Was Aldo Leopold Right about the Kaibab Deer Herd?

Dan Binkley,[1,2,3]* Margaret M. Moore,[4] William H. Romme,[1,2] and
Peter M. Brown[1,5]

[1]Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, Colorado 80523, USA;
[2]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523, USA; [3]Natural Resource Ecology
Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA; [4]School of Forestry, Northern Arizona University, Flagstaff,
Arizona 86011, USA; [5]Rocky Mountain Tree-Ring Research Inc., 2901 Moore Lane, Fort Collins, Colorado 80526, USA

ABSTRACT

In ecology textbooks prior to the 1970s, Aldo Leopold's classic story of predator control, over-population of deer, and habitat degradation on the Kaibab Plateau during the 1920s epitomized predator regulation of herbivore populations. However, the story disappeared from texts in the late 20th century after several papers noted uncertainties in estimations of the deer population and provided alternative explanations. We re-examined the case study by determining the age structure of aspen (*Populus tremuloides* Michx.) on the plateau. Aspen comprises the majority of deer browse in the summer, and the absence of a normal cohort of aspen from the 1920s would indicate deer over-population. The number of aspen (at 1.4 m) dating to the 1920s was an order of magnitude lower than the null expectation. Other periods of unusual numbers of aspen included high numbers of aspen dating to the 1880s and 1890s (when regular sur-face fires ceased), few aspen dating from 1953 to 1962 (after a second irruption of the deer population), and very high numbers from 1968 to 1992 (coincident with widespread logging). These convergent lines of evidence support the idea of extreme deer herbivory in the 1920s, consistent with food limitation of deer at high populations (bottom–up control) and predation limitation at low deer populations (top–down control). Some uncertainty remains within the overall story, and this level of ambiguity is common in case studies that involve population ecology, land management, and people at the scale of 1,000 km² and 100 years. A complete version of the Kaibab deer story and its history would be a valuable, realistic case study for ecology texts.

Key words: deer population; irruption; Kaibab Plateau; Grand Canyon; fire history.

INTRODUCTION

The story of the Kaibab deer herd formed a cornerstone of population ecology from the 1920s (compare Elton 1927) through the early 1970s (compare Dasman 1964; Kormandy 1969; Owen 1971; Ricklefs 1973). The classic form of the story was often attributed to Aldo Leopold (1943), who reported that reducing the population of predators on the Kaibab Plateau led to an irruption of the

deer population, degradation of habitat, and lower carrying capacity for deer. The deer herd on the Kaibab Plateau was the focus of major controversies between the National Park Service and the USDA Forest Service, a landmark dispute between Arizona and the federal government over wildlife and hunting rights, and even a colorful attempt to drive deer across the Grand Canyon that was fictionalized in a novel by Zane Grey (Grey 1924; Young 2002). Rachel Carson (1962) used the Kaibab deer story in *Silent Spring* to convince readers of the importance of predators, and the story appeared in most ecology textbooks to show

that top predators are critical for controlling ecosystem food webs.

Confidence in the story began to erode when Caughley (1970) highlighted the paucity and inconsistency of the original data. He suggested that if a deer irruption actually occurred, the driver might have been release of the deer from food competition with livestock after massive livestock reductions at the end of the 19th century. The role of predation in regulating food webs was also challenged by ecologists and land managers in the 1960s and 1970s. Increasing confidence in the control of food webs by primary production rather than predation contributed to the adoption of the ''natural regulation'' policy by the US. National Park Service. Populations of ungulates were expected to stabilize at ''natural'' levels controlled by food supply (National Research Council 2002). Some texts began to use Leopold's Kaibab deer story not as an example of ecological principles but as a warning about the dangers of unwarranted credulity (Dunlap 1988; Botkin 1990). Colinvaux (1973, 1986) went so far as to claim that the Kaibab story had been exposed as fiction, that the anecdote was known to be without value, and that the history was not true. Most recent textbooks simply omit mention of the once-classic tale (Molles 1999; Krebs 2001; Ricklefs 2001; Smith and Smith 2001) or use it as an example of poor ecology (Stiling 2002). Some scientists remain convinced of the role of mammalian herbivores in shaping the structure and function of ecosystems (for example, Paine 2000), so the underlying idea of top–down control of populations retains some support even if the Kaibab example was inconclusive.

Does the classic Kaibab deer story warrant confidence as a landscape-level demonstration of the importance of predation in regulating food webs, or is the value of the story limited to a historical account of misguided ecology? Mitchell and Freeman (1993) reviewed a wealth of primary sources apparently not examined by Caughley (1970) and concluded that a deer irruption and die-off had occurred, but that the drivers included both reductions in predation (including human hunting) and livestock competition, followed by overbrowsing, severe drought, and a change in the long-term fire regime. Young (2002) provided the most thorough synthesis of the story; his primary conclusion was that whatever the real dynamics of the deer population might have been, the Kaibab deer story is an excellent example of the interaction of science, conservation, politics, and management.

