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ANTIQUITY OF SOUTHERN APPALACHIAN GRASS BALDS: THE ROLE OF KEYSTONE MEGAHERBIVORES

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ABSTRACT.—The origin and persistence of the high elevation grass balds of the southern Appalachians have been the subject of a long standing controversy that now threatens the preservation of this community, with its unique array of plants and animals. Those who claim that the balds are the result of recent, anthropogenic factors are content to allow successional processes to obliterate most balds. On the other hand, those who believe that balds are, in many cases, natural and quite ancient communities argue for their study and preservation. On the basis of information drawn from regional history, community ecology, agricultural studies and paleontology, we hypothesize that open grasslands probably always existed locally in mountain landscapes and elsewhere in the Southeast during the Pleistocene and that these areas were maintained and modified initially by large keystone herbivores, later by bison, elk and deer and, since about 1840, by domestic livestock. The rapid decline of the grass balds today may be largely attributed to the absence of large herbivores, and the best method for restoring them and conserving their rare biota may involve the reintroduction of wild or domestic animals in the future.

KEYWORDS.—grass balds, keystone species, megaherbivores

Southern Appalachian grass balds are areas of naturally occurring treeless vegetation located on well-drained sites below the climatic treeline in predominantly forested regions (Mark, 1958) and are dominated by herbaceous plants, especially grasses, sedges, and forbs. About 90 grass balds of various types have been described in the southern Appalachians, from the Great Smoky Mountains through the Balsam and Roan Mountain massifs to the mountains of southwestern Virginia (Wells, 1937; Mark, 1958; Ramseur, 1959; Gersmehl, 1970). These grasslands, familiar in the past to both local Indian peoples and early European settlers, have started to disappear as successional

processes now favor rapid forest invasion. The origin of these balds has remained largely unexplained, and their past and future maintenance is highly controversial for a variety of scientific, political, and economic reasons. For, if the origin and persistence of these biologically diverse balds can be attributed to recent anthropogenic factors - either the activity of pre-colonial native Americans or later white settlers - then one might dismiss the community as a human artifact, unworthy, except in a few special cases, of any concerted preservation efforts.

On the other hand, if the balds are judged to be the result of natural phenomena, perhaps dating from the late Pleistocene and later influenced by human activity, then one can make a strong case for expending political effort and financial resources to study and maintain them. Over the past 20 years some individuals and agencies have come to consider all these areas as recent human artifacts—largely the products of European agricultural practices—and have limited their concern to species of rare plants, scenic considerations, and the protection of a few small remnants of the original formation (Lindsay and Bratton, 1979; Sutter and White, 1994). We would maintain that such a conclusion not only ignores the diversity of animal species associated with the balds, but overlooks the dynamic ecological and evolutionary processes which are potentially part of their history. We would also maintain that the kind of academic training we biologists receive, which emphasizes particular groups of organisms, narrow allegiance to disciplines and a preoccupation with the here and now rather than process and history is the main cause of the conceptual problems surrounding the balds.

Before reviewing a hypothesis and some arguments about bald origins and maintenance (Weigl and Knowles, 1995), we need to make a few necessary distinctions. We in no way wish to insist that all grass balds had the same origin and that all are ancient. Many are clearly the products of human activity in the 19th and 20th centuries, and almost all have been modified to varying degrees by local people, as documented by Gersmehl (1970) and Lindsay and Bratton (1979). Our major interest centers on the so called "natural" balds mentioned by Peterson (1981), Smathers, (1981), Wilson (1991) and others which clearly have more complex histories. These may be found on many of the mountain ridges of western North Carolina and Virginia.

Hypothesis

Based on available information from many sources discussed below we advance the idea that some form of grassy area has persisted in the upper elevations of these mountains from at least the late Pleistocene and that these areas have been maintained to a major degree by large mammalian herbivores. In fact the distinctive animal and plant assemblages of the grass balds may well be the result of a disturbance regime involving successive groups of keystone herbivores. Furthermore, the recent absence of these animals is a major factor in bald disappearance.

Origins and antiquity.

In the controversy over bald origins and maintenance two divergent schools of thought have developed. One school holds that balds are natural features of the landscape and existed over a vast number of years. Its adherents have invoked factors such as frost damage, soil conditions, insect pathogens, fire, and interactions between climatic change and forest migration at ecotones (Edson, 1894, Harshberger, 1903; Clements, 1936; Gates, 1941; Billings and Mark, 1957; Mark, 1958). While they have documented the severe conditions and some of the history of these mountain grasslands, no one theory has been adequate to explain these communities. The other school of thought has emphasized anthropogenic factors. Early members of this school proposed that native Americans cleared the balds for hunting and campgrounds (Wells, 1936; 1938; 1956), but there is virtually no archeological evidence to support this possibility. Recent papers claim that European agricultural practices are responsible for the balds (Gersmehl, 1970; Lindsay and Bratton, 1979): that settlers cleared areas to graze livestock, and that with the decline in mountain farming, the balds will, and maybe should, be allowed to disappear. Unfortunately this has been a much invoked argument - with all its portentious implications for mountain conservation.

