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Comparative Studies of Food Habits and Digestive Tracts in Two *Apodemus* Species

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Feeding experiments using three pairs of food items, analysis of the scaling of digestive organs and microscopic observation were examined in two woodland rodent species, ***Apodemus argenteus*** and ***A. speciosus.*** Comparing the values of selective indices between acorns and three species of insects, it was shown that ***A. argenteus*** has more intensive preference to insects than does ***A. speciosus.*** Both the mean ratio of the caecum length to stomach and intestine length (CL/TL) and the ratio of caecum length to the small intestine length (CL/SIL) in ***A. speciosus*** were significantly larger than those in A. ***argenteus.*** Compared to ***A. speciosus,*** distributions of goblet cells stained with PAS in ***A. argenteus*** were dense and homogeneous at most of positions of the small intestines. These characteristics in the small intestine suggest that A. ***argenteus*** depends on more homogeneous and proteinic foods, and support the results from our feeding experiments. From what described above, it was implied that these differences in potential food habits are related to the characteristics of foraging behavior, habitat utilization and territoriality in the two ***Apodemus*** species.

INTRODUCTION

Studies of food habits in small mammals have been mainly based on microscopic analyses of feces or stomach contents and on preference experiments in the laboratory (Hansson, 1985). In *Apodemus argenteus* and *A. speciosus*, which are Japanese woodland rodents, several reports on analyses of stomach contents (Mizushima and Yamada, 1974; Tachikawa and Murakami, 1976) reveal that the two species have both granivorous and insectivorous characteristics. Still, research on the food habits of the two species often fails to illuminate the differences between the two species: however, it is accepted that *A. argenteus* depends on animal food more than *A. speciosus* (Maeda *et al.*, 1984). Laboratory experiments on food preference among woodland rodents showed that quality and/or abundance of usable foods affect the diet selection (Hansson, 1985). It was shown that availability of foods in both the laboratory and field experiments affects the diet choice of *Apodemus* species (Holisova, 1975; Sone, 1990). Therefore, there is a great need for further examination of experimental conditions concerning combination and availability of food items to objectively explain differences in food habits between the two species.

A. argenteus and *A. speciosus* are sympatric species with segregated microhabitats, which is explained as a mechanism for reducing interspecific competition (Shioya *et al.*, 1990). Difference in food habits are an important factor in facilitating coexistence of

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*Present address: Wildlife Ecology Laboratory, Forestry and Forest Products Research Institute, Ministry of Agriculture, Forestry and Fisheries, Ibaraki 305, Japan sympatric species (M'Closkey, 1976; Rosenzweig, 1981). Namely, differences in microhabitat usage in small mammals depend on food habit or foraging behaviors (Rosenzweig, 1991). Therefore, understanding of the histology and histochemistry of digestive organs is necessary for revealing differences in the trophic characters of small mammals.

In these two species, most of the studies on the digestive organs have used macroanatomical observations. Although some studies analysed the relationships between the ratio of caecum length to small intestine length and food habits (Miyao *et al., 1960;* Maeda *et al.,* 1984), histological analyses were never done. Mucilage cells, which serve in the protection of mucosal epithelium in the stomach and intestines, are related to the activity of digestion of protein in the diet (Martin, 1961). There is hence the possibility of explaining differences in food habits between species by numerical analyses of mucilage cells. However, most studies only compare gastric histology among species with extremely various food habits (Horner *et al.,* 1965 for Rodentia; Kamiya and Pirlot, 1975 for Chiroptera; Lüthje, 1976 for Rodentia; Suzuki et al., 1986 for Primates). Because no appreciable difference in interspecific macroanatomical morphology was found, little attention has been given to the small intestine, whose real functions are absorption and digestion.

The aim of this paper is to compare the preference to animal food of the two *Apodemus* species based on the results of feeding experiments with three pairs of acorns and insects, and to discuss the histological characters of the gastric organs and small intestines, which are related to the food habits in both species.

