB in Callosciurinae provided by Hayssen (2008): $\log_{10}(\text{BM}) = -3.91 + 2.73 \times \log_{10}(\text{HB})$ ($R^2 = 0.947$). After dissection, alimentary tracts were fixed and preserved in 10% formalin solution or preserved at -20°C . To measure alimentary tract, we placed materials on a dissecting plate and removed mesenteries to make alimentary tract straight. Then, lengths of small intestine (SI) (duodenum, jejunum, and ileum), cecum (CC), and colon (CL) (proximal and distal colon and rectum) were measured to the nearest 5 mm by a tape measure. The cecum served as the defining border between small intestine and colon. Length of the large intestine (LI) was calculated by summing CC and CL lengths, and the total intestine (TI) length was calculated by summing SI and LI lengths.

We examined the relationship between BM and the relative length of the alimentary tract. To remove the effect of body size from the alimentary tract length, we calculated ratios of the alimentary tract length to HB (SI/HB, CC/HB, CL/HB, LI/HB, and TI/HB). We also calculated the ratio of LI to SI (LI/SI). This ratio emphasizes large intestine involvement in the dietary process and the tendency toward herbivory (Snipes 1994). In order

Table 1. Food habits of squirrel species examined in this study (n = number of samples)

Species	Common name	n	Food habits (references)
<i>Callosciurus erythraeus</i>	Pallas's squirrel	4	fruit, seed (Lurz et al. 2013)
<i>Callosciurus notatus</i>	plantain squirrel	1	fruit (Payne et al. 1985)
<i>Callosciurus prevosti</i>	Prevost's squirrel	1	fruit (Payne et al. 1985)
<i>Glaucomys volans</i>	southern flying squirrel	1	fruit, seed (Harlow and Doyle 1990)
<i>Petaurista alborufus</i>	red and white giant flying squirrel	2	leaf, fruit (Lee et al. 1986)
<i>Petaurista leucogenys</i>	Japanese giant flying squirrel	2	leaf, fruit, seed (Ando et al. 1985; Kawamichi 1997)
<i>Petaurista petaurista</i>	red giant flying squirrel	1	leaf, fruit, seed (Shafique et al. 2006)
<i>Petaurista philippensis</i>	Indian giant flying squirrel	1	leaf, fruit (Nandini and Parthasarathy 2008; Koli et al. 2013)
<i>Pteromys volans</i>	Siberian flying squirrel	1	leaf, seed (Airapetyants and Fokin 2003; Asari et al. 2008)
<i>Sciurus lis</i>	Japanese squirrel	1	fruit, seed (Tamura 1997)
<i>Sciurus stramineus</i>	Guayaquil squirrel	2	fruit, seed (Merrick et al. 2012)
<i>Sciurus vulgaris</i>	Eurasian red squirrel	1	fruit, seed (Lurz et al. 2005)
<i>Tamiasciurus hudsonicus</i>	American red squirrel	1	seed (Steele 1998)

to conduct interspecific comparisons, we used averages of both BM and the relative lengths of the alimentary tract for species with more than one sample; *C. erythraeus* ($n = 4$), *Pe. alborufus* ($n = 2$), *Pe. leucogenys* ($n = 2$), and *S. stramineus* ($n = 2$), respectively. Then, we calculated the Spearman rank correlation coefficient (r_s) between the respective lengths and body mass with 95% confidence intervals. All statistical analyses were with R program ver. 2.8.1. (R Development Core Team 2008).

Results and discussion

Fig. 1 (a–e) shows the relationships between BM and relative lengths of the alimentary tract. Relative length of the cecum was positively correlated with body mass in arboreal squirrels ($r_s = 0.59$, Fig. 1b). It indicates that larger *Petaurista* species may have longer cecum, which provides them an elongated fermentation chamber. The significant correlation between LI/SI and BM indicates

