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COMPARATIVE MORPHOLOGY OF THE GASTROINTESTINAL TRACT IN THE FEEDING SPECIALIST *SCIURUS ABERTI* AND SEVERAL GENERALIST CONGENERS

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Abert's squirrel (*Sciurus aberti*) is a highly specialized mammal dependent upon ponderosa pine (*Pinus ponderosa*) for a significant part of its yearly diet. For up to six months of the year, these squirrels only eat ponderosa pine phloem, which is a high-fiber, low-quality diet. We compared gross morphologies of the gastrointestinal tract in specialized Abert's squirrels to those of generalist fox squirrels (*S. niger*) and found that Abert's squirrels have significantly longer gastrointestinal tracts with greater tissue surface area and weight than do fox squirrels. Published data describing the eastern gray squirrel (*S. carolinensis*) and the western gray squirrel (*S. griseus*) indicate that these generalist species have body weights and a gut morphology very similar to that of the fox squirrel. We conclude that the morphology of the digestive tract of Abert's squirrel has become adapted to its low-quality diet.

Key words: *Sciurus aberti,* Abert's squirrel, *Sciurus niger,* fox squirrel, ponderosa pine, gastrointestinal tract morphology, digestion

Abert's squirrels (*Sciurus aberti*) are feeding and habitat specialists that live in ponderosa pine (*Pinus ponderosa*) forests of the Rocky Mountains. Abert's squirrels are remarkable due to their degree of dependence upon ponderosa pine as a food plant; cones and pollen strobili, as well as hypogeous fungi that are mycorrhizal with ponderosa pines, are their preferred food sources. Because Abert's squirrels do not cache food, when these preferred food sources are unavailable during winter, they eat less nutritional food sources. For up to six months of the year, they survive by feeding predominantly on the cortical tissue (primarily phloem) of small twigs (Keith, 1965; States et al., 1988), which is a low-quality (i.e., low amounts of digestible carbohydrates, proteins and fats), high-fiber diet (Snyder, 1992). For example, dry ponderosa phloem contains <1% N, 4–6% non-structural (i.e., digestible) carbohydrates, and 4–11% tannins and related polyphenols. The bulk of the remainder is cellulose, lignin, and other plant structural elements; it has the general consistency of sawdust (Snyder, 1992). This dependence on one species of plant is remarkable and renders the biology of Abert's squirrels as worthy of attention as that of other specialized mammalian herbivores, such as the koala (*Phascolarctos cinereus*) and the giant panda (*Ailuropoda melanoleuca*). The extent to which dietary specialization has affected the evolution of morphology in these specialist herbivores is of special relevance in the context of recent comparative studies of digestive systems from evolutionary perspectives (Chivers and Langer, 1994; Foley and Cork, 1992; McWilliams et al., 1997).

Previous research has demonstrated that Abert's squirrels choose to feed only on certain ponderosa pines. They select these trees based on the chemical composition of the resin, flow rate of the resin, and nutritive value (Snyder, 1992). Snyder (1993)

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and Snyder and Linhart (1998) concluded that due to this selection of specific trees and the damage inflicted upon these trees, Abert's squirrels can have a significant impact on the evolutionary dynamics of ponderosa pines. However, whether or not ponderosa pines have had any evolutionary influence on Abert's squirrels has not been examined. In this study, we ask if there is any evidence that Abert's squirrel evolved a digestive system that allows it to obtain adequate nutrition from the low-quality food that the phloem of ponderosa pines provides.

Cork (1994) summarizes the predicament facing mammals that eat high fiber diets by stating that such mammals appear to follow two alternative strategies for fulfilling their energy requirements: 1) an "intake-maximizing" strategy of passing food through the gut as rapidly as possible to maximize the quantity of food processed, or 2) a "retention-maximizing" strategy of delaying the passage of food through the gut to maximize digestion. Pandas exemplify the "intake-maximizing" strategy; an average 80–125 kg panda eats 10–18 kg of bamboo/day (Schaller et al., 1985), which is equal to ca. 15% of its body weight. Conversely, koalas compensate for the low quality of a eucalyptus-leaf diet by extending the mean retention time of digesta (Hume, 1982) by virtue of their significantly enlarged gastrointestinal tract and an especially large cecum.

