FOOD HABITS AND EVOLUTIONARY RELATIONSHIPS OF THE TASSEL-EARED SQUIRREL (*SCIURUS ABERTI*)

JACK S. STATES AND PETER J. WETTSTEIN
jstates@rmisp.com
Department of Biology, Northern Arizona University,
Flagstaff, AZ 86011 (JSS)
Department of Surgery and Immunology, Mayo Foundation,
Rochester, MN 55905 (PJW)

ABSTRACT.—The present distribution of the Abert's, or tassel-eared squirrel, *Sciurus aberti*, is confined to forests dominated by ponderosa pine, *Pinus ponderosa*, in the southern Rocky Mountains and the montane islands of Arizona, New Mexico, and northern Mexico. A review of the current knowledge on the six known subspecies is presented with a focus on the relationship of food habits and foraging behavior to their restricted distribution patterns, genetic diversity, and evolutionary history. Genetic analyses of *S. aberti* resulted in the recognition of a minimum of four subspecies in geographically separated assemblages. Two notable features of foraging behavior common to all subspecies were the strong feeding preference shown for sporocarps of hypogeous fungi and their selective herbivory on the inner bark of ponderosa pine. No other sciurid within the range of Abert's squirrels was found to exhibit this particular year-round foraging pattern. The squirrels appear to play an important ecological role as dispersal agents for the spores which they defecate following consumption of the sporocarps. Upon germination, spores of hypogeous fungi form obligate mutualistic associations with ponderosa pine roots (mycorrhizae), and thereby enhance seedling survival and forest regeneration. Availability of fungi for food appears to be linked to squirrel distribution and abundance. Squirrel feeding preferences for certain pines was found to be related to the terpene composition of resin in the inner bark. A review of literature on terpene-related, selective herbivory of conifers revealed a remarkable coincidence in the geographic distribution of the subspecific assemblages of squirrels relative to the biochemical classification of ponderosa pine host in their particular region, a classification based on the genetically controlled monoterpene composition of xylem resin. These studies are discussed as a putative example of coevolution: adaptation, interaction, and interdependence of Abert's squirrels with ponderosa pine and associated mycorrhizal fungi over a long period of time.

INTRODUCTION

The "tassel-eared" or "Abert's" squirrel, *Sciurus aberti*, is the only arboreal squirrel in North America known to be a strict ecological associate with a single, widespread conifer species, ponderosa pine (*Pinus ponderosa)*. Although ponderosa pine is found throughout mountainous regions from Canada to central Mexico, the modern distribution of this squirrel extends only from the eastern side of the Rocky Mountains, from extreme south-central Wyoming and northern Colorado, south to the Sierra Occidentale in western Durango, Mexico (Hall and Kelson, 1959). The distribution pattern of the Abert's squirrel is discontinuous and confined for the most part to montane "islands" of various size separated by expanses of non-forested and unsuitable habitat.

The geographically isolated squirrel populations exhibit both a wide range of coat coloration and enough morphological variability to justify the recognition of two species and eight subspecies (Hall and Kelson, 1959). *S. kaibabensis* and *S. aberti* were recognized as separate species primarily on the basis of striking differences in coat color and color pattern. The Grand Canyon of the Colorado

In M.A. Steele, J. F. Merritt, and D. A. Zegers (eds.). 1998.
Ecology and Evolutionary Biology of Tree Squirrels. Special
Publication Virginia Museum of Natural History

River separates these two populations from one another and their geographic isolation has been considered to be the major factor responsible for speciation by divergence. Although frequently cited in contemporary biology textbooks (Keeton and Gould, 1993) as an example of allopatric speciation via geographic separation, biologists still disagree as to whether the two populations have reached the level of full species. In a comprehensive review of morphometric data of all taxa in the subgenus *Otosciurus*. Hoffmeister and Diersing (1978) recognized as valid only one species, *S. aberti aberti*, and five other subspecies. Compounding this taxonomic debate is strong controversy over theories proposed to account for the modern geographic distribution of Abert's squirrel subspecies and mechanisms of dispersal (Davis and Brown, 1989; Lomolino et al., 1989). The need for explanations regarding the fragmented distribution patterns, the close association with ponderosa pine, and the evolutionary history of the Abert squirrel was the most compelling reason for our current research.

This paper reviews current knowledge on the six subspecies of tassel-eared squirrels, focusing on what the authors and others have researched concerning the relationship of food habits and foraging behavior to their restricted distribution on montane islands of ponderosa pine in the Southwest. Combined with the results of our studies on genetic diversity and divergence in *S. aberti* subspecies, this information is discussed as a putative example of coevolution: Abert squirrel adaptation, interaction, and interdependence with ponderosa pine and its associated mycorrhizal fungi over a long period of time.