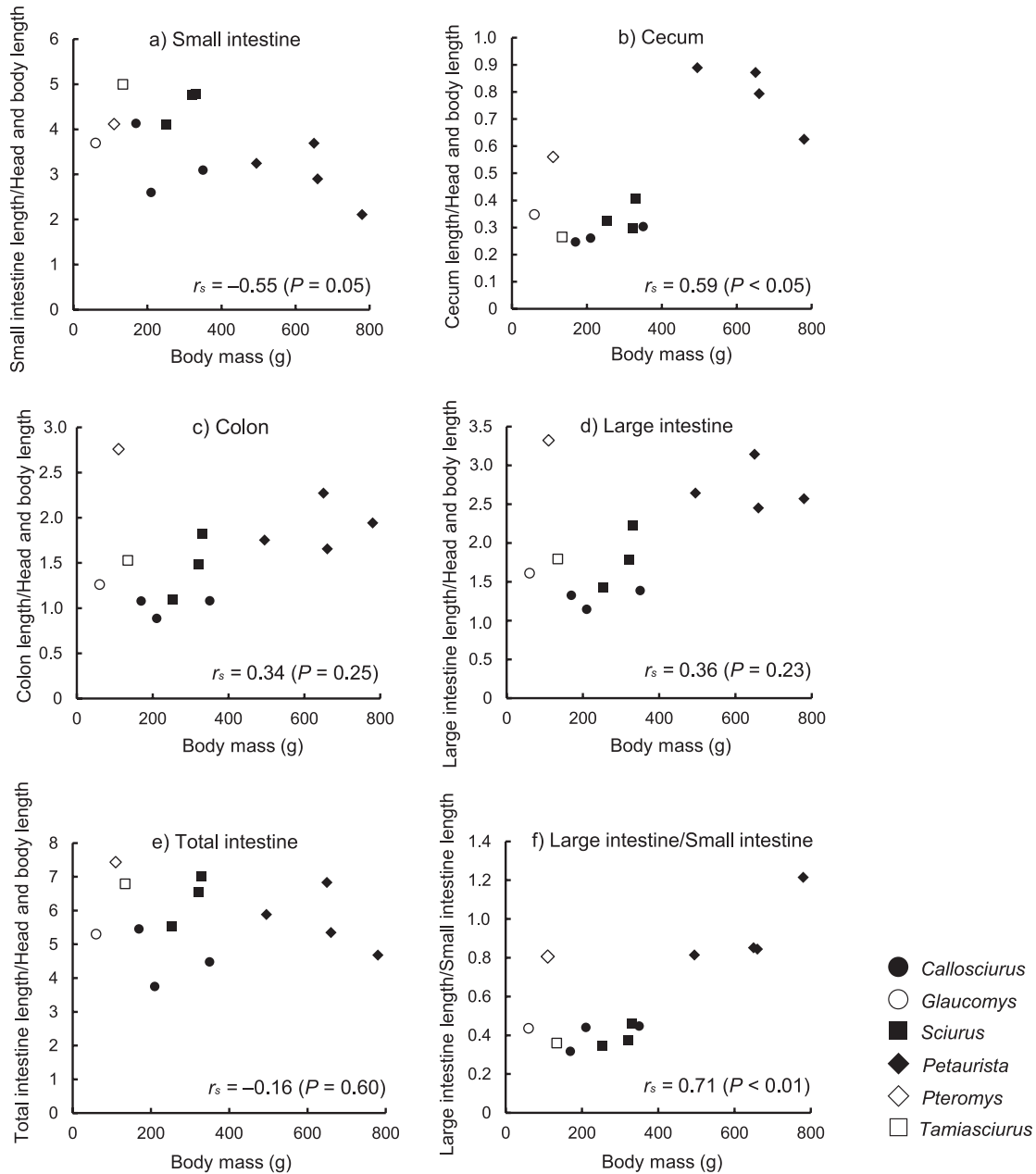


Fig. 1. Relationships between body mass (g) and the relative lengths of alimentary tract in 13 arboreal squirrel species from six genera: *Callosciurus* (closed circles), *Glaucomys* (open circles), *Petaurista* (closed diamonds), *Pteromys* (open diamonds), *Sciurus* (closed squares), and *Tamiasciurus* (open squares); a) small intestine, b) cecum, c) colon, d) large intestine, e) total intestine, and f) large intestine/small intestine.