Abert's squirrels do not consume large volumes of food daily. During a 3-year study in Arizona, States et al. (1988) found that these squirrels clip an average of 25 twigs/day throughout winter. Feeding involves preliminary peeling and discarding of the outer bark, consumption of the phloem, and finally discarding the woody core (Snyder, 1992). Thus, an estimate of phloem weight per twig is an accurate measure of food intake. If each clipped twig contains an average weight of 1.6 g of phloem (Y. Linhart, in litt.), Abert's squirrels eat ca. 40 g of phloem/day. For a 500–600 g Abert's squirrel, this means that they consume ca. 6–8% of their body weight daily, suggesting that they are not using the "intake-maximizing" option. To test if a relatively long gastrointestinal tract associated with the "retention-maximizing" strategy can enable the Abert's squirrel to feed exclusively on a fibrous and low-quality diet, we compared the gastrointestinal tracts of specialist Abert's squirrels to those of generalist fox squirrels (*S. niger*) along with published data on two other generalists: the eastern gray squirrel (*S. carolinensis*), and the western gray squirrel (*S. griseus*).

Fox squirrels are feeding generalists whose year-round diet consists primarily of fruits, berries, grains, seeds, buds, insects, some phloem from various deciduous trees, and human leftovers (Lechleitner, 1969). The nutritional value of such a diet is much higher than that of Abert's squirrels. For example, buds, seeds, insects, and related foods can be expected to contain nitrogen at levels one order of magnitude greater than the ≤0.5% of pine phloem in winter, and fiber contents that are at least one order of magnitude lower (Kramer and Kozlowski, 1979; Salisbury and Ross, 1985; Strong et al., 1984). The fox squirrels that we studied belong to the subspecies *S. niger rufiventer* (Armstrong, 1972). In this region, fox squirrels tend to have a body weight of 500–900 g, comparable to the body weights of Abert's squirrels.

Interspecific comparisons of various mammals that are specialized herbivores indicate that length, surface area, and capacity of digestive tracts are markedly larger than in omnivorous species of comparable size (Chivers and Langer, 1994). Such characteristics also can vary intraspecifically as a function of diet. For example in various rodents, total capacity of the digestive tract and relative size of the cecum and colon can increase with diminishing food quality (Chivers and Langer, 1994; Young Owl and Batzli, 1998). Our predictions, based on previous interspecific analyses, were that Abert's squirrels would have a significantly enlarged cecum and that those differences should be much larger than the intraspecific variation observed to be associated with diet and seasonality in other species.

MATERIALS AND METHODS

We compared *S. aberti ferreus* and *S. niger rufiventer*. We used road-killed specimens with intact viscera and relatively minor external damage. All were collected along the Colorado Front Range near Boulder, Denver, and Colorado Springs. After opening the abdominal cavity, we removed the entire gastrointestinal tract, first severing the stomach from the esophagus at the cardiac sphincter. We separated the stomach from the small intestine at the pyloric sphincter and the small intestine from the cecum at the ileocecal sphincter. We separated the cecum from the proximal colon just after the junction between the cecum and the ileum. We detached the colon from the anus at the standardized distance of 3.5 cm from the rectum. That 3.5 cm was added to all of our measurements for colon length. However, we were unable to calculate weight and surface area for that missing 3.5-cm section, so weight and surface area measurements for the colon were uniformly low.

After separating the gastrointestinal tract into the stomach, small intestine, cecum, and colon, we measured lengths of each of these sections. For the stomach and cecum, we measured the lesser and greater curvatures and then averaged those values.

We weighed each of the separate organs when they were full and empty. To cleanse the stomach and cecum, we cut them along both their lesser and greater curvatures and gently washed out the internal contents. We cleansed the small intestine and colon in the same manner after cutting them into several pieces of ca. 15 cm and then cutting these segments lengthwise from one end to the other.

To measure the surface area, we used a technique adapted from Chivers and Hladik (1980) and Young Owl (1994). After weighing the stomach, small intestine, cecum, and colon, we traced the tissue pieces onto paper without stretching or enlarging the surface area. We proceeded to trace the paper outlines onto aluminum foil with a known surface area:weight ratio and then cut out and weighed these aluminum foil pieces. By multiplying the aluminum foil weight by the surface area:weight ratio, we were able to obtain accurate surface area measurements for stomach, small intestine, cecum and colon. According to Young Owl (1994), surface area gives a truer picture of mammalian gastrointestinal tract size than length and can be measured more accurately than volume. For all comparisons that met assumptions of normality and homoscedasticity, we used one-way analysis of variance (ANOVA). For those comparisons that did not meet those assumptions, we used the Kruskal-Wallis non-parametric test (Cody and Smith, 1997).