DIET COMPOSITION AND FORAGING BEHAVIOR

Much of the ecological and biogeographical literature on tassel-eared squirrels has focused on the identification of factors accounting for their strict ecological dependence on ponderosa pine for food and habitat. Their food habits and foraging behavior are unusual in several respects. Diets of Abert's squirrels invariably include fungi, mycelium and fruiting bodies of hypogeous fungi (truffles) and epigeous fungi (mushrooms) that often approach 100% of the stomach volume in some seasons (Stephenson, 1975; Kotter and Farentinos, 1984*a*; States, 1985). These fungi are known to form obligate, mutualistic symbioses with ponderosa pine rootlets as mycorrhizae (Heidmann and Cornett, 1986; Riffle, 1989). Because the squirrels serve as a dispersal vector for the mycorrhizal fungi they consume, it is also probable that they indirectly influence the distribution of their pine host (Fogel and Trappe, 1978; Kotter and Farentinos , 1984*b*; Molina et al., 1992).

Another significant aspect of foraging behavior that illustrates a unique association of Abert's squirrels with ponderosa pine is their use of inner bark (phloem). Whereas other tree squirrels only occassionally strip or chew the bark from live trees, selecting it as a supplement to their usual diet (Gurnell, 1987), Abert's squirrels consume inner bark on a year-round basis and it constitutes a major portion of their winter diet. They characteristically focus their herbivory on the terminal branches in the upper portions of the canopy. Here, twig segments of variable length and distance from the apical bud are excised and the outer bark is systematically "peeled" away. The thin layer of exposed phloem is separated from the underlying woody xylem, and eaten. The remaining twig, terminal needle cluster, and apical bud is dropped to the ground (sometimes apical buds are also eaten). This pattern of defoliation and the highly visible carpet of clippings and peeled twigs serve as reliable indicators of presence and distribution of the squirrel (Keith, 1965; Hall, 1981).

The squirrels also demonstrate a strong feeding preference for specific trees; selective feeding that often results in the virtual defoliation of the "target" tree tops (Snyder, 1993). Several factors that seem to play a role the in selective herbivory of inner bark include carbohydrate content (Thomas, 1979), ease of peeling (Pederson and Welch, 1985), and the amount and diversity of terpenes in the sap (Farentinos et al., 1981, Zhang and States, 1991). Gaud et al. (1993) observed repetitive feeding to be limited to 25% of the stand and that the likelihood of being a favored tree increased with tree size and reproductive maturity. As a result of selective foraging a significant decline in tree growth and reproductive fitness of target trees has been documented (Snyder, 1993). In ponderosa pine, organic components, such as terpenes, appear to be under genetic control (Smith, 1977), and their presence and diversity has been used to resolve their taxonomy. Thus, Abert's squirrels, through selective herbivory, may serve as an agent in natural selection, and over many years of dependent association, influence the phylogenetic history of ponderosa pine.

Although Abert's squirrels are the only tree squirrel to establish year-round residence in pure stands of ponderosa pine in the Southwest, home ranges of other tree squirrels overlapping ecotones where ponderosa pine is mixed with other conifer and hardwood species. The pine squirrel, *Tamiasciurus hudsonicus*, is occassionally found with Abert's squirrels in areas of higher elevation where Douglas fir is mixed with ponderosa pine. Their diet, principally of seed cones, also includes fruiting bodies of mushrooms and truffles (Smith, 1968) as well as occasional terminal buds and some inner bark (J. S. States, in litt). The Arizona gray squirrel, *Sciurus arizonensis*, occupies woodland and riparian habitats with mixed conifer and deciduous trees at lower elevations and exhibits limited mycophagy (Shewmaker, 1987). The ground-dwelling sciurids which are most frequently encountered in the under-story of ponderosa pine stands include chipmunks, *Tamias*, the golden-mantled ground squirrel, *Spermophilus lateralis*, and the rock squirrel, *Spermophilus variegatus*. These squirrels are known mycophagists (Maser et al., 1978) and although they are potential competitors, their densities are low in stands of ponderosa pine, apparently due to the lack of understory vegetation (Hall and Kelson, 1959).

We examined the stomach contents of four subspecies of Abert's squirrels (*S. a. aberti, S. a. kaibabensis, S. a. chuskensis, S. a. ferreus*) and the three most frequently encountered squirrels foraging within Abert's habitat, as listed above. Samples were collected in the autumn, a period when the highest quantity and diversity of food items are available (Stephenson, 1975, Theobald, 1983). The fidelity of selective herbivory on ponderosa pine and mycophagy on its associated mycorrhizal fungi by Abert's squirrels seems to be more pronounced than that of any other sciurid in its range (Table 1). No recognizable tissues of inner bark were found in any squirrel other than the Abert's subspecies. Hypogeous fungi were consumed by all taxa in greater quantity than epigeous fungi. Although available to all squirrels sampled, fungi were consumed in greater quantity by all four Abert's subspecies, 58% of the stomach volumes, compared to 23% for the other squirrels. Stomach contents of the other squirrels were more diverse and contained many items not consumed by the four subspecies.