We would be surprised if grass balds and other open grasslands had not been repeatedly formed - and in some cases obliterated - in the Pleistocene and Holocene. First, the idea that the whole region east of the Mississippi was one solid forest is increasingly untenable as coastal plain savannahs, Piedmont prairies, Tennessee and Kentucky barrens and prairie peninsulas become well documented and as the descriptions of early explorers are rediscovered. Secondly, the vegetation reconstructions of the Delcourts (1980) and other paleobotanists (Woodward, 1985) indicate that periods of glacial advance were associated with climates so severe on high mountain peaks that forest vegetation was frequently replaced by

semi-tundra and open grassland—terrain which would have been particularly attractive to the large cold adapted herbivores of the time. In addition, palynological data from a mountain bog reveal that some high elevation sites were not forested 3000 years ago, but supported open areas of heath and other plants (Shafer, 1986). Third, we have the richness of Indian lore and legend about grass balds. These traditions have been much maligned and dismissed by Waterman (1914) and Gersmehl (1970), but such a response may be premature and ill considered in the light of the veracity of Indian knowledge about a host of other subjects during the settlement of North America. Also, one has only to think of the geographical descriptions of the Old Testament or Schliemann's use of Homeric legend to locate Troy to grasp the accuracy of many folk traditions.

Finally, what is the evidence from the colonial period? One reads frequently that there are no reports of grass balds until rather late in the 19th century and that the first settlers in the mountains immediately started to clear the peaks (Gersmehl, 1970). Let us take these subjects one at a time. In Virginia the first descriptions of balds come from the writings of John Lederer in 1669 and John Sinclair in 1747 (Keith Langdon, personal communication). In North Carolina, descriptions date from at least the eighteenth century. In surveying the North Carolina-Tennessee boundary in 1799 John Strother wrote in his diary: "There is no shrubbage grows on the tops of this mountain for several miles, say, five... The prospects from the Roan Mountain is more conspicuous than any other part of the Appalachian Mns" (in Wilson, 1991). At the same time (1799-1814) John Lyon's journal also described the treeless nature of Roan (Ewan and Ewan, 1963; Peterson, 1981), attributing it to cold and wind. By the 1830's Elisha Mitchell found that little had changed at Roan: "...the top of the Roan may be described as a vast meadow (about nine miles in length..), without a tree to obstruct the prospect; where a person may gallop his horse for a mile or two, with Carolina at his feet on one side, and Tennessee on the other" (in Wilson, 1991). In 1855, T.L. Clingman described the "naked slopes and fantastic peaks" of the Craggy Mountains at a time when no significant settlement had occurred in the region (Smathers, 1981). Thus, there are early records of balds by visitors and explorers.

The next question then becomes, were the grass balds described by these travelers the result of European settlement? In almost all cases the answer is no. To obtain information on conditions in the mountains and on settlement patterns we had to go back to early censuses, maps, county histories and traveler's descriptions.

One must keep in mind that until the later part of the 18th century Cherokee peoples continued to have a dominant influence by both treaty and presence in the mountains. In spite of earlier losses to western militias the Cherokee were able to mount attacks on Eatons Station and Ft. Watauga in 1776 (in northeastern Tennessee) and fought battles with South Carolina troops in 1779. In fact it was only with the explusion of the southeastern Cherokee in the Trail of Tears episode as late as 1838-39 that the Indian presence was largely removed.

In the face of Indian residents and harsh conditions, settlement in the mountains was slow and uneven. Most people passed through or around the mountains to the rolling lands and river valleys of eastern Tennessee and southwestern Virginia (Cappon, 1976). As is clear from the reports of Brickell in 1730 (Smathers, 1981) and Bartram in 1775 (Van Doren, 1955) and the Delcourts' (1980) pollen studies, grassy openings and savannahs were present in the larger mountain valleys, and it appears that these areas were settled first. The men who fought at the Battle of Kings Mountain in 1780 came mostly from west of the mountains in Tennessee. After a night at the famous shelving rock near the present town of Roan Mountain in Tennessee, they camped on the Roan massif on what, from their descriptions, could only have been part of a bald (Cooper, 1964). By 1790 the whole Toe River valley between the Black Mountains, Grandfather and Roan had only 80 families, maybe 300 people in all (Sheppard, 1935). By the census of 1840 the counties near the higher mountains had only a few thousand inhabitants each, and these mostly in the lowlands (U.S. Department of State, 1990; De Bow, 1990). Finally, while the people on the good land surrounding the mountains and in the broad valleys around Asheville might have been major cattle and sheep raisers, this was uncommon until later in the closed mountain valleys. Here hogs were the major meat animals, benefiting with their owners from the abundant acorn and chestnut crops (Cooper, 1964). Hogs do not commonly forage in grasslands, and there are many descriptions of the relatively few cattle and sheep sharing the woodlands with hogs.