RESULTS

We dissected seven Abert's squirrels and eight fox squirrels (Table 1). Mean body weights of the two species were remarkably similar and did not differ significantly ($P = 0.67$). The mean head and body lengths were not significantly different ($P = 0.33$). All measurements of gastrointestinal tract length differed significantly between the two species (Fig. 1). The stomach ($P \leq 0.01$), small intestine ($P < 0.05$), cecum ($P \leq 0.001$), colon ($P \leq 0.001$) and overall length of the gastrointestinal tract ($P \leq 0.001$) were significantly longer in Abert's squirrel than in the fox squirrel. Weights for the empty stomach and small intestine were not significantly different whereas tissue weights of the cecum ($P < 0.05$), colon ($P \leq 0.001$) and complete gastrointestinal tract ($P < 0.05$) were significantly larger in Abert's squirrel. The only section of the gastrointestinal tract that was not significantly different in surface area was the small intestine. Surface areas of the stomach ($P \leq 0.01$), cecum ($P \leq 0.001$), colon ($P \leq 0.001$) and the total surface area for the entire gastrointestinal tract ($P \leq 0.001$) were significantly larger in Abert's squirrel.

DISCUSSION

The specialized Abert's squirrel had a markedly different gastrointestinal morphology from that observed or reported in the generalist fox, eastern gray, and western gray squirrels (Table 1). All of these sciurid species had similar body weights, and

TABLE 1.—*Body and gastrointestinal tract measurements of* Sciurus aberti *(specialized herbivore,* n = *7, this study),* S. niger *(omnivore,* n = *8, this study),* S. carolinensis *(granivore,* n = *17, from Schieck and Millar, 1985), and* S. griseus *(generalized herbivore,* n = *1, from Young Owl, 1994).*

	S. aberti		*S. niger*			*S. carolinensis*		
Character	$\bar{X}$	*SE*	$\bar{X}$	*SE*	*P*[a]	$\bar{X}$	*SE*	*S. griseus*
Body weight (g)	511.7	22.9	532.2	38.7	n.s.[b]	523.0	23.0	520.0
Head and body length (cm)	30.5	1.1	31.8	0.7	n.s.[b]			
Lengths (cm)								
Stomach	12.0	0.6	9.6	0.4	≤0.01[b]			
Small intestine	166.6	10.8	144.0	2.0	<0.05[c]	212.0	6.0	
Cecum	19.8	1.8	11.5	0.4	≤0.001[c]	10.1	0.4	
Colon	73.5	3.5	48.0	1.3	≤0.001[c]	49.5	1.2	
Total	271.8	14.2	213.1	2.4	≤0.001[c]			
Empty weights (g)								
Stomach	4.6	0.5	3.8	0.3	n.s.[b]			
Small intestine	8.8	1.2	6.5	0.6	n.s.[b]			
Cecum	3.9	0.5	2.0	0.2	<0.05[c]			
Colon	5.8	0.5	3.1	0.4	≤0.001[b]			
Total	23.1	2.5	15.4	0.8	<0.05[c]			
Surface areas (cm^2)								
Stomach	84.6	6.7	54.5	4.4	≤0.01[b]			44.0
Small intestine	304.6	40.7	216.3	12.2	n.s.[c]			209.0
Cecum	91.4	9.1	40.6	1.9	≤0.001[c]			17.0
Colon	158.9	12.7	84.9	5.6	≤0.001[c]			79.0
Total	639.5	61.2	396.3	14.9	≤0.001[c]			349.0

[a] Statistical significance comparing *S. aberti* and *S. niger*.

[b] Because of normality of data, comparisons with analysis of variance.

[c] Because of non-normality of data, comparisons with Kruskal-Wallis test.

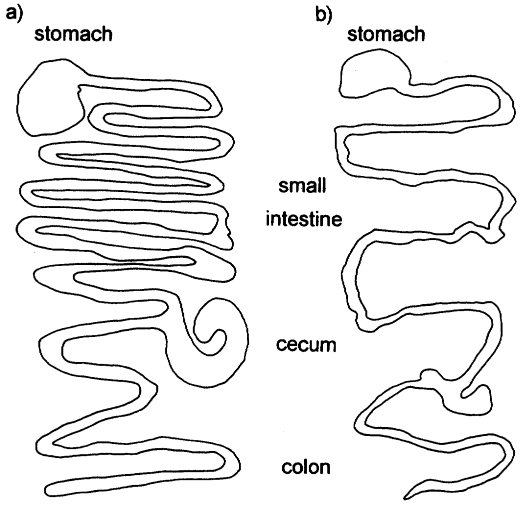

FIG. 1.—Gastrointestinal tracts of a) an Abert's squirrel (*Sciurus aberti*) and b) a fox squirrel (*S. niger*).