MATERIALS AND METHODS

1. Feeding experiments

The preference experiment trials were conducted in an enclosure (1 : w : h=30× 60 x 40cm). The temperature was maintained at approximately 20°C. Numbers and kinds of food items used in each of the experiment were as follows: 30 acorns of *Quercus glauca* and 30 beetles of *Melolontha satsumaensis* in experiment 1; 10 acorns of Q. *glauca* and 30 domestic flies *Musca domestica* in experiment 2; 30 acorns of Q. *glauca* and another 30 acorns which included the parasitic larvae of *Curculio sikkimensis* in experiment 3. In each of the experiments, ten wild-caught mice (5 ♂♂ : 5 ♀♀) of each of the two *Apodemus* species were used. All adult *Apodemus* mice used in these experiments were trapped at Mt. Tachibana-yama (367m) north of Fukuoka City in April 1989. Each of the individuals was starved for 12 hrs prior to the trials and introduced singly into the enclosure at 1900 h. The enclosure had two kinds of food items and water. Consumption was recorded and cached items were checked on the following day at 0100 h. Trials in each experiment were repeated three times for each individual. Mean values of both Ivlev's selective index (Ivlev, 1961) and Jacobs's index (Jacobs, 1974) were calculated for each species, and compared between the species using Mann-Whitney U-tests.

2. Histological methods

For histological analyses, adult *A. argenteus (56* ♂: 5 ♀♀) and *A. speciosus* (5 ♂♂:

5 ♀♀) were also captured in November 1990 at a location similar to that in the preference experiments described above. The gastrointestinal tract was extracted from the abdominal cavity after killing individuals by etherization. For macroanatomical measurements of digestive tracts, the stomach and intestine length (TL), small intestine length (SIL), and caecum length (CL) in fresh condition were recorded. Stomachs and small intestines to be used for comparative histological studies were fixed in Bouin's fixative. For the gastric organs, segments were taken from both the cardiac and fundic regions. For the small intestines, segments of 5 mm length were taken at each of five positions at 4, 20, 40, 60 and 80% of the length of the tracts from the proximal to the distal side. One group of these segments was embedded in paraffin wax after dehydration, and then sectioned at 6 μm and stained with haematoxylin and eosin. The others were embedded in Technovit 7100 (Kulzer Co., Ltd.) and sectioned at 4 μ m, employing haematoxylin and periodic acid Schiff (PAS) technique for microscopic observation of goblet cells. To statistically analyse differences in the function of proteinic digestion of food-stuff in the small intestines, numbers of the goblet and other cells were counted at ten points at each of the villi and crypts per segment. In the two species, frequency of appearance of the goblet cells was compared, i.e. the ratio of goblet cells to all cells.

RESULTS

1. Feeding experiments

In experiment 1, the mean numbers of acorns and *M. satsumaensis* per trial selected by A. *argenteus* were 1.5 and 2.6, respectively, while A. *speciosus* selected 4.9 acorns and 4.4 beetles per trial on average (Table 1). Both species almost exclusively attacked at the basal part of the hemelytra of *M.* satsumaensis and fed on the abdominal material, excluding the cuticle. Mean values of both Ivlev's selective index and Jacobs's index were

Table 1. Results of feeding experiment 1 comparing two **Apodemus** species, using acorns of *Quercus glauca* and adults of *Melolontha* ***satsumaensis*** as diet.

	A. argenteus		***A. speciosus***	
	acorn	*M.* ***satsumaensis***	acorn	*M.* ***satsumaensis***
n	1.5	2.6	4.9	4.4
ri	0.366	0.634	0.527	0.473
pi	0.5	0.5	0.5	0.5
	┌	$p<0.001$	┐	
Ei	-0.155	0.118	0.026	−0.028
		└	$p<0.001$	┘
	┌	$p<0.001$	┐	
Di	− 0.268	0.268	0.054	−0.054
		└	$p<0.001$	┘

n, mean numbers of food items eaten; r, mean proportions of food items eaten in diet; p_i, mean proportions of food items in food; E_i, means of Ivlev's selective index $= \frac{r_i-p_i}{r_i+p_i}$; D_i, means of Jacobs's index $= \frac{r_i-p_i}{r_i+p_i-2r_ip_i}$ Significant differences are estimated using the Mann- Whitney U-test.

significantly different between the two species (U-tests, $ps<0.001$): *A. argenteus* more intensively selected *M. satsumaensis* than did *A. speciosus*.