We tested a hypothesis that might shed light on whether the deer population irrupted in the 1920s as Aldo Leopold (and almost all of this contemporaries) believed. Young shoots of aspen (*Populus tremuloides* Michx.) comprise the majority of deer browse during summer on the Kaibab Plateau (Rasmussen 1941; Bostick 1949; Hungerford 1970) and we hypothesized that aspen regeneration would necessarily be impaired during periods when high browsing pressure by deer (or livestock) led to massive deer mortality. If the deer population irruption in the 1920s was real, aspen regeneration on the Kaibab Plateau should have been far lower than normal during this period. If the aspen cohort matched the long-term trend for the plateau, the population of deer was unlikely to have been high enough to degrade habitat. Support of this hypothesis would indicate that the classic story may have been true, because the deer population apparently did irrupt, but this would not be a direct test of whether the irruption resulted from predation release.

Our hypothesis was in line with unquantified observations of excessive browsing of *Populus*, *Quercus*, and shrubs during the period when the deer population was reported to be high (Adams 1925; Mann 1941; Russo 1964). Some previous work lent preliminary support to this hypothesis. In 1935, McHenry noted that very few *Populus tremuloides* trees were under 20 years of age in Grand Canyon National Park, asserting that Lepold's conclusion that deer browsing had effectively limited the aspen reproduction ''is an inescapable fact as one looks through the forest to see practically no new, young growth.'' Rasmussen (1941) noted:

> Ordinarily a forest of this type contains a great number of seedling aspens, but the numbers that are present on the plateau from 1929 to 1931 could almost be enumerated... [and] few young trees established during the period of 1916–1932. Only the exceptional tree has been able to grow tall enough to get out of reach of the deer during that period.

Merkle (1962) determined that size distribution was irregular in the *Populus tremuloides* of the North Rim, with abundance in the smallest (under 1 m tall) and largest size (over 6 m tall) classes and almost complete absence in intermediate sizes, which Merkle assumed was due to the intense browsing by deer in the 1920s. When Moore and Huffman (2004) examined the ages of trees invading meadows on the Kaibab Plateau, they noted an absence of aspen dating to the 1920s.

We also used other sources of information to develop a more complete picture, determining whether convergent lines of evidence support the overall Kaibab deer story. We examined patterns in

climate, fire regime, livestock populations, logging, and hunting by humans. If the overall story were supported by several lines of evidence, then the Kaibab Plateau could be useful as a combined ecological and sociological case study at the scale of landscapes, centuries, ecosystems, and societies.

METHODS

Background on the Kaibab Plateau

The Kaibab Plateau rises from the desert in northern Arizona, USA, and covers about 1,800 km^2 between about 2,200 and 2,750 m; our assessment of aspen age structure was spread across the 1,300 km^2 within the Kaibab National Forest. Ponderosa pine (*Pinus ponderosa* Dougl ex Laws.) dominates over about half of this area. The rest of the plateau is apportioned almost equally among mixed conifer forests [comprised of spruce (*Picea engelmannii* Parry ex Engelm., *Picea pungens* Engelm.), fir (*Abies concolor* (Gord & Glend.) Lindl. ex Hildebr., *Abies lasiocarpa* (Hook.) Nutt.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)], spruce forests, aspen-dominated forests, and meadows (Joy 2002). Aspen also occurs as a widespread minor component across the plateau, except for the lowest (and driest) ponderosa pine forests to the north.

Human use of the plateau extends back several thousand years. At the time of European settlement in the late 1800s, Ute tribes hunted deer on the plateau annually, in part for deer hides to trade with Navajos (Young 2002). John Wesley Powell and co-workers surveyed the plateau and the surrounding regions in the 1870s, and cattle and sheep began grazing the plateau in the late 1870s and early 1880s. Lang and Stewart (1910) performed a reconnaissance of the plateau to examine its potential for timber and other uses, and they highlighted the evidence of repeated surface fires in developing the open forests of the plateau.

The Grand Canyon Game Preserve was established in 1906, and the federal government prohibited deer hunting. Shooting of predators continued and perhaps increased on behalf of livestock interests; predator reduction programs were not aimed initially at increasing the deer population (Young 2002). Forest Service personnel developed estimates of the deer population almost annually beginning in 1908. Estimated numbers rose from an initial 4,000 to a plateau of 30,000 from 1923 through 1930, followed by a decline to 9,000 by 1940 (Mann 1941). Other estimates were provided by local ranchers; the highest estimate was 100,000 deer in 1924. The Forest Service later concluded (Mann 1941) that its earlier estimates of the deer population from the 1920s ''were far below actual numbers,'' and revised estimates rose to a maximum of 100,000. One Forest Service Ranger (B. Swapp) estimated that the population dropped by 60% from 1924 to 1926, although his peak estimate was 50,000 rather than 100,000 deer. This information was used by Rasmussen (1941) to produce the curve in the classic story (Figure 1) of a 20% annual rate of increase in the deer population from 1904 to 1924, with a peak of 100,000 deer followed by a 60% decline over several years. The Forest Service and Arizona Department of Game and Fish continued to estimate deer populations through the 20th century.