In summary then, the Indian presence, settlement patterns, population size, and local economics suggest that settlers would have had little impact on remote mountain tops until the 1830's or 40's, well after there exist fairly good

descriptions of grass balds. And it is only at this time that Gersmehl (1970) and others start to document human modification of mountain peaks and slopes.

Rare plant assemblages

Although the balds support a number of rare animals and animal communities, these have not yet been well studied, and it is the plants that have received the most renown. The presence of a large assemblage of relict, disjunct and rare plant species which are mostly confined to balds or other open habitats, and which are generally intolerant of closed forest, suggests that these plants evolved, migrated and survived in similar open communities over an extensive period of time - probably on the order of thousands of years (Table 1). The chances that the whole assemblage could have invaded the balds from rock outcrops in the 150 years or less since the onset of human disturbance seems unlikely, especially where the outcrops are small and few in number. In addition, the kinds of species-area constraints deduced from island biogeography studies suggest that small, isolated outcrops are not likely to support large, diverse populations for long periods. In fact, many of the outcrops at Roan Mountain, which have now been overgrown by alder or rhododendron, fail to support much of anything in the way of plants or animals underneath. Clearly, data on reproduction, genetics, longevity and dispersal mechanisms are badly needed to understand plant migrations—but at present such data do not exist. Ironically, the people who so vehemently argue that rock outcrops are entirely adequate reservoirs for this diverse group of plants are, in most cases, the very same individuals who are most vocal about the necessity of preserving these plants on the balds today. Finally, it is important to mention here that these plants continue to exist on the balds in spite of a century and a half of livestock grazing.

Recent grazing and maintenance.

Of the original high elevation grasslands, including balds and man-made pastures, it appears that only those which are now grazed or browsed by livestock (or have been recently mowed) have maintained any semblance of their size, open character, or species composition (DeSelm and Murdock, 1993). All of the rest have undergone rapid succession since the cessation of grazing. Such succession typically involves the invasion of trees at the bald edges and the progressive dominance of such plants as blackberry (*Rubus*), blueberry (*Vaccinium*), *Rhododendron* and *Angelica* in open areas. Such changes also appear to be associated with a decline in the diversity and number of various small vertebrates which inhabit the balds or use them seasonally (Weigl, unpublished data). Thus it is clear that any agency which cuts back woody overgrowth and suppresses succession helps maintain the balds, and that domestic livestock have assumed this function for over 150 years.

Impact of past megaherbivores.

While the impact of grazing and browsing by domestic animals has received some attention in the literature, the influence of large herbivores in the past has either been overlooked or dismissed (Weigl and Knowles, 1995). Prior to 11,000 BP (7,000 years after the last glacial maximum) a more diverse fauna occupied the region. Using Kurtén and Anderson's (1980) review of the ranges of Pleistocene mammals as a guide, Weigl (1986) postulated that up to 20 species of large herbivores could have inhabited the southern Appalachians (Table 2). These included mammoth, mastodon, horse, bison, musk oxen, caribou and ground sloth. Such animals possessed great climatic tolerance, high mobility, immense strength, and diverse dietary requirements and would have been capable of occupying and radically modifying high elevation habitats, especially grassland—forest mosaics.

Two types of information subsequently lent support to this idea.

a)Excavations at Saltville, Virginia - an area of ancient stream deposits dated at 10-11,000 years BP and within 200 miles of all the grass balds - have unearthed many of the megaherbivores mentioned earlier (Table 2; McDonald and Bartlett, 1983; McDonald, 1990). Thus there can be little question of the existence of megaherbivores in the region.

b)In the past few years Owen-Smith (1987; 1988; 1989) has published a number of papers based on his research in Africa and North America in which he puts forward his "keystone megaherbivore hypothesis". He found that large herbivores in relatively small numbers were able to maintain the openness of certain habitats and in the process create suitable conditions for a whole variety of other organisms. In fact, it appears that large herbivores, vegetation structure, and species diversity have a long history of interdependence.