In experiment 2, the mean numbers of acorns and *M. domestica* selected per trial by A. *argenteus* were 1.5 and 10.6, respectively, while these values were 7.0 and 11.0 in A. *speciosus*. Also, the parts of the fly bodies on which the mice began to feed were different in each attacked fly. The flies were consumed almost completely except for the indigestible wings and cuticle segments. Results in experiment 2 were similar to those obtained in experiment 1: mean values of both Ivlev's selective index and Jacobs's index were significantly different between the two species (U-tests, $ps<0.001$) . This shows that *A. argenteus* selected *M. domestica* more strongly than did *A. speciosus* (Table 2).

Table 2. Results of feeding experiment 2 comparing two *Apodemus* species, using acorns of Q. glauca and adults of *Musca domestica* as diet.

	A. argenteus		*A. speciosus*	
	acorn	M. *domestica*	acorn	*M. domestica*
n	1.5	10.6	7.0	11.0
r_i	0.122	0.877	0.388	0.611
Pi	0.25	0.75	0.25	0.75
		$p<0.001$		
E_i	− 0.344	0.078	0.040	− 0.019
			$p<0.001$ -	
	7	p <0.001		
D_i	− 0.454	0.454	0.312	− 0.312
			$p<0.001$	

See Table 1 for explanations of symbols.

In experiment 3, *A. argenteus* selected 1.1 sound acorns and 9.5 acorns parasitised by larvae of C. *sikkirnensis* per trial on average, whereas *A. speciosus* selected 4.6 and 9.8, respectively. The larvae were removed from acorns and completely consumed by both species. Mean values of the two indices of each of the food items were significantly different between the two species (U-tests, $ps<0.01$-0.001). *A. argenteus*

Table 3. Results of feeding experiment 3 comparing the two *Apodemus* species, using acorns of *Q. glauca* and the ones including parasitised by larvae of *Curuculio sikkimensis* as diet.

	A. argenteus		*A. speciosus*	
	acorn	C. *sikkimensis*	acorn	C. *sikkimensis*
n	1.1	9.5	4.6	9.8
r_i	0.103	0.896	0.319	0.680
Pi	0.5	0.5	0.5	0.5
		$p<0.001$		
E_i	− 0.656	0.283	-0.220	0.152
			$p<0.001$	
		$p<0.001$		
D_i	-0.792	0.792	-0.361	0.361
			$p<0.01$	

See Table 1 for explanations of symbols.

more strongly selected C. *sikkimensis* in comparison with A. *speciosus* (Table 3).

2. Histology of stomachs and small intestines

The mean lengths from stomach to rectum (TL) were 387.3 mm (s.d.=22.1) in A. *argenteus* and 490.4 mm (s.d.=41.0) in A. *speciosus* (Table 4). Mean ratios of the small intestine length to these total lengths (SIL/TL) were 0.679 (s.d.=0.099) in A. ***argenteus*** and 0.673 (s.d.=0.135) in A. *speciosus*, and did not differ significantly (U-tests, $p>0.05$). On the other hand, the mean ratios of the caecum length to the total length (CL/TL) were 0.091 (s.d.=0.011) in A. ***argenteus*** and 0.101 (s.d.=0.013) in A. *speciosus*, and the ratios of caecum length to the small intestine length (CL/SIL) were 0.134 (s.d.=0.032) and 0.150 (s.d.=0.073), respectively, and there were significant differences in these ratios between the species (U-tests, $ps<0.05$). Additionally, all of the ratios of TL, SIL, and CL to cube roots of body weight were not significantlly different between the two species (U-tests, $ps>0.05$).

Table 4. Comparison of measurements of digestive tracts between the two *Apodemus* species on the basis of means (s.d.) of stomach and intestine length (TL), small intestine length (SIL), caecum length (CL), and cube root of body weight ($\sqrt[3]{BW}$).

	A. argenteus	*A. speciosus*	p
TL mm	387.3 (22.1)	490.4 (41.0)	
SIL / TL	0.679 (0.099)	0.673 (0.135)	ns
CL / TL	0.091 (0.011)	0.101 (0.013)	< 0.05
CL / SIL	0.134 (0.032)	0.150 (0.073)	< 0.05
TL / $\sqrt[3]{BW}$	146.4 (9.03)	147.8 (11.50)	ns
SIL / $\sqrt[3]{BW}$	99.4 (6.18)	99.5 (7.74)	ns
CL / $\sqrt[3]{BW}$	14.5 (0.90)	14.9 (1.16)	ns

ns, not significant by using Mann-Whitney U-test.