As inhabitants of conifer forests, both squirrels consume similar diet items, but a long term diet study of pine squirrels indicated little or no preferential feeding on inner bark (Smith, 1970). This temperance may be explained by observations of apparent difficulty in digestion. In comparative feeding trials where captive squirrels were fed perforce on inner bark, very little of the structural plant tissue was digested by pine squirrels in contrast to its nearly complete reduction by Abert's squirrels (J.S. States, in litt). In addition, pine squirrels typically larderhoard massive caches of cones and aggressively defend them. In striking contrast, Abert's squirrels scatterhoard small caches of pine cones and acorns and exhibit no defensive behavior. Because pine squirrels have been found to occur within ponderosa pine forests outside the geographic range of Abert's squirrels, they could be viewed as habitat generalists, and the separation of the two may be partly due to differences in utilization of food resources. Cone crops of ponderosa pine are highly variable and

Table 1.—*The occurrence of selected food items in the stomachs of Abert's squirrels* (Sciurus) *and associated sciurids collected during autumn in ponderosa pine forests. Values indicate average percent (%) of diet by volume in stomachs. Number of stomachs examined* = (n).

		Food Item (%)					
	n	Seed	Plant matter	Inner bark	All fungi	Hypogeous fungi	Epigeous fungi
S. a. aberti	10	28.7	1.8	7.0	60.2	47.7	12.5
S. a. kaibabensis	10	40.2	1.2	7.8	50.8	45.0	5.8
S. a. chuscensis	10	30.0	1.0	12.0	57.0	57.0	0.0
S. a. ferreus	10	29.7	0.5	5.6	64.2	48.9	15.3
S. arizonensis	10	26.3	64.9	0.0	8.8	5.7	3.1
Tamiasciurus hudsonicus	9	66.5	3.5	0.0	30.0	17.5	12.5
Spermophilus lateralis	3	10.0	62.5	0.0	27.5	22.5	5.0
Spermophilus variegatus	2	2.0	73.5	0.0	24.0	24.0	0.0

unreliable as a food source for both squirrels (Larson and Schubert, 1970). The ability of Abert's squirrels to specially utilize inner bark and hypogeous fungi as alternative food resources may account, in part, for their predominance in ponderosa pine forests.

The importance of fungi in diets of squirrels has been well documented. Austin (1990) found the nutrient content of truffles and mushrooms to be comparable to that of pine seed and inner bark. He concluded that the nutrient levels of fungi should satisfy energetic demands of Abert's squirrels during periods when other primary foods are in short supply. Fruiting bodies of mycorrhizal fungi and inner bark constitute a major portion of their diet on annual basis (Fig. 1). Although total caloric values (kcal\g dry weight) of these fungi are lower (4.4) than pine seed (6.2), they are available in all seasons, and when produced in abundance, contribute to increased body weight (Austin, 1990). In a comparison of biweekly body weights of four, live trapped, free-ranging squirrels through four seasons, States et al. (1988) reported a winter weight loss that paralleled the decrease in availability of fungi, as evidenced by their presence in fecal contents (Fig. 2). Mycophagy has also been reported to be nutritionally advantageous on the basis that fungi are energetically less expensive to consume (Smith, 1970), and they provide higher concentrations of metabolic salts, sodium, potassium, and magnesium, than any other major diet item (Austin, 1990).

Because of their dietary importance, the availability of fungi seems to be critically important in regulating squirrel distribution and abundance. Mortality in Abert's squirrels was related to the depth of snow cover which limited the availability of food resources on the ground (Stephenson and Brown, 1980). States et al. (1988) reported a marked increase in inner bark consumption coincident with increased snow depth, and a corresponding decrease in truffle and availability of seed cones. Also, home ranges of Abert's squirrels were shown to fluctuate in accordance with food supply.