Table 2. Squirrel materials examined in this study and preserved in the Laboratory of Wildlife Biology, Obihiro University of Agriculture and Veterinary Medicine, Japan

Species	Identity number	Sex	Dissecting date	Supplier	BM (g)	HB (mm)	Alimentary tract length (mm)				Relative length of the alimentary tract						
							SI	CC	CL	LI	TI	SI/ HB	CC/ HB	CL/ HB	LI/ HB	TI/ HB	LI/ SI
<i>Callosciurus erythraeus</i>	12151208-1	M	Dec 15, 2015	M. Yasuda	180	214	1145	75	300	375	1515	5.33	0.35	1.40	1.75	7.08	0.33
<i>Callosciurus erythraeus</i>	12151208-2	M	Dec 15, 2015	M. Yasuda	199	213	745	40	200	240	985	3.50	0.19	0.94	1.13	4.62	0.32
<i>Callosciurus erythraeus</i>	12151208-3	M	Dec 15, 2015	M. Yasuda	137	206	710	40	140	180	890	3.45	0.19	0.68	0.87	4.32	0.25
<i>Callosciurus erythraeus</i>	12151208-4	M	Dec 15, 2015	M. Yasuda	162	197	840	50	255	305	1145	4.26	0.25	1.29	1.55	5.81	0.36
<i>Callosciurus notatus</i>	Cno-1*	M	Jan 13, 1995	-	210	†192	500	50	170	220	720	2.60	0.26	0.89	1.15	3.75	0.44
<i>Callosciurus prevosti</i>	Cpr-1*	M	Oct 19, 1993	-	350	†231	715	70	250	320	1035	3.10	0.30	1.08	1.39	4.48	0.45
<i>Glaucomys volans</i>	S9*	M	Sep 9, 1996	-	60	115	425	40	145	185	610	3.70	0.35	1.26	1.61	5.30	0.44
<i>Petaurista alborifus</i>	S5*	F	June 3, 1996	-	615	405	1180	310	560	870	2050	2.91	0.77	1.38	2.15	5.06	0.74
<i>Petaurista alborifus</i>	S7*	M	June 9, 1996	-	705	420	1215	345	810	1155	2370	2.89	0.82	1.93	2.75	5.64	0.95
<i>Petaurista leucogenys</i>	No.1*	F	Feb 9, 1990	-	730	418	1530	355	1015	1370	2900	3.66	0.85	2.43	3.28	6.94	0.90
<i>Petaurista leucogenys</i>	No.14*	F	June 11, 1991	-	570	397	1480	355	840	1195	2675	3.73	0.89	2.12	3.01	6.74	0.81
<i>Petaurista petaurista</i>	S10*	F	Sep 20, 1996	-	495	405	1315	360	710	1070	2385	3.25	0.89	1.75	2.64	5.89	0.81
<i>Petaurista philippensis</i>	S2	F	Apr 12, 1996	P-C. Kuo	780	440	930	275	855	1130	2060	2.11	0.63	1.94	2.57	4.68	1.22
<i>Pteromys volans</i>	S3*	M	Apr 17, 1996	-	110	125	515	70	345	415	930	4.12	0.56	2.76	3.32	7.44	0.81
<i>Sciurus lis</i>	Si-1	M	June 28, 2016	Morioka Zoo	252	200	820	65	220	285	1105	4.10	0.33	1.10	1.43	5.53	0.35
<i>Sciurus stramineus</i>	Sst-1*	F	Oct 22, 1994	-	380	230	1025	90	340	430	1455	4.46	0.39	1.48	1.87	6.33	0.42
<i>Sciurus stramineus</i>	Sst-2*	F	Aug 10, 1995	-	280	215	1100	90	465	555	1655	5.12	0.42	2.16	2.58	7.70	0.51
<i>Sciurus vulgaris</i>	Svu-1**	F	Jul 28, 1996	-	322	235	1120	70	350	420	1540	4.77	0.30	1.49	1.79	6.55	0.38
<i>Tamiasciurus hudsonicus</i>	Thu-1	F	Dec 8, 2015	Awaji Farm Park	134	170	850	45	260	305	1155	5.00	0.27	1.53	1.79	6.79	0.36

BM = Body mass, HB = Head-body length, SI = length of small intestine, CC = Cecum, CL = Colon, LI = Large intestine, TL = Total intestine.

* Individuals obtained commercially from pet stores in Japan.