Microscopic observations in the fundic region of the gastric organs revealed that maximum ratios of thickness of the *Tunica muscularis* to the whole cross layer were approximately 15% in A. ***argenteus*** and 20% in A. *speciosus*. Chief cells, which were stained violet with haematoxylin, were sparse in the neck region of the gastric gland in both species, while they were relatively dense in the basal region. The ratios of the thickness of this high density region to the depth of the gastric gland were 50% in A. ***argenteus*** and 30% in ***A.*** *speciosus*. Parietal cells, including granules stained red with eosin, were scattered in both species, and the distribution patterns of parietal cells were not different. In the cardiac region, the ratio of thickness of mucous layer to the whole of the stomach layer ranged from 14-20% in both species. Maximum ratios of *Tunica muscularis* to thickness of the whole cross layer were approximately 25% in ***A. argenteus*** and 30% in ***A.*** *speciosus*. Significant differences in these values were not found between the two species (U-tests, $ps>0.05$).

On the basis of microscopic observations of the small intestines, the villi region was shown to be 3 to 5 times thicker than the *Tunica muscularis* in both species and the species did not essentially differ in the scaling of villi. In the basal region of the crypts

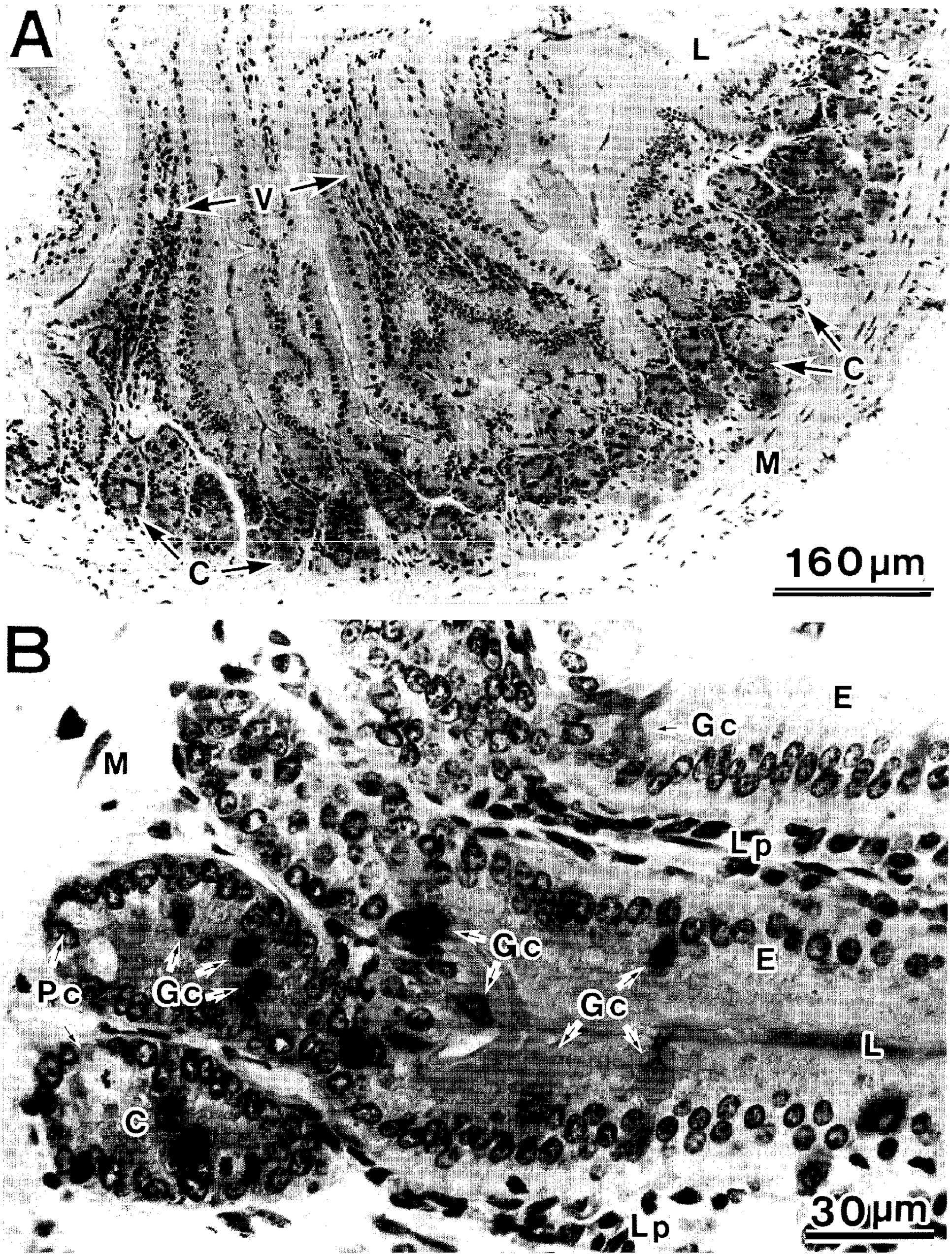

Fig. 1. Photomicrographs showing the small intestine of *Apodemus argenteus* stained with PAS and haematoxylin. A, Cross section at the jejunum; B, Cross section at the ileum. Note the presence of many goblet cells (Gc) in deeper site of crypts (C). E, epithelium; L, lumen; Lp, lamina propria mucosae; M, *Tunica muscularis;* Pc, Paneth's cell; V, villi.