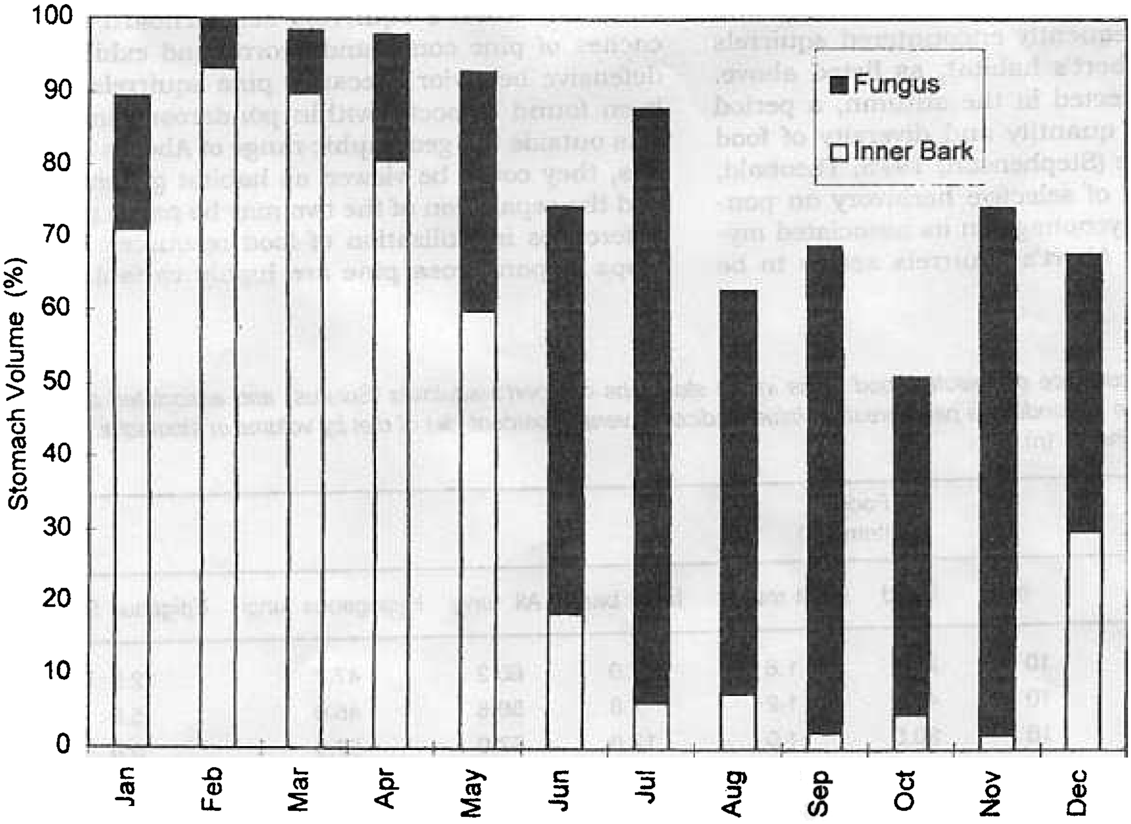

Fig. 1.—Occurrence of fungi and inner bark in stomach contents of Abert's squirrels sampled monthly in a ponderosa pine forest. Values are the monthly averages of the percentage stomach volume occupied by each item in 10 stomach samples.

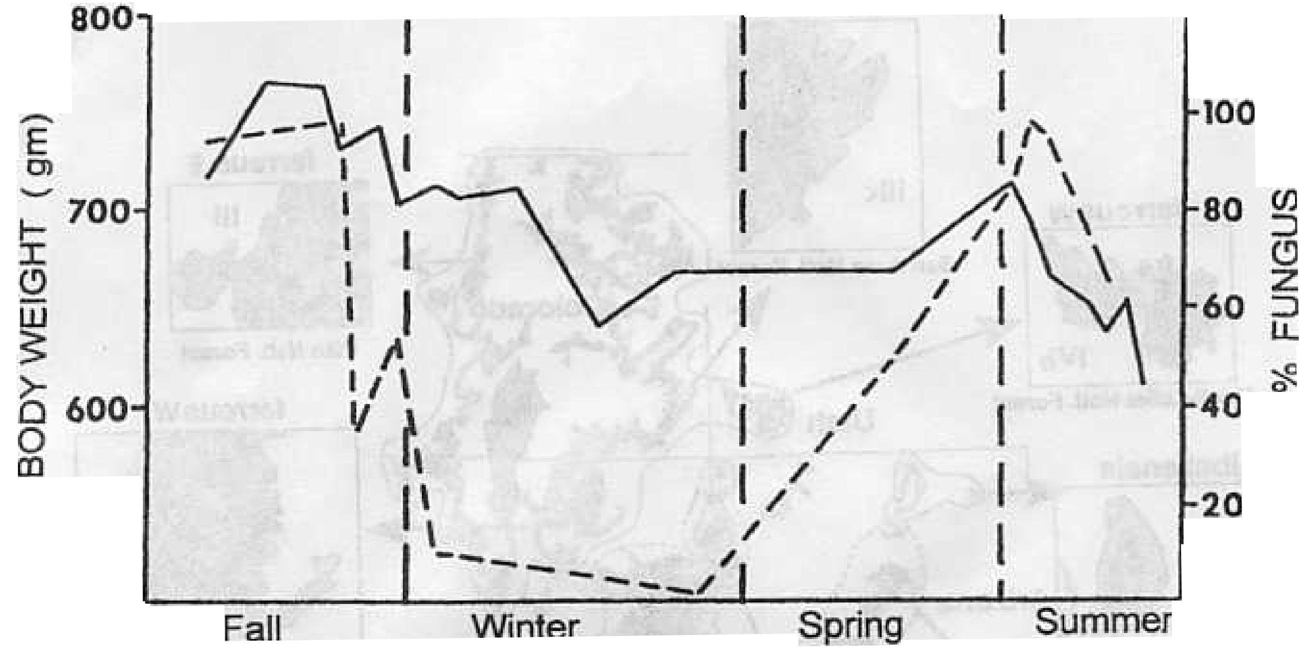

Fig. 2.—Body weights (solid line) of Abert's squirrels compared to fungal content of feces (dotted line) over a year in Coconino National Forest, Arizona (From States et al., 1988).