In the past few years a number of reports have come to light describing similar phenomena: the South African and Serengeti savannahs (Owen-Smith, 1987; McNaughton, 1994), The New Forest (Putnam, 1986) and Wiltshire Downs in England, Dutch salt marshes and the Carmargue of France (Gordon and Duncan, 1988). In all of these areas

TABLE 1.—*RARE, SENSITIVE, AND RELICT PLANTS OF THE ROAN MOUNTAIN GRASS BALDS*

Species (Common Name)	State Status (North Carolina)*	Federal Status*	Southern Appalachian Endemic?	Pleistocene Relict?
Agrostic mertensii (Arctic Bentgrass)	C			X
Alnus viridis ssp. crispa (Green Alder)	C			
*Calamagrostic canadensis*** (Canada Reedgrass)	SR			X(?)
Carex aenea (Bronze Sedge)	E			X
Carex misera (Wretched Sedge)	SR	3C	X	
Carex oligosperma (Few-seeded Sedge)	C			
*Delphinium exaltatum*** (Tall Larkspur)	E-SC	C2		
Deschampsia flexuosa (Hair Grass)			X	
Epilobium ciliatum (Purpleleaf Willowherb)	SR			
Geum geniculatum (Bent Avens)	T	C2		
Geum radiatum (Spreading Avens)	E	E	X	
Hedyotis purpurea var. *montana* (Roan Mountain Bluet)	E	E	X	
Huperzia appalachiana (Fir Clubmoss)	C			X
Hypericum graveolens (St. John's-Wort)			X	
Hypericum mitchellianum (St. John's-Wort)			X	
*Liatris helleri*** (Heller's Blazing Star)	T-SC	T	X	
Lilium grayi (Gray's Lily)	T-SC	C2	X	
Lilium philadelphicum (Wood Lily)	C			
Minuartia groenlandica (Greenland Sandwort)	C			X
Platanthera peramoena (Purple Fringeless Orchid)	C	3C		
Poa palustris (Swamp Bluegrass)	SR			
Potentilla tridentata (Three-toothed Cinquefoil)				X
Prenanthes roanensis (Roan Rattlesnake Root)	SR	3C	X	
Rhytidium rugosum (Golden Tundra-moss)	SR			X
Senecio schweinitzianus (Schweinitz's Groundsel)	E			
*Trisetum spicatum*** (Soft Trisetum)	E			X
Xanthoparmelia monticola (A Foliose Lichen)	C			

*Source: U.S. Fish & Wildlife Service, Asheville, North Carolina; and the North Carolina Natural Heritage Program. Many of these species are also listed by the state of Tennessee.

**Represented in historical collections; may now be extirpated from Roan Mountain.

Key to North Carolina status codes:

E - Endangered. Any species of plant whose continued existence as a viable component of the State's flora is determined to be in jeopardy.
T - Threatened. Any species of plant likely to become an endangered species within the forseeable future.
SC - Special Concern. Any species of plant which requires population monitoring.
C - Candidate. Species which are very rare in North Carolina, generally with 1-20 populations in the state, generally substantially reduced in numbers by habitat destruction. These species are also either rare throughout their ranges or disjunct in North Carolina from a main range.
SR - Significantly Rare. Species which are very rare in North Carolina, generally with 1-20 populations in the state, generally substantially reduced in numbers by habitat destruction. These species are generally more common somewhere in their ranges.

Key to federal status codes:

E - Endangered. A taxon that is threatened with extinction throughout all or a significant portion of its range.
T - Threatened. A taxon that is likely to become endangered in the foreseeable future.
C2 - Candidate 2. A taxon for which there is some evidence of vulnerability, but for which there are not enough data to support listing as endangered or threatened at this time.
3C - Candidate 3C. A taxon that has proven to be more abundant or widespread than previously believed and/or those that are not subject to any identifiable threat.

TABLE 2.—*LATE PLEISTOCENE MAMMALS OF THE SOUTHERN APPALACHIANS**

Scientific Name	Common Name	Comments
*Megalonyx jeffersonii***	Ground Sloth woodlands, forest	Ox-size;
Eremotherium rusconii	Ground Sloth	3 tons; diet of twigs and leaves
Glossotherium harlani	Ground Sloth	
Equus complicatus	Horse	
Equus fraternus	Horse	
Equus spp.**	Horses	
Tapirus veroensis	Tapir	
Myohyus nasutus	Longnose Peccary	Deer-size
Platygonus vetus	Liedys Peccary	Large
Platygonus compressus	Peccary	Wild boar-size; herd animal
Odocoileus virginianus	Whitetail Deer	
Sangamona fugitiva	Fugitive Deer	
*Rangifer tarandus***	Caribou	
Alces alces	Moose	
*Cervalces scotti***	Stag Moose	
Cervus elaphus	Elk	
Symbos cavifrons	Woodland Muskox	
*Bootherium bombifrons***	Harlans Muskox	
*Bison latifrons***?	Giant Bison	
Bison bison	Bison	
*Mammut americanum***	American Mastodon	
Mammuthus jeffersonii	Mammoth	
*Mammuthus primigenius***,****	Woolly Mammoth	