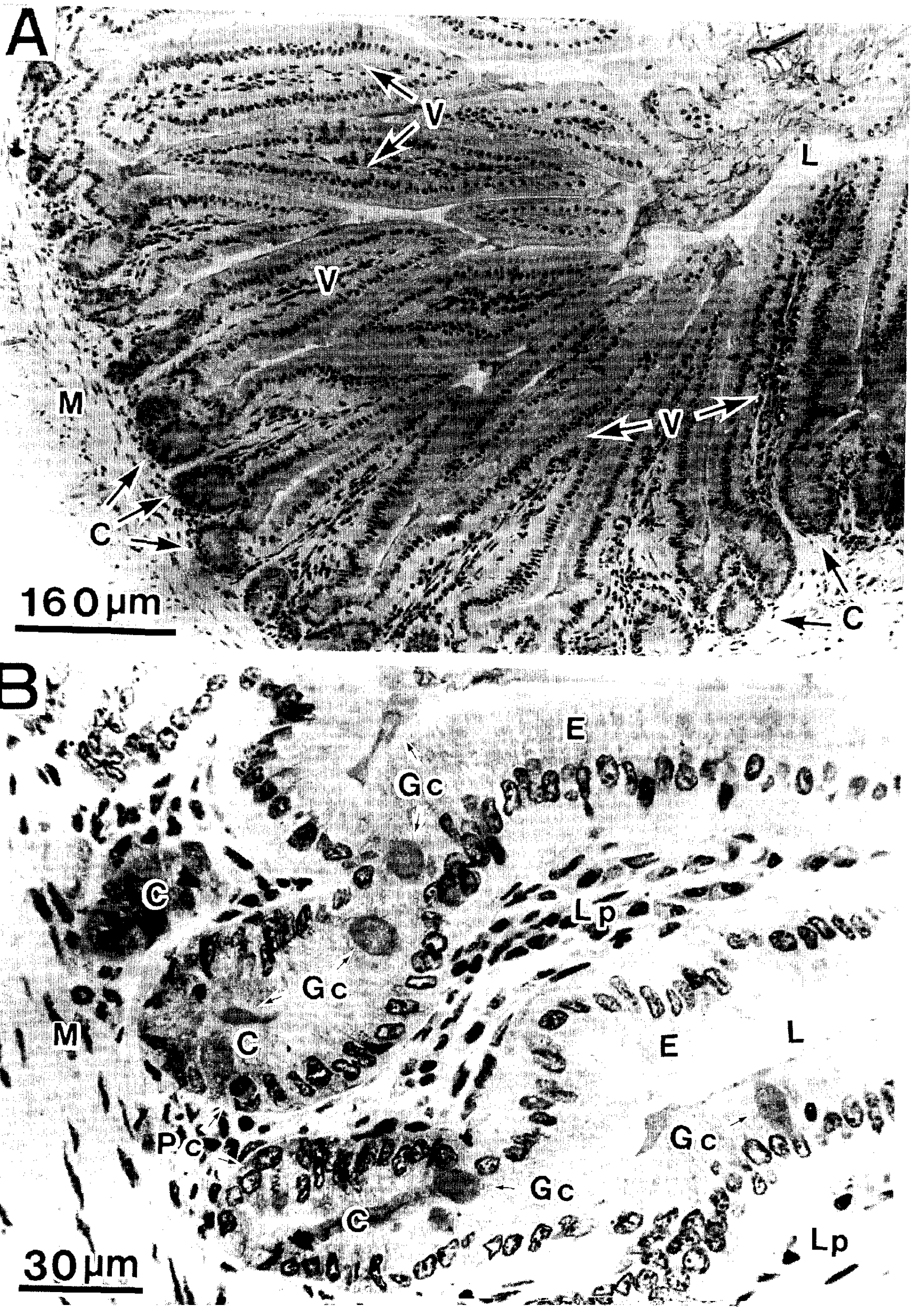

Fig. 2. Photomicrographs showing the small intestine of *Apodemus speciosus* stained with PAS and haematoxylin. A, Cross section at the jejunum. Note the sparse presence of goblet cells (Gc) in deeper site of crypts (C); B, Cross section at the ileum. Goblet cells are dense in comparison with those at the jejunum. E, epithelium; L, lumen; Lp, lamina propria mucosae; M, *Tunica muscularis*; Pc, Paneth's cell; V, villi.