therefore, we did not need to scale any of the measurements. The gastrointestinal tract of the Abert's squirrel was significantly longer, had a significantly larger surface area, and had a larger tissue weight than fox squirrels. The largest differences were found in the length, weight, and surface area measurements of the cecum and colon, indicating that the hindgut of the Abert's squirrel is particularly enlarged. Most of the food that the Abert's squirrel ingests is fiber, which cannot be broken down until it reaches the cecum. Consequently, the large hindgut of the Abert's squirrel may enable symbiotic microbes to digest the food and perhaps detoxify the digesta, which, in the case of ponderosa pine, include terpenes, resin acids, and tannins (Snyder, 1992; Y. Linhart, in litt.). Sciurids have never been shown to be caecotrophic or to possess a colonic separation mechanism, either of which would enable Abert's squirrel to minimize the loss of fermentable digesta and symbiotic microbes in the feces. We suggest that future research could demonstrate that Abert's squirrel utilizes one of these digestive strategies. Because the food cannot be digested in the foregut, it is reasonable that the small intestine would not be significantly larger in the Abert's squirrel. Indeed, this lack of enlargement of the small intestine has been observed in several small mammals including sciurids (Schieck and Millar, 1985). However, the stomach of the Abert's squirrel had both significantly greater length and surface area than the stomach of the fox squirrel, yet tissue weights were not significantly different. This suggests that Abert's squirrel either has a significantly lighter stomach or that it stuffs as much food as possible into its stomach and thereby stretches it. Because the first option is unlikely, these data suggest that Abert's squirrel may maximize both intake and retention within the constraints imposed by its size and arboreal ecology.

Comparisons with published data of the two other sciurid species indicate that these generalists are very similar to the fox squirrel in their gastrointestinal tract measurements and thus significantly different from the Abert's squirrel. Only the gastrointestinal lengths were available for the eastern gray squirrel; its small intestine length is larger than either that of the Abert's or fox squirrel, but the cecum and colon lengths are comparable with those of the fox squirrel. The surface area measurements for the western gray squirrel also are significantly different from those of Abert's squirrel.

We interpret the large differences observed between the specialist Abert's squirrel and the other generalist squirrel species as being relevant in an evolutionary context. We propose that gut morphology in Abert's squirrels has changed as a result of the selective pressures generated by the need for this species to maximize the food value of its low-quality diet. Gut morphology can vary in rodents as a function of changes in diet, condition of given individuals, and seasonality (Hammond and Wunder, 1995; Young Owl and Batzli, 1998). Most such reports typically show a range of variation of 5–20%. Our results show that differences between Abert's and other squirrels are usually much more pronounced (Table 1). Besides differences in length, our measurements of surface area, which are thought to illustrate gastrointestinal tract differences more accurately (Young Owl, 1994), show that the cecum of Abert's squirrel is on average 125% larger, the colon 87% larger, and the overall gastrointestinal tract 61% larger than those of the fox squirrel. The difference in the cecum is especially notable and consistent with the enlarged cecum characteristic of other specialized herbivores such as koalas. In addition, none of the females used in this study were pregnant or lactating and both our Abert's and fox squirrels were collected during several seasons, so seasonal changes were accounted for. Thus, although morphology of the digestive tract in the squirrels may vary intraspecifically to some degree, the magnitude of the interspecific differences we observed is consistent with published comparisons of herbivores and omnivores both within and among families (Hume, 1994; Schieck and Millar, 1985) and leads us to suggest that there has been adaptation of the Abert's squirrels to their diet of pine phloem.

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LITERATURE CITED

ARMSTRONG, D. M. 1972. Distribution of mammals in Colorado. Monograph of the Museum of Natural History, The University of Kansas, 3:1–415

CHIVERS, D. J., AND C. M. HLADIK. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. Journal of Morphology, 166:337–386.

CHIVERS, D. J., AND P. LANGER (eds.). 1994. The digestive system in mammals: food, form and function. Cambridge University Press, Cambridge, United Kingdom.

CODY, R. P., AND J. K. SMITH. 1997. Applied statistics and the SAS programming language, Fourth ed. Prentice-Hall Inc., Upper Saddle River, New Jersey.

CORK, S. J. 1994. Digestive constraints on dietary scope in small and moderately-small mammals: how much do we really understand? Pp. 337–369, *in* The digestive system in mammals: food, form and function. (D. J. Chivers and P. Langer, eds.). Cambridge University Press, Cambridge, United Kingdom.

FOLEY, W. J., AND S. J. CORK. 1992. Use of fibrous diets by small herbivores: how far can the rules be "bent"? Trends in Ecology and Evolution, 7:159–162.