GENETIC DIVERSITY AND DIVERGENCE

Analysis of genetic relatedness within subspecies of *S. aberti* was conducted early in our research (Wettstein and States, 1986*a*, 1986*b*). We examined the diversity of gene families in the major histocompatibility complex genes and found little evidence to indicate divergence between *S. a. aberti* and *S. a. kaibabensis*. More definitive estimates of divergence using mitochondrial DNA analysis of restriction site polymorphisms (Wettstein et al., 1994), allowed us to recognize, from among the four subspecies present in the United States, two major squirrel assemblages: 1) an *aberti : kaibabensis* group; and 2) a *chuscensis : ferreus* group. Using sequences of the entire cytochrome-*b* gene from samples of all six subspecies of *S. aberti*, we confirmed and extended our previous results in the recognition of three major, geographically separated subspecies assemblages: 1) *barberi:durangi* in the western Sierra Madre of Mexico; 2) *ferreus:chuscensis* in the central and southern Rocky Mountains; and 3) *aberti:kaibabensis* in the Colorado Plateau region of Arizona and New Mexico (Wettstein et al., 1995).

Our proposed subspecies groups are in general agreement with the morphological classification and patterns of geographic distribution proposed by Hoffmeister and Diersing (1978). But there are some notable exceptions (Fig. 3). The populations from the San Juan Mountains(Colorado), Santa Fe National Forest (New Mexico), and Manti-LaSal National Forest (Utah) originally designated as *S. a. aberti*, clearly possess mitochondrial DNA of *S. a. ferreus*. Using analysis of neighbor joining and maximum parsimony we identified what appeared to be a level of substructuring of the *S. a. ferreus* population (Wettstein et al., 1995). Consequently, the range of *S. a. ferreus*, depicted in Fig. 2, has been divided into an eastern (E) and a western (W) population geographically separated by low elevation associated with the Rio Grande river drainage (Fig. 3). The high degree of genetic relatedness between *S. a. aberti* and *S. a. kaibabensis* is supportive of the reluctance expressed by Hoffmeister and Diersing (1978) to provide subspecies status for *S. a. kaibabensis* on the basis of morphometric similarities.