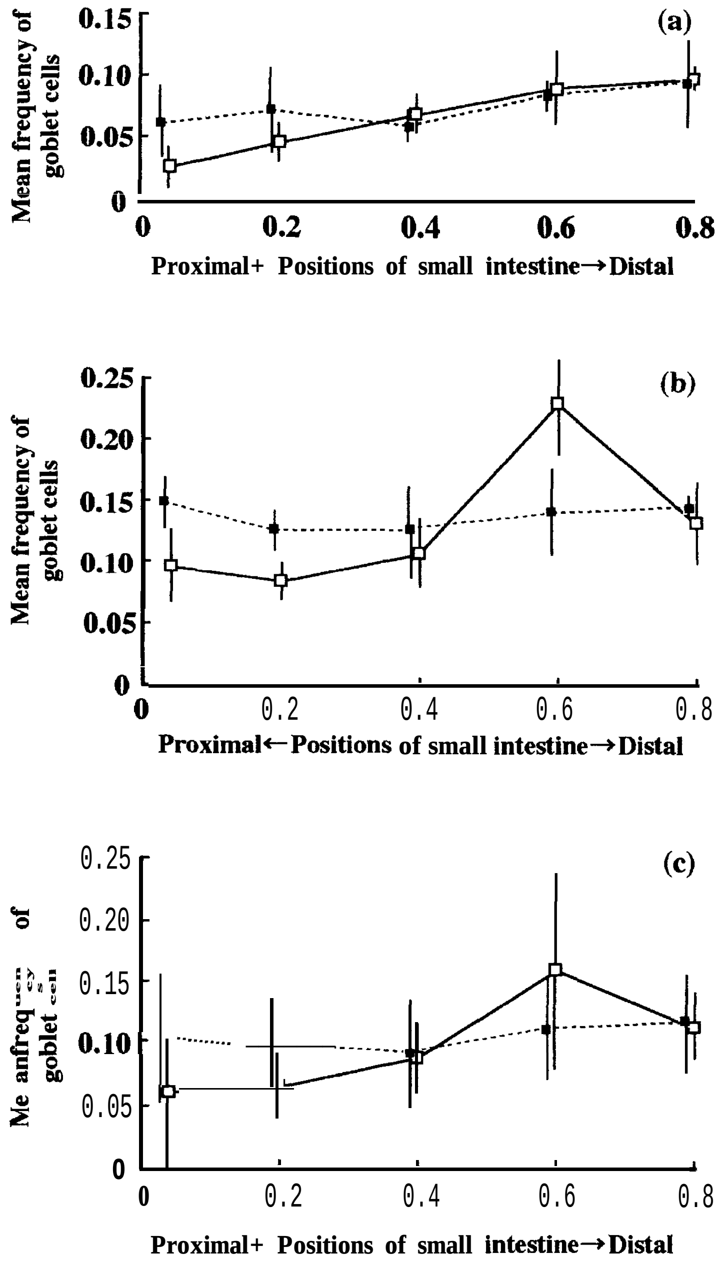

Fig. 3. Changes of frequency in appearances of goblet cells in accordance with the five positions from the proximal to distal side of the small intestines. Each graph indicates the changes in villi (a), crypts (b), and overall (c), respectively. Vertical bars represent standard deviations. ■ -..W, *Apodemus argenteus*;□—□, *A. speciosus*.

the appearance of several Paneth's cells and the intensity of the reaction of the cytoplasm in the basal side of those cells to haematoxylin were not qualitatively different in the two species.

The goblet cells of the small intestines in both species were conspicuously identified with PAS (Figs 1 and 2). The microphotographs illustrate that the goblet cells were distributed sparsely in the villi and densely in the crypts. Compared to A. *speciosus*, in *A. argenteus* a large number of the cells in the crypts showed a more intensive reaction to the PAS technique.

Mean values of the frequency of appearance of goblet cells in the villi in the small intestines were 0.073 (s.d.=0.027) for *A. argenteus* and 0.065 (s.d.=0.031) for *A. speciosus*. Furthermore, in the crypts the mean values of *A. argenteus* and *A, speciosus* were 0.137 (s.d.=0.027) and 0.129 (s.d.=0.060), respectively; the standard deviation in *A. speciosus* was more than twice that in *A. argenteus*. The mean ratio of the frequency of the goblet cells in the crypts to that in the villi was 1.94 in *A. argenteus* and 1.73 in *A. speciosus*, accordingly, goblet cells of *A. argenteus* were concentrated more intensively in the crypts than those of *A. speciosus* (U-tests, $p<0.05$).

In comparison with frequency of appearance of goblet cells in the villi in relation to the five positions from the proximal to distal end of the small intestines, the values of the standard deviations were small at each of the five positions in both species. Especially, in *A. argenteus*, there was little change in the values extending over the whole small intestine (Fig. 3). In the crypts, the frequency of appearances of goblet cells was higher in *A. argenteus* than in *A. speciosus* at most positions of the small intestine. Additionally, those in the villi were rather homogeneously similar between the two species.