** Road-killed individual collected by authors.

† These values were calculated by transforming the equation for predicting BM from HB in Callosciurinae, $\log_{10}(\text{BM}) = -3.91 + 2.73 \times \log_{10}(\text{HB})$ ($R^2 = 0.947$) provided by Hayssen (2008).

larger *Petaurista* species may be more folivorous (Fig. 1f), which agrees with their reported food habits (Table 1). Murphy and Linhart (1999) reported that the specialized herbivorous the Abert's squirrel (*S. aberti*) had a significantly longer cecum than the omnivorous fox squirrel (*S. niger*) and the granivorous eastern gray squirrel (*S. carolinensis*). From January to June, the Abert's squirrel only eats high-fiber and low-quality ponderosa pine (*Pinus ponderosa*) phloem, suggesting that the alimentary tract morphology of the Abert's squirrel has become adapted to their low-quality diets. Therefore, the developed fermentation chamber of larger *Petaurista* species in our study may reflect feeding adaptations to folivory.

Petaurista squirrels had large LI/SI of 0.74–1.22 (Table 2). These are comparable to specialized herbivores such as rabbits (0.8), guinea pigs (0.9), and spalaxs (1.0) (Snipes 1994). Miyao (1972) reported the LI/SI values for two individuals of *Pe. leucogenys*: 1.14 and 1.47. Large intestine of *Petaurista* was almost the same length as small intestine and might be a structural adaptation to folivory. The LI/SI of granivorous and frugivorous species were 0.25 to 0.51 (Table 2). *Petaurista* species had higher CC/HB than other squirrels (Fig. 1b). Thus, the largest difference between *Petaurista* and other squirrels is in cecum rather than colon length, indicating that the cecum of *Petaurista* is particularly elongated as a fermentation chamber. *Petaurista* species have a developed cecum for the adaptation to folivory, not only morphologically, but also physiologically. Cecal microbiota of *Pe. alborufus lena* has great metabolic potential for converting diverse plant materials into absorbable nutrients (Lu et al. 2012). Of the two sympatric flying squirrel species in Japan, *Pe. leucogenys* more easily digests fibers than *Pt. momonga* (Okubo et al. 2015).

Of the small squirrels, *Pt. volans* had the longest colon and large intestine (Table 2 and Fig. 1c and d) and thus, its LI/SI ratio was relatively large (Table 2 and Fig. 1f). Therefore, the elongated large intestine of this species seems to be associated with folivory. Actually, leaves are one of their main food items (Airapetyants and Fokin 2003; Asari et al. 2008). *Pteromys volans* occurs in the subarctic regions, from Finland and the Baltic countries through Siberia to Korea and Hokkaido Island, Japan (Hanski et al. 2000). It lives where the availability of fruits and masts is limited. Contrary to this, *G. volans*, which is granivorous and smaller than *Pt. volans*, is associated with oak-hickory (*Quercus* and *Carya*) forests in the temperate region in the North American Continent (Thorington et al. 2012). In the present study, its cecum

was shorter than that of *Pt. volans*. Although both *Pt. volans* and *G. volans* are small-sized flying squirrels occurring in the Northern Hemisphere, each species could have adapted to different habitat, showing different alimentary tract length. Moreover, frugivorous *C. erythraeus* (Payne et al. 1985) and *C. notatus* (Tamura 2011), which have a shorter cecum, occur in subtropical and tropical regions where fruits are abundant. Thus, morphological differences in alimentary tract length between *Pt. volans* and other small arboreal squirrels may reflect geographical distribution of food resources. Even in ungulates, there are exceptions to the Jarman-Bell Principle; for instance, the giraffe (*Giraffa camelopardalis*), the largest ruminant, does not feed on high-fiber grass (e.g., Takatsuki 1991). Feeding adaptation of *Pt. volans* would be an exception because of its northernmost distribution among arboreal squirrels.

The SI/HB ratio suggests that smaller arboreal squirrels might have longer small intestines ($r_s = -0.55$, Fig. 1a). Based on LI/SI ratio (Fig. 1f) and food habits of all species (Table 1), we suggest that smaller squirrels feeding mainly on fruits and seeds have elongated small intestine. In mammals, the small intestine is the primary site of enzymatic digestion and the site for absorption of carbohydrates, amino acids, and fatty acids (e.g., Lavin et al. 2008). Elongation of a tubular alimentary tract is one way to increase an absorptive surface (Snipes 1994). Since fruits and seeds, in general, contain abundant carbohydrates and fatty acids, development of the small intestine may show the adaptation of arboreal small squirrels to their diet. Previous studies (Lavin et al. 2008; Lovegrove 2010), however, show that diet does not significantly affect the small intestine length in mammals. Further studies should examine adaptations of the small intestine to diets.

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