Investigations of Aspen Age Structures

We examined the age of aspen trees in three investigations in the fall of 2002 and summer of 2003. The primary investigation was a plateau-wide descriptive study of the age structure of aspen within the Kaibab National Forest. The secondary investigations were small experimental studies of the age structure in the vicinity of an old ranger station, where hunting dogs were said to have kept deer away, and inside and outside a fenced exclosure established by the Forest Service in 1927.

For the primary investigation, we mapped a 1 × 1 km grid across the Kaibab National Forest portion of the Plateau, and then randomly selected grid numbers for sampling points. Forest attributes were characterized at 21 sampling points, with ten measurement subplots at each point. Five of the subplots were arrayed at 100 m intervals along an eastward transect; five others were arrrayed along a westward transect offset 100 m to the south. All data from the ten subplots were averaged to provide a single representation of the sampling point. At each subplot, we used calibrated wedge prisms to determine the basal area of aspen (1.15 m^2/ha basal area factor) and conifers (4.59 m^2/ha basal area factor, for a description of point sampling with prisms, see Avery and Burkhart 2002). Each aspen included within the prism's range was cored at 1.4 m to determine tree age at that height and at 0.2 m to determine the number of years taken to reach 1.4 m. We expected that aspen trees would need to surpass a height of 1.4 m to escape the major impact of deer browsing; we also expected that the time interval between the lower and upper ages would increase during periods with heavy browsing.

Tree core dates were determined by standard dendrochronological techniques at the Ecological
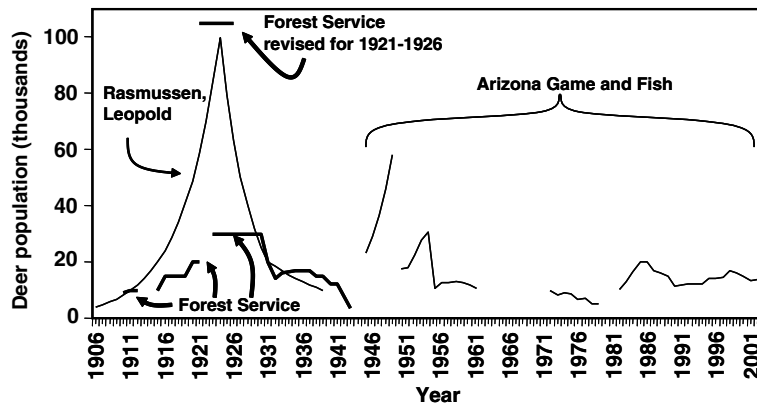
Figure 1. Estimates of the deer population in the 1920s appeared to differ substantially between the pattern preferred by Rasmussen (1941) and Leopold (1943) and those of the forest supervisors. The apparent contradiction had disappeared before Rasmussen and Leopold published their estimates, as Forest Supervisor Walter Mann (1931, 1941) revised the forest supervisor estimates to more than 100,000 in the mid 1920s. Deer populations showed a second peak in the early 1950s (Russo 1964) and have ranged between 5,000 and 20,000 since then (Barlow and McCulloch 1984; J. Goodwin, personal communication).

Restoration Institute at Northern Arizona University. The age of the cores was determined mainly by crossdating with marker years (notable years were 1996, 1977, 1976, 1971, 1961, 1956, 1951, 1934, 1904, 1902, 1899, 1896, 1880, 1879, 1864, 1847, 1845, and 1836). About three-fourths of the trees were cross-datable, and most of those lacking good marker years were younger than 1970. Ring counts and counts corrected by marker years were within 3–5 years on cores more than 150 years old, so we are confident that all ages are accurate within about 3–5 years (and most are precise to a single year).

The data set provided an estimate of the age structure of aspen currently found on the plateau. We expected that the average pattern would be an exponentially declining number of trees with increasing age, reflecting a null expectation of constant rate of recruitment and a constant proportional rate of mortality through time. We estimated this null expectation by fitting a line to the $\log_{10}$ of tree numbers per km^2 for 5-year age classes of aspen. Periods that deviated by more than one standard error (SE) from this general trend would be considered ''not normal,'' and probably driven by special factors that did not apply in general over the time course. We tested whether more time was required for trees to grow from 0.2 to 1.4 m in height during periods with few aspen trees by comparing these periods versus all other periods with a t-test (with unequal variances).