HAMMOND, K. A. AND B. A. WUNDER. 1995. Effect of cold temperatures on the morphology of gastrointestinal tracts of two microtine rodents. Journal of Mammalogy, 76:232–239.

HUME, I. D. 1982. Digestive physiology and nutrition of marsupials. Cambridge University Press, Cambridge, United Kingdom.

———. 1994. Gut morphology, body size and digestive performance in rodents. Pp. 315–323, *in* The digestive system in mammals: food, form and function. (D. J. Chivers and P. Langer, eds.). Cambridge University Press, Cambridge, United Kingdom.

KEITH, J. O. 1965. The Abert squirrel and its dependence on ponderosa pine. Ecology, 46:150–163.

KRAMER, P. J., AND T. T. KOZLOWSKI. 1979. Physiology of woody plants. Academic Press, New York.

LECHLEITNER, R. R. 1969. Wild mammals of Colorado: their appearance, habits, distribution, and abundance. Pruett Publishing Company, Boulder, Colorado.

MCWILLIAMS, S. R., D. AFIK, AND S. SECOR. 1997. Patterns and processes in the vertebrate digestive system. Trends in Ecology and Evolution, 12:420–422.

SALISBURY, F. B., AND C. ROSS. 1985. Plant physiology. Third ed. Wadsworth Publishing Company, Belmont, California.

SCHALLER, G., J. HU, W. PAN, AND J. ZHU. 1985. The giant pandas of Wolong. The University of Chicago Press, Chicago, Illinois.

SCHIECK, J. O., AND J. S. MILLAR. 1985. Alimentary tract measurements as indicators of diets of small mammals. Mammalia, 49:93–104.

SNYDER, M. A. 1992. Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. Ecology, 73:1730–1741.

———. 1993. Interactions between Abert's squirrel and ponderosa pine: the relationship between selective herbivory and host plant fitness. The American Naturalist, 141:866–879.

SNYDER, M. A., AND Y. B. LINHART. 1998. Subspecific selectivity by a mammalian herbivore: geographic differentiation of interactions between two taxa of *Sciurus aberti* and *Pinus ponderosa.* Evolutionary Ecology, 12:755–765.

STATES, J. S., W. S. GAUD, W. S. ALLRED, AND W. J. AUSTIN. 1988. Foraging patterns of tassel-eared squirrels in selected ponderosa pine stands. Pp. 425–431, *in* Symposium Proceedings, Management of Amphibians, Reptiles, and Small Mammals in North America. (R. C. Szaro, K. E. Severson, and D. P. Patton, eds.) United States Forest Service General Technical Report RM-166, Fort Collins, Colorado.

STRONG, D. R., J. H. LAWTON, AND R. SOUTHWOOD. 1984. Insects on plants. Harvard University Press, Cambridge, Massachusetts.

YOUNG OWL, M. 1994. A direct method for measurement of gross surface area of mammalian gastrointestinal tracts. Pp. 219–233, *in* The digestive system in mammals: food, form and function. (D. J. Chivers and P. Langer, eds.). Cambridge University Press, Cambridge, United Kingdom.

YOUNG OWL, M., AND G. O. BATZLI. 1998. The integrated processing response of voles to fiber content of natural diets. Functional Ecology, 12:4–13.

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LINKED CITATIONS

- Page 1 of 2 -

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Literature Cited

Effect of Cold Temperatures on the Morphology of Gastrointestinal Tracts of Two Microtine Rodents

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Journal of Mammalogy, Vol. 76, No. 1. (Feb., 1995), pp. 232-239.

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http://links.jstor.org/sici?sici=0022-2372%28199502%2976%3A1%3C232%3AEOCTOT%3E2.0.CO%3B2-1

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James O. Keith

Ecology, Vol. 46, No. 1/2. (Jan., 1965), pp. 150-163.

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http://links.jstor.org/sici?sici=0012-9658%28196501%2946%3A1%2F2%3C150%3ATASAID%3E2.0.CO%3B2-2

Selective Herbivory by Abert's Squirrel Mediated by Chemical Variability in Ponderosa Pine

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Ecology, Vol. 73, No. 5. (Oct., 1992), pp. 1730-1741.

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Interactions between Abert's Squirrel and Ponderosa Pine: The Relationship between Selective Herbivory and Host Plant Fitness

Marc A. Snyder

The American Naturalist, Vol. 141, No. 6. (Jun., 1993), pp. 866-879.

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M. Young Owl; G. O. Batzli

Functional Ecology, Vol. 12, No. 1. (Feb., 1998), pp. 4-13.

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