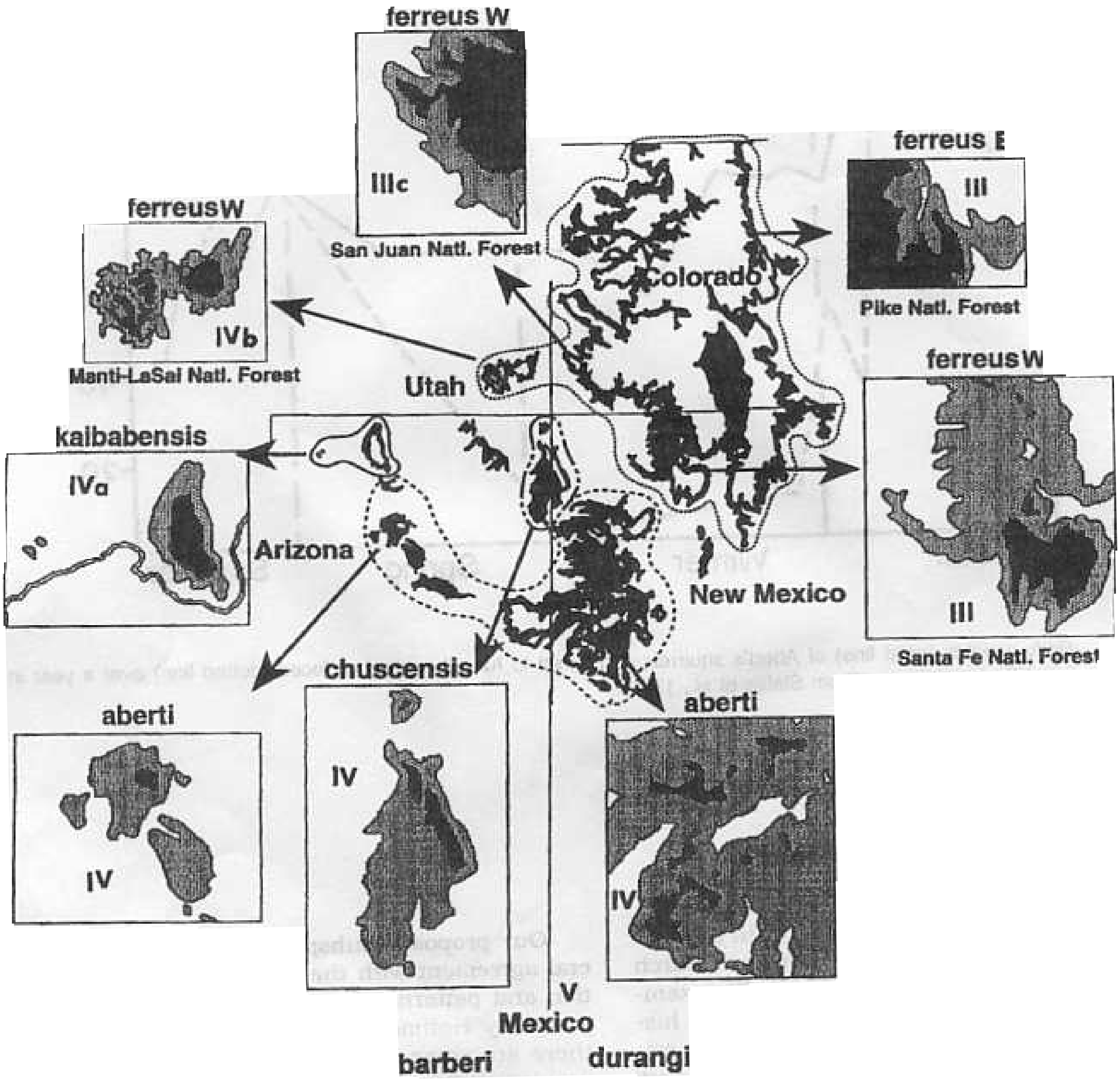

Fig. 3.—Geographic location of subspecies of *Sciurus aberti* and their inferred ranges from an analysis of genetic diversity and divergence. Shaded areas in the full map correspond to ponderosa pine habitat of Abert's squirrels, the light shaded areas in the insert maps indicate high elevation mixed conifer habitat of red squirrels, and the patterned lines encompass subspecies ranges. Roman numerals indicate the biochemical region assigned to ponderosa pines by Smith (1977). Modified from Wettstein et al.(1996).

PATTERNS OF ADAPTATION AND EVOLUTION

In the preceding account we illustrated the relationships that define the ecological "niche" relationships of Abert's squirrels with their pine habitat highlighting the selective nature of their foraging on inner bark of terminal twigs from target trees, pine seeds, and hypogeous fungi, which form mycorrhizal symbionts with pine roots. On the basis of nucleotide divergence, a minimum of four subspecies occupying separate geographc regions were identified and arranged into separate, genetically related assemblages. Based on these analyses, we postulate that the subspecies became genetically distinct sometime before the Wisconsin glacial period about 2 mya (Wettstein et al., 1995). Geographically, the distribution of ponderosa pine far exceeds that of the squirrel populations. However, the subspecies appear to be restricted to well defined montane islands of the southwestern United States and northern Mexico in localities where their host is always present.

In view of a possible historical association of nearly two million years, we are prompted to speculate here on the co-evolutionary relationships that may have developed. Like the squirrels, ponderosa pine is genetically diverse and the species has been separated into several varieties and races (Conkle and Critchfield, 1988). Smith (1977) separates the geographic range of races of ponderosa pine into five chemical regions whose boundaries are defined by the genetically controlled monoterpene composition of xylem resin. There is a surprising coincidence in the geographic distribution of the species assemblages of the squirrels and the monoterpene regions that characterize the host range: *barberi:durangi* = region V;. *aberti;kaibabensis* = region IV; and *ferreus:chuscensis* = region III (Fig. 2). A lesser degree of coincidence for individual subspecies was observed in situations where their host trees contain unique percentages of one or more of the five major monoterpene components. For example, large, possibly sub-regional shifts in terpene ratios within region IV (Smith, 1977), were noted for the north Kaibab plateau occupied by *S. a. kaibabensis* and for the Manti-LaSal forest occupied by *S. a. ferreus* E. We have designated these regions as IVa and IVb in Fig. 3. The selective foraging behavior of Abert's squirrels suggests that they may play a major role as agents of natural selection in their association with their biochemically diverse pine hosts. Farentinos et al. (1981) found amounts of monoterpenes to be significantly lower in twigs collected from trees selected by *S. a. ferreus* for consumption of inner bark. Furthermore, *a*-pinene was the best single predictor of tree selection, i.e. greater concentrations in the inner bark resulted in a higher degree of avoidance by the squirrels.

Trees in biochemical region III have large amounts of 3-carene, moderate amounts of myrcene and *b*-pinene, and small amounts of *a*-pinene and limonene (Smith, 1977). In contrast, inner bark resins of trees in region IV have very high proportions of *a*-pinene and 3-carene, with smaller amounts of *b*-pinene, myrcene, and limonene. Inner bark from trees selected for feeding by *S. a. aberti* contained high amounts of *a*-pinene which did not appear to influence their herbivory. Three monoterpenes present in low concentrations, myrcene, sabinene, and terpinolene, appeared to be the most important feeding deterrents in non-feed trees in *aberti* habitats (Zhang and States,1991).

A parallel example of selective feeding behavior involves the comparative feeding habits of the mountain pine beetle (*Dendroctonus ponderosae*) on two biochemically diverse races of ponderosa pine in California (Region II) and the Rocky Mountains (Region III). In California, Sturgeon (1979) observed marked avoidance of trees with high limonene content resulting larger numbers of pines with high concentrations of limonene and fewer numbers of trees with high *a*-pinene concentrations. This pattern was not detected in pine beetle interactions with the Rocky Mountain population, but there was a significantly higher biochemical diversity of pines in this region (Sturgeon and Mitton, 1986). We suggest that the selective and distinctive feeding habits, documented in both herbivores, help to maintain the characteristic biochemical diversity of the ponderosa pine races with which they are associated.