One of the secondary investigations was prompted by a small article in a 1935 edition of *Grand Canyon Nature Notes:* ''In marked contrast

to . . . the Kaibab Forest, one finds rather extensive reproduction of aspen in the vicinity of the Quaking Aspen Ranger Station. . . Here a number of hounds are kept and, of course, no deer come near'' (McHenry 1935). The cabin was built circa 1910 and was used intermittently by Forest Service rangers until the mid-1920s, when E. Vaughn obtained a special use permit to live there. She expanded the water source at the site, built an additional cabin and corral, and kept hunting dogs until the early 1940s (J. Vaughn and D. Lund, personal communication). We relocated the site of this station and placed three prism plots (which encompassed 38 trees) at random within the aspen stand that bordered the meadow. If the age structure of this stand showed substantial recruitment during periods of low recruitment across the plateau, we would infer that deer played a major role in aspen recruitment (rather than other plateau-wide factors).

The other secondary investigation included relocating a small (8 × 8 m) exclosure established in 1927 (Bostick 1949). The original study included 41 pairs of plots (fenced and nearby unfenced) established between 1925 and 1927, with about 15 pairs within the range of aspen on the plateau. Assessments of the plots in the 1930s and 1940s concluded that ''all (fenced) plots showed recovery'' (Russo 1964). Using a set of photos taken in 1930, 1942, and 1948, we relocated one of these exclosure sites (plot 28) near Dry Park. The designated unfenced plot was about 10 m distant from the fence. We determined the size, number, and age of all trees in the fenced plot and the unfenced plot.
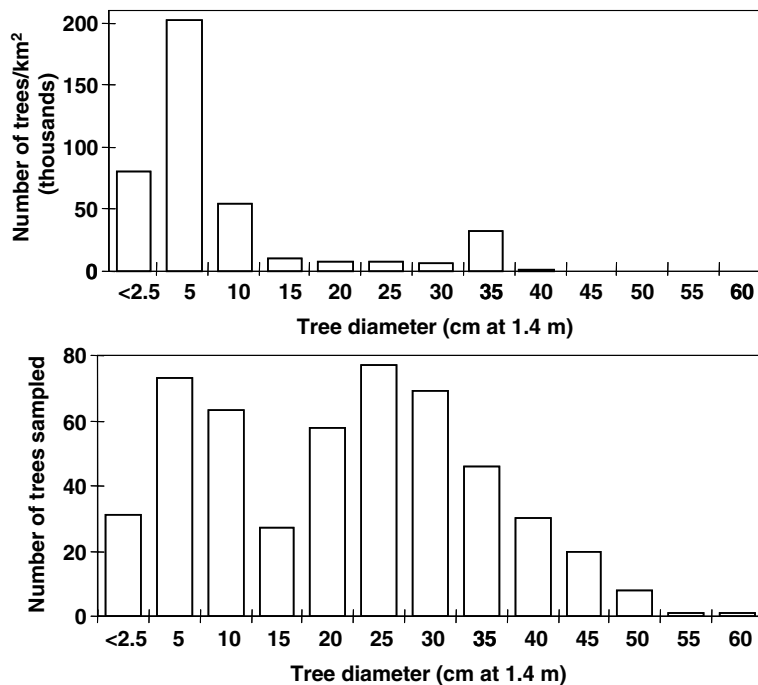
Figure 2. Size distribution of aspen on the Kaibab Plateau (*upper*) and size distribution of aspen trees sampled in the prism plots.

Similar to the secondary study at Quaking Aspen Springs, we expected that aspen inside the exclosure would have an age structure that included stems from periods when recruitment was rare across the landscape.

Finally, we considered the broader context of potential drivers of aspen recruitment. We examined the possible role of climate as a driver of the age structure of aspen by relating age structure to (a) ring-width chronologies for 15 of the oldest aspens in our sample, (b) a ponderosa pine ring-width chronology from the same area, (c) precipitation measures from the South Rim of the Grand Canyon National Park, and (d) Palmer drought severity indices (PDSI) derived from Cook and others (1999) for the North Kaibab area. We used published and archived records to explore the potential aspen impacts of altered fire regime (Fulé and other 2002, 2003), livestock populations (Lang and Stewart 1910; Mann 1931; 1941; Bostick 1949), deer populations (Kimball and Watkins 1951; Russo 1964; Barlow and McCulloch 1984; and unpublished records from the Arizona Game and Fish Department, J. Goodwin, personal communication) and logging (Sesnie and Bailey 2003).

RESULTS

Primary Descriptive Investigation

The basal area of aspen averaged 2.9 m^2/ha (SE among 21 sample points = 0.5), comprising 14% of the total forest basal area of 20.5 m^2/ha (SE = 1.2). Aspen basal area did not correlate with conifer basal area ($P = 0.5$). Aspen were widespread across the plateau; only one of the 21 sample points had no aspen, and more than half of all subplots had at least one aspen stem. The size distribution of trees declined exponentially with increasing tree diameter (Figure 2). If age structure had been determined based on fixed-area sampling plots, our representation of ages would have been heavily weighted by the abundance of young, small-diameter stems. The prism approach resulted in a more even distribution of sample trees by size class, rather than by number of stems/ha (Figure 2).