*Compiled from Kurtén and Anderson (1980)
**Presence confirmed by fossil excavations in Saltville, Virginia
***Not listed for the southern Appalachians in Kurtén and Anderson (1980)

the structure and diversity of the community results from wild or domestic keystone herbivores. Just recently, Nature Conservancy biologist Alan Weakly was quoted suggesting that the newly discovered and apparently ancient Piedmont prairies of North and South Carolina are the result of bison grazing in addition to fire and soil conditions (Horan, 1995).

About 10,000 years ago North America's megafauna died out quite suddenly. However, on the basis of skeletal remains, place names, and the early reports of such travelers as Lawson, Logan, and Bartram, it is clear that substantial populations of elk, deer and bison occupied the open lands of the southeast and very likely became the dominant herbivores in mountain grasslands. The domestic livestock of a later era, then, merely maintained an ancient ecological process.

Not only are animals now being used widely to control vegetation (Poore and Green, 1992), they have been found to have unexpected side effects. At Roan Mountain, after a small area had been grazed by goats, hundreds of the rare Gray's lily (*Lilium grayi*) seedlings were found growing in one of the empty paddocks (pers. obs.). Plants may flourish because of herbivory, not in spite of it.

SCENARIO

The above arguments provide evidence which is consistent with a megaherbivore keystone hypothesis and suggest the following scenario (Weigl and Knowles, 1995) with regard to the history of the southern Appalachian grass balds.

During the glacial episodes of the late Pleistocene, severe climatic conditions could have repeatedly deforested the higher peaks of the southern mountains. Some of these ridge systems or peaks became the permanent habitat or

summer feeding grounds of an array of large grazers and browsers capable of maintaining open grasslands or of forest-grass mosaics, which in turn provided upland habitat for both plants and smaller animals. During periods of more moderate conditions (between glacial advances) some areas continued to be occupied by herbivores, while others (less suitable peaks?) became reforested. The persistence of disjunct, open habitat provided the basis for the survival of rare, and relict species of small plants and animals which could not have tolerated closed forest. At the time of the great megafaunal extinction 10-11,000 years ago, bison, elk, and deer may have replaced the earlier herbivores, but perhaps at a loss of some grasslands because of their lower impact on forest succession. Starting 150 years ago, the mixed herds belonging to European settlers, the metal ax, and perhaps occasional fire further modified and extended the remaining grass balds or made new ones. By the 1940s and 1950s mountain farming went into decline and lands were purchased for parks, national forests and recreation. Finally without their herbivores the balds started to disappear.

IMPLICATIONS FOR RESEARCH AND CONSERVATION

If the above scenario has merit, then it forces us to consider the balds in a much broader historical context, to accept the idea that large animals can have a profound effect on the distribution and evolution of vegetation, and to attempt to formulate rational conservation measures. This, in turn, might lead to the following actions.

1) Research on rare plants which goes beyond localization and plant-by-plant protection to include studies of demography, genetics, reproductive mechanisms, and the possible impact of animals on dispersal and establishment. Recently, a major part of an issue of *Ecology* was given over to just this point (Schemske et al., 1994). Almost no work of this kind has been carried out to date.
2) Study and protection of animal species, both vertebrate and invertebrate, found on or near the balds. Because these are more difficult to study and because most work has been done on plant species, such animals have often been ignored in management decisions. In addition, our preoccupation with endangered species and popular organisms has often made us blind to the unique assemblages of currently non-threatened and less charismatic forms found in mountain habitats, and has led to the management of entire regions for one or a few species but not the community as a whole.
3) Research on the effect of combinations of grazers and browsers on the maintenance and re-establishment of the grass balds. This would probably involve carefully controlled studies using domestic herbivores, but wild species (elk, bison, etc.) might be reintroduced in some areas. In spite of all the concern expressed over the last quarter century, no carefully designed research of this kind has been conducted. Such work might lead to long-term preservation strategies that come closest to replicating natural evolutionary and ecological processes that are part of grass bald history, and have a real chance of preserving this special community.

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