Hypogeous fungi form obligate, mycorrhizal associations with ponderosa pine and they are dependent on animals, especially squirrels, for spore dispersal. The pines are dependent to a large extent on mycorrhizal fungi for their mineral nutrition and in this regard several hypotheses have been advanced for co-evolution of these fungi with their tree associates (Fogel, 1992). Very little is known regarding aspects of speciation in hypogeous fungi but on an evolutionary scale they exhibit high species diversity and are known to form species specific associations with host trees (Molina et al., 1992). Hypogeous fungi have apparently undergone rapid morphological divergence in response to selective pressures of cold, arid environments (Bruns et al., 1989). The rapid evolution of ponderosa pine before and during the Pleistocene epoch, and its adaptation to strongly seasonal climates and drier sites in western North America was presumably enhanced by mycorrhizal associations which gave them an adaptive advantage over other species in stressful environments (Axelrod, 1986). It can be reasonably assumed that ectomycorrhizal fungi made adaptive responses to the adaptive radiation of the host.

Finally, the putative co-evolution of ectomycorrhizal host trees with ponderosa pine has had an impact on the squirrels as well. Hypogeous fungi make a substantial contribution to the diets of the rodents which disperse their spores. They provide considerable energy and mineral nutrition, and they are clearly favored in *S. aberti* foraging behavior. Their availability during seasons when other food items are in short supply may be a critical factor influencing the distribution and emigration of Abert's squirrels. For example, the relationship between climate and fungus availability may account for the failure of these squirrels to successfully occupy ponderosa pine forests north of the 41st parallel in North America. We conclude that continued study of the apparent interactive relationships among squirrels, pines, and fungi will contribute significantly to an understanding of their evolutionary history.

ACKNOWLEDGMENTS

The authors gratefully acknowledge access to study areas and scientific collecting permits issued by: the U. S. Park Service, Grand Canyon National Park, AZ; the U. S. Forest Service for the Coconino, Coronado, and Kaibab National Forests, AZ; the Arizona Game and Fish Department, Phoenix, AZ.; the New Mexico Department of Game and Fish, Santa Fe, NM; the Navajo Fish and Wildlife Branch, Navajo Nation, Window Rock, AZ; and the Colorado Division of Wildlife, Denver, CO. This research was supported in part by grants GM-41260 and GM-41399 from the National Institutes of Health and by a faculty grant to the senior author by Northern Arizona University, Flagstaff, AZ.

LITERATURE CITED

AUSTIN, W. J. 1990. The foraging ecology of Abert squirrels. Ph.D. dissertation, Northern Arizona University, Flagstaff, 279 pp.

AXELROD, D. I. 1986. Cenozoic history of some western American Pines. Annals of the Missouri Botanical Garden 73:565-641.

BRUNS, T., R. FOGEL, T. J. WHITE, AND J. PALMER. 1989. Accelerated evolution of a false truffle from a mushroom ancestor. Nature, 339:140-142.

CONKLE, M. T., AND W. B. CRITCHFIELD. 1988. Genetic variation and hybridization of ponderosa pine. Pp. 27-43, *in* Ponderosa pine: the species and its management (D. M. Baumgartner and J. E. Lotan, eds.). Washington State Cooperative Extension, Pullman, 281 pp.

DAVIS, R., AND D. E. BROWN. 1989. Role of post-pleistocene dispersal in determining the modern distribution of Abert's squirrel. The Great Basin Naturalist, 49:425-424.

FARENTINOS, R. C., P. J. CAPRETTA, R. E. KEPNER, AND V. M. LITTLEFIELD. 1981. Selective herbivory in tassel-eared squirrels: role of monoterpenes in ponderosa pine chosen as feeding trees. Science, 213:1273-1275.

FOGEL, R., 1992. Evolutionary processes in truffles and false-truffles: evidence from distribution of hypogeous fungi in the Great Basin, USA. Micologiae Vegetazione Mediterranea, 7:13-30.

FOGEL, R., AND J. M. TRAPPE. 1978. Fungus consumption (mycophagy) by small mammals. Northwest Science, 52:1-31.

GAUD, W. S., W. S. ALLRED, AND J. S. STATES. 1993. Tree selection by tassel-eared squirrels of the ponderosa pine forests of the Colorado Plateau. Pp. 56-63, *in* Proceedings of the 1st Biennial Conference on Research in Colorado Plateau National Parks. United States Department of Interior, National Park Service Publication NPS/NRNAU/NRTP-93/10, Flagstaff, Arizona, 186 pp.

GURNELL, J. 1987. The natural history of tree squirrels. Facts on File Publications, New York, 201 pp.

HALL, J. G. 1981. A field study of the Kaibab squirrel *Sciurus aberti kaibabensis* in Grand Canyon National Park, Arizona, USA. Wildlife Monographs, 75:1-54.

HALL, J. G., AND KELSON, K. R. 1959. The Mammals of North America. Vol. I. The Ronald Press Company, New York. 1:xxx + 1-546 + *79*.

HEIDMANN, L. J., AND Z. J. CORNETT. 1986. Effect of various nutrient regimes and ectomycorrhizal inoculations on field survival and growth of ponderosa pine container seedlings in Arizona Tree Planters Notes, 37:15-19.