The maximum age of sampled aspens was more than 200 years, and tree diameter related moderately well to tree age (Figure 3). Many trees larger than 20 cm in diameter had decayed heartwood, preventing age determination. Three-fourths of the trees less than 15 cm diameter (average age, 50 years) were solid and datable, but up to three-fourths of the trees greater than 35 cm diameter (average age, 130 years) had rotten interiors. Our analyses of the age class distributions of trees is based only on the datable trees; the actual number of trees by age class would be higher (especially in larger size classes) than number of datable trees, but this would not bias our evaluation of periods with unusually large (or small) numbers of aspen.

The age structure of aspen on the Kaibab Plateau generally followed a typical pattern for all-aged forests, with number of trees decreasing exponen-
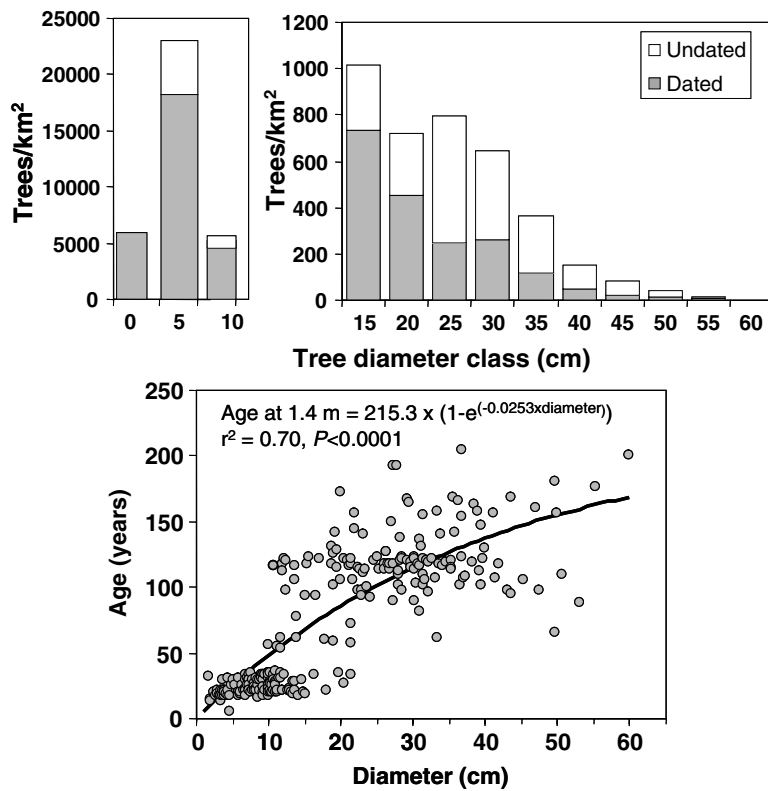
Figure 3. Number of trees per km^2 (*upper*); trees with rotten interiors were not datable and comprised about 10–40% of trees less than 20 cm in diameter and 50–80% of trees larger than 20 cm. The relationship between diameter and age (*bottom*) was highly significant, but there was high variation within diameter classes.

tially with age (Figure 4). However, two periods had substantially more aspen than expected: 1877–1886 and 1967–1992. The numbers of aspen dating from these periods were more than an order of magnitude greater than expected from the long-term trend. Two other periods showed lower than expected numbers of aspen. The number of aspen was more than an order of magnitude lower than the null expectation from 1913 to 1937, with the exception of 1923–1927, when numbers of aspen reached just 25% of the long-term trend. The second major period with significantly fewer than expected aspen was 1953–1962; none of our 234 cores dated to this period.

Across all periods, aspen required an average of 5.0 years to grow from 0.2 to 1.4 m (Figure 5). The intervals differed strongly among periods, with significantly longer periods for the 1920s and 1930s than for other periods (no trees were encountered for the 1950s). During this period with few aspen trees, trees that reached the height of 1.4 m (and survived to the present) were already several decades old at 0.2 m. The success of these few old trees may have depended on the accumulation of carbohydrate reserves to support a rapid height increase beyond the reach of deer, or an age-related decline in the palatability of shoots to deer.
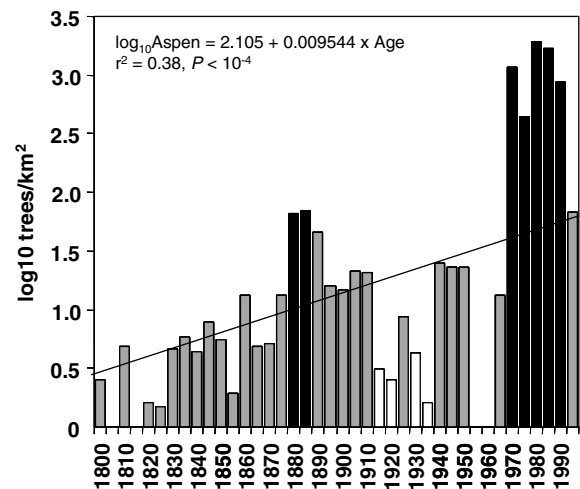

Figure 4. Density of aspen in the North Kaibab Ranger District by 5-year classes. *Black bars* indicate numbers more than one Standard error (SE) above the long-term average; *open bars* (as well as the absent bars from 1953–1962) indicate numbers more than one SE below the average.