DISCUSSION

Ratios of animal food in the stomachs of *A. speciosus* were often similar to those in *A. argenteus*, or were higher in some cases than in *A. argenteus* because of great variations in the ratio in each the species (Igarashi, 1972; Mizushima and Yamada, 1974; Ota *et al.*, 1977). Generally, it has been suggested that *A. argenteus* depends on animal food more than *A. speciosus* (Tachikawa and Murakami, 1976; Maeda *et al.*, 1984). In each of our feeding experiments which varied both the benefit and cost of foraging, values of Ivlev's selective index and Jacobs's index of insects in *A. argenteus* were significantly greater than in A. *speciosus*. The differences were greater in the two experiments using motile insects, *M. satsumaensis* and *M. domestica*, than in the others using parasitised acrons. Previous research showed that food habits of *Apodemus* mice in Japan were more insectivorous than those of the same genus in Europe (Tachikawa and Murakami, 1976). Our results support the belief that *A. argenteus* depend on animal food more than *A. speciosus*.

Values of CL/SIL have been found to be higher in herbivorous Microtinae, *Microtus montebelli*, *Clethrionomys rufocanus bedfordiae*, and *Eothenomys smithii* and lower in four species of the genera *Mus* and *Rattus*, which feed on nutritious food in areas close to human, and granivorous and insectivorous *A. argenteus* and *A. speciosus* have moderate values of CL/SIL with slightly higher values in *A. speciosus* than in *A. argenteus*

(Miyao, 1970). Our measurements also showed that both CL/ TL and CL /SIL were significantly higher in A. *speciosus* than in A. ***argenteus,*** and were consistent with the above view. Considering that there were no significant differences between the two species in the scaling of CL and cube root of body weight, it is implied that this distinction as to CL is very obscure.