HOFFMEISTER, D. F., AND V. E. DIERSING. 1978. Review of the tassel-eared squirrels of the subgenus *Otosciurus*. Journal of Mammalogy, 59:402-413.

KEETON, W. T., AND J. L. GOULD. 1993. Biological Science. Fifth edition. W. W. Norton & Company. New York. 1194 pp.

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

KOTTER, M. M., AND R. C. FARENTINOS. 1984*a*. Tassel-eared squirrels as spore dispersal agents of hypogeous mycorrhizal fungi. Journal of Mammalogy, 65:684-687.

———. 1984*b*. Formation of Ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. Mycologia, 76:758-760.

LARSON, M. M., AND G. H. SCHUBERT. 1970. Cone crops of ponderosa pine in central Arizona including the influence of Abert squirrels. USDA Forest Service Research Paper RM-58, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. Pp.15.

LOMOLINO, M. V., J. H. BROWN, AND R. DAVIS. 1989. Island biogeography of montane forest mammals in the American Southwest. Ecology, 70:180-194.

MASER, C. J., J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal small-mammal interrelationships with emphasis on Oregon coniferous forests. Ecology, 59:799-809.

MOLINA, R., H. MASSICOTTE, AND J. M. TRAPPE. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. Pp. 357-423, *in* Mycorrhizal functioning: an integrative plant-fungal process. (M. F. Allen, ed.). Chapman & Hall, New York.

PEDERSON, J. C., AND B. L. WELCH. 1985. Comparison of ponderosa pines as feed and nonfeed trees for Abert squirrels. Journal of Chemical Ecology, 11:149-157.

RIFFLE, J. W. 1989. Field performance of Ponderosa, Scots, and Austrian pines with ectomycorrhizae in prairie soils. Forest Science, 35:935-945.

SHEWMAKER, J. A. 1987. Fungal Consumption by the Arizona gray squirrel (*Sciurus arizonensis*). M.S. thesis. Northern Arizona University, Flagstaff, 50 pp.

SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs, 38:31-63.

———. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs, 40:349-371.

SMITH, R. H. 1977. Monoterpenes of ponderosa pine xylem resin in western United States. USDA Forest Service Technical Bulletin, 1532, 48 pp.

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

STATES, J. S. 1985. Hypogeous mycorrhizal fungi associated with ponderosa pine: sporocarp phenology. p.271, *In* Proceedings of the 6th North American Conference on Mycorrhizae (R. Molina, ed.) Forest Research Laboratory, Corvallis, OR. (abstract).

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* Management of Amphibians, Reptiles, and Small Mammals in North America. Proceedings of the Symposium (R. Szaro, K. Severson, and D. Patton, eds.). Forest Service- USDA General Technical Report RM-166, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, 455 pp.

STEPHENSON, R. L. 1975. Reproductive biology and food habits of Abert's squirrels in central Arizona. M. S. thesis, Arizona State University, Tempe, 66 pp.

STEPHENSON, R. L., AND D. E. BROWN. 1980. Snow cover as a factor influencing tassel-eared squirrel mortality. The Journal of Wildlife Management, 44:951-955.

STURGEON, K. B. 1979. Monoterpene variation in ponderosa pine xylem resin related to western pine beetle predation. Evolution, 33:803-814.

STURGEON, K. B., AND J. B. MITTON. Biochemical diversity of ponderosa pine and predation by bark beetles (Coleoptera: Scolytidae). Journal of Economic Entomology, 79:1064-1068.

THEOBALD, D. 1983. Studies on the biology and habitat of the Arizona gray squirrel. M. S. thesis, Arizona State University, Tempe, 49 pp.

THOMAS, G. R. 1979. The role of phloem sugars in the selection of ponderosa pine by the Kaibab squirrel. M. S. thesis, San Francisco State University, California, 62 pp.

WETTSTEIN, P. J., AND J. S. STATES. 1986*a*. The major histocompatibility complex of tassel-eared squirrels. I. Genetic diversity associated with Kaibab squirrels. Immunogenetics, 24:230-241.

———. 1986*b*. The major histocompatibility complex of tassel-eared squirrels. II. Genetic diversity associated with Abert squirrels. Immunogenetics, 24:242-250.

WETTSTEIN, P. J., P. LAGER, L. JIN, J. STATES, T. LAMB, AND R. CHAKRABORTY. 1994. Phylogeny of mitochondrial DNA clones in tassel-eared squirrels *Sciurus aberti*. Molecular Ecology, 3: 541-550.

WETTSTEIN, P. J., M. STRAUSBACH, T. LAMB, J. STATES, R. CHAKRABORTY, L. JIN, AND R. RIBLET. 1995. Phylogeny of six *Sciurus aberti* subspecies based on nucleotide sequences of cytochrome *b*. Molecular Phylogenetics and Evolution, 4:150-162.

ZHANG, X., AND J. STATES. 1991. Selective herbivory of ponderosa pine by Abert squirrels: a re-examination of the role of terpenes. Biochemical Systematics and Ecology, 19:111-115.