Secondary Experimental Investigations

The pure aspen stand near the site of the former Quaking Aspen Ranger Station was largely consistent with the aspen age structure across the pla-
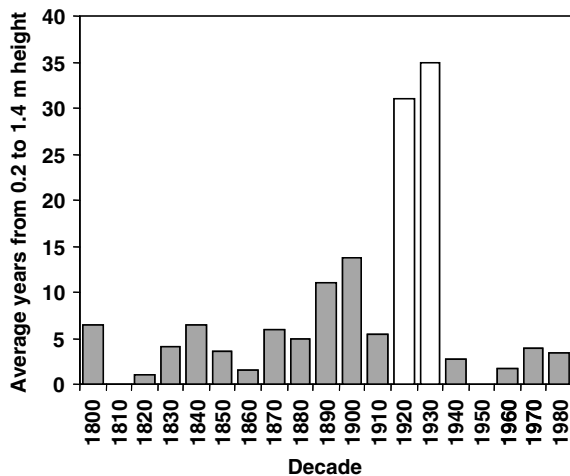
Figure 5. The number of years between stem age at 0.2 and 1.4 m averaged 5.0 for all periods other than 1920s and 1930s (no trees encountered for the 1950s), when the only successful recruitment (and survival to the present) occurred on trees older than 30 years at 0.2 m (periods with *white bars* differ from solid bars at *P* < 0.02).

teau, with no aspen trees dating from the 1920s, or from 1953 to 1962 (Figure 6). However, the high density of trees from the 1930s is anomalous relative to the plateau at large, and is consistent with expectations of hunting dogs keeping deer away from the mid-1920s through the early 1940s.

The exclosure showed rapid proliferation of aspen after fencing in 1925 (Figures 6 and 7), but no aspen established outside the fence between 1910 and 1960. Records taken in 1930, 1942, and 1948 also indicated substantially more conifer reproduction inside the fence than outside. Field notes from 1928 stated that outside the fence "aspen regeneration is 90% utilized." These impacts of deer browsing had a strong legacy over the next five decades. In 2003, the fenced plot had the equivalent of 3,570 aspen/ha (average diameter, 14.6 cm; basal area, 60.2 m^2/ha), along with 6,010 spruce/ha (average diameter, 13.1 cm; basal area, 80.7 m^2/ha). The unfenced control plot had the equivalent of 780 aspen/ha (average diameter 6.2 cm; basal area, 2.2 m^2/ha) and 5,760 spruce/ha (average diameter, 8.1 cm; basal area, 29.5 m^2/ha). Interestingly, substantial recruitment occurred within the exclosure in the 1950s, a period with very little aspen establishment across the plateau.

DISCUSSION

The age structure of aspen forests on the Kaibab Plateau supported the classic story of extremely

high deer populations in the 1920s, Many fewer aspen date to the 1920s, when the deer irruption was reported (Figure 4), relative to the long-term pattern in aspen numbers. The only successful aspen recruitment during this period was found in areas protected from deer by fences or dogs, along with a few decades-old trees that managed to grow tall enough to escape deer browse. The age structure also had three other anomalous periods: dramatically higher numbers of aspen in the 1880s/1890s and from 1968 to 1992, and very low numbers from 1952 to 1963. We cannot demonstrate cause-and-effect relationships in this historical pattern, but we can examine the timelines of potential driving factors of climatic variation, fire regimes, livestock and deer populations, and logging for consistency with each of the anomalous periods.

Climatic Variation

Climate variations did not appear to have a major influence on the age structure of aspen on the Kaibab Plateau. Based on 5-year classes, the pine ring-width chronology (Figure 8) correlated well with the drought index (r^2 = 0.45, P < 10^{-5}), but the correlation of drought with the aspen chronology was weak (r^2 = 0.10, P = 0.07). This may reflect a greater sensitivity of annual pine increment to climate; the coefficient of variation in average (5-year) ring widths was 22% for pines and just 14% for aspen. The pine chronology also related better to the annual precipitation recorded on the South Rim of the Grand Canyon (r^2 = 0.27, P = 0.03) than did the aspen chronology (r^2 = 0.00, P = 0.88). The pine chronology showed markedly stressful conditions for 1873–1884, and 1893–1897 and a prolonged, mildly stressful period from 1943 to 1972. Favorable conditions for pine lasted from 1863 to 1867, 1903 to 1912, 1933 to 1937, and 1973 to 1982. The aspen ring-width chronology indicated stressful conditions from 1800 through 1822 (except for a better period from 1808 to 1812), from 1853 to 1862, and from 1873 to 1882, and 1973 to 1982. Periods with favorable conditions were 1823–1832, 1887–1892, and 1958–1972.