Under reproductive conditions, A. ***argenteus*** uses more homogeneous microhabitats than ***A.*** *speciosus* (Shioya et al., 1992). ***A.*** *argenteus* is relatively selective in its nutrient demand. Further, the body weight of ***A. argenteus*** is 0.3 to 0.5 times that of ***A.*** *speciosus* and the basal metabolic rate (3.18 ml O_2/g•h) of ***A. argenteus*** is approximately twice as large as that (1.57 ml O_2/g . h) of ***A.*** *speciosus* (Sekijima, 1993). On this basis it is predicted that mammals having higher metablolic rates require more nutritious foods (Jarman, 1974; Kleiber, 1975). From this, it follows that ***A. argenteus*** tends to require animal protein.

Comparison of the cells of the mucous layer and the fundus gland of the stomach revealed no substantial differences between the two species. However, the ratio of the thickness of the fundus gland region to the whole thickness in ***A. argenteus*** was larger than that in ***A.*** *speciosus*. Also, the ratio of the thickness of the region showing a high density of chief cells which produce pepsinogen, a precursor of pepsin, to the whole thickness in ***A. argenteus*** was superior to ***A.*** *speciosus*. These facts suggest that the gastric organ of ***A. argenteus*** is more adapted to proteinic digestion than that of ***A.*** *speciosus*.

The function of goblet cells in the intestinal tract has not yet been completely clarified. However, it is indisputable that the mucoprotein and acidic sulfate-mucopolysaccharide secreted from the cells have the function of lubricating and protecting the mucosal epithelium (Kurosumi ***et al.,*** 1981). It is recognized that the more insectivorous species in the Chiroptera (Pteropodidae, Vespertilionidae, Rhinolophidae, Hipposideridae and Phyllostomatidae) have a higher density of cells in the stomach which stain with PAS (Kamiya and Pirlot, 1975). In *Microtus*, an herbivorous vole species, the number of these cells is extremely small (Golley, 1960). This difference seems to show the importance of their function in protection against autolysis in animals feeding on higher proteinic foods.

In this connection, the distribution of goblet cells stained with PAS in ***A.*** *argenteus* was denser and more homogeneous at most positions of the small intestine than in ***A.*** *speciosus*. This fact suggests that ***A.*** *argenteus* depends on more homogeneous and proteinic foods, and is consistent with the results of our feeding experiments. In ***A.*** *argenteus*, territoriality and monogamy have been observed (Oka, 1992). These characters are consistent with the restrictions in resource utilization in this species because such restrictions would reduce the qualitative heterogeneity of habitats which affects mating systems in animals (Emlen and Oring, 1977). In contrast with ***A.*** *argenteus*, in ***A.*** *speciosus* the large variation in distribution of goblet cells at different positions in the small intestine of individuals seems to support adaptation for euryphagous behaviour.

A. argenteus has a smaller body weight and a smaller stomach volume than ***A.*** *speciosus*. Therefore, ***A. argenteus*** needs to increase absorptivity. The fact that the distribution of goblet cells in this species are concentrated in the crypts may be adaptive for increasing the number of goblet cells without extremely decreasing absorptivity. In small mammals, there are in fact correlations between mean ratio of mucosal surface area to serosal area in the small intestine and the degree of dependence on animal foods (Barry, 1976). Therefore, the tendency to depend on animal foods in A. *argenteus* is consistent with the distribution pattern of goblet cells. In general, quality of diet affects the ratio of goblet cells to mucosal epithelium cells in small intestines (Kurosumi ***et al.,*** 1981). Considering the results from our feeding experiments, it seems reasonable to suppose that differences in distribution patterns of goblet cells between the two species reflect variances in their food habits. This implication may propose that there are substantial differences between the two ***Apodemus*** species in the nutritional components of diet.

The above implies that histological characters in these two woodland *Apodemus* species reflect qualitative differences in potential food habits. The smaller ***A.*** *argenteus* depends on animal foods, while A. *speciosus* is not completely adaptive to absorption of animal foods and has promoted more euryphagous characteristics. It is suggested that these differences in potential food habits are related to the traits of foraging behavior, habitat utilization and territoriality in the two species.

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