The anomalously high number of aspen from the 1880s and 1890s included periods of both low and high ring-width increments for aspen and pine. From 1915 through the 1930s, the low numbers of aspen trees corresponded to a prolonged period of average climatic conditions based on the aspen and pine chronologies and the measured precipitation. The increase of aspen in the 1880s and 1890s
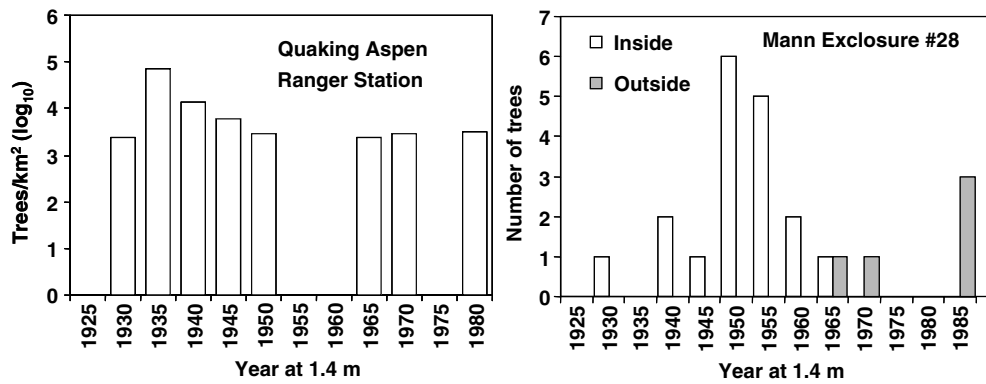
Figure 6. The age structure for aspen at the former site (*left*) of the Quaking Aspen Ranger Station (where hunting dogs were said to have kept deer away) showed abundant aspen from the 1930s through the early 1950s, but no stems dated from the 1920s or from 1953–1962. Aspen recruitment was strong inside the 8 × 8 m exclosure (see Figure 7), particularly in the 1950s when recruitment was extremely low across the plateau; recruitment was absent in the open plot outside the exclosure until the 1960s.
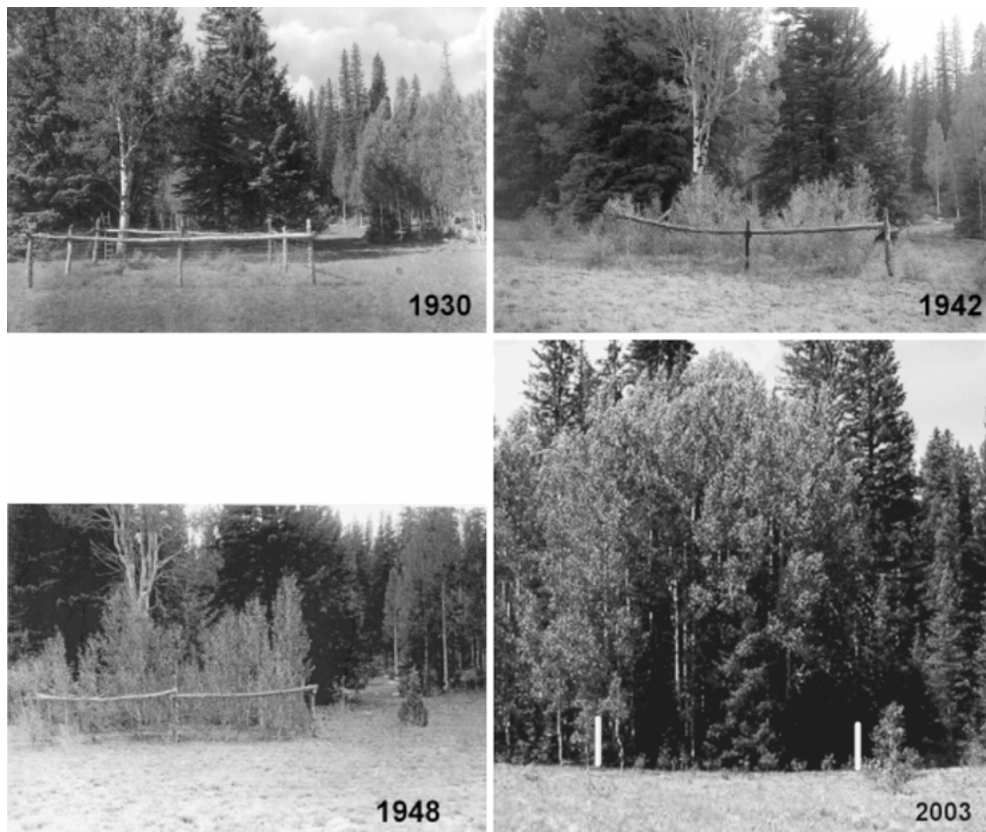

Figure 7. Aspen established in plot 28 shortly after fencing of the exclosure in 1927, with the tallest trees reaching 1.4 m in the 1930s and exceeding 4 m by the end of the 1940s. *White bars* in 2003 indicate location of original corner posts. (Historical photos from archives at the North Kaibab Ranger District; 2003 photo by D. Binkley). For a pictures of Leopold observing this exclosure, see Ripple and Beschta 2005.

showed no clear relationship to climate stress, and the dearth of aspen from 1915 through the 1930s was unrelated to climatic stress.

Fire Regime

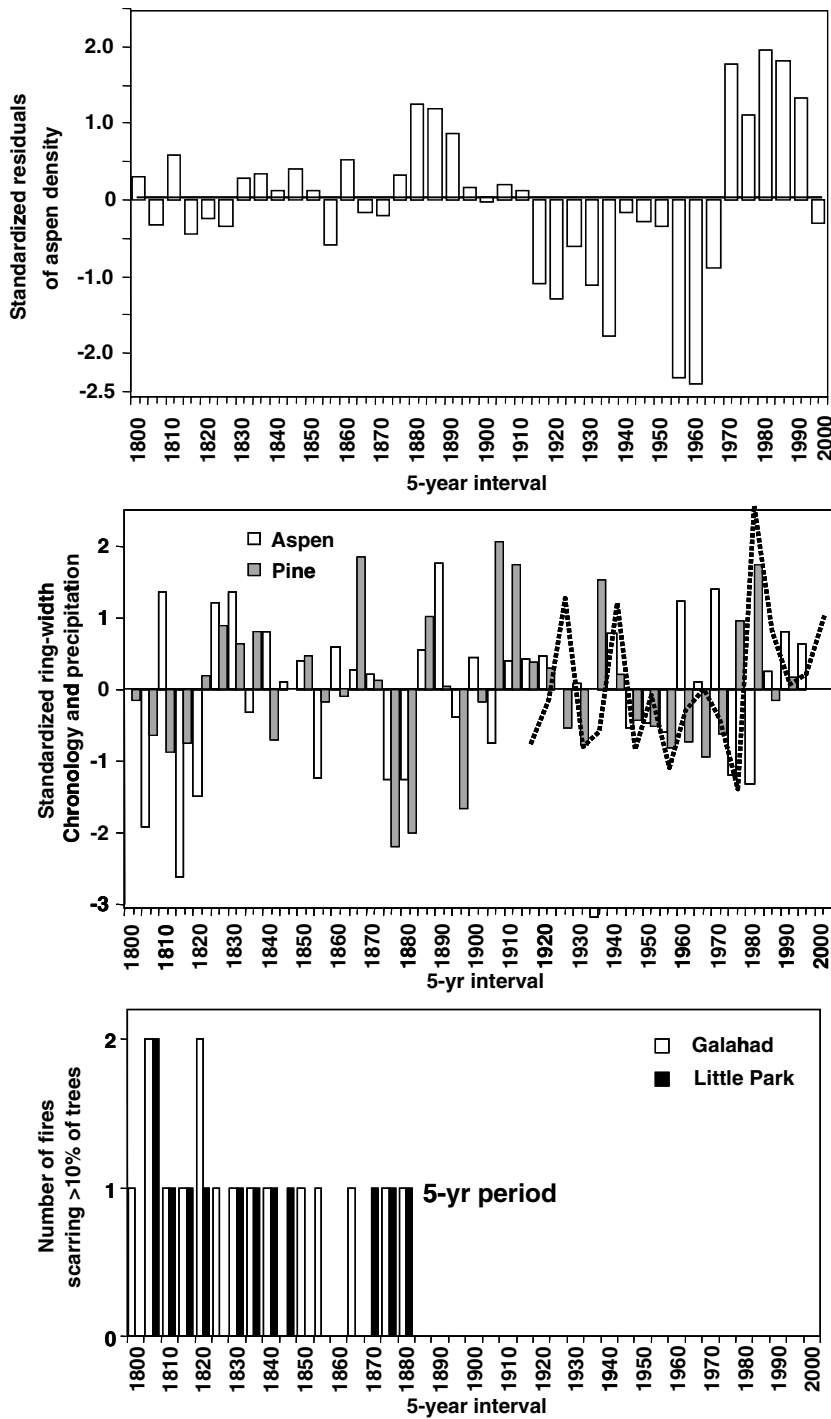A change in the fire regime appears to be a likely driver of the increase in aspen in the 1880s and

Figure 8. Standardized residuals of the long-term trend in aspen age structure (*top graph*; derived from Figure 4) did not correspond to climate stress as indexed by conifer-ring width (*bars*) or precipitation (*dashed lines*; *middle graph*), but aspen number increased by more than an order of magnitude following cessation of the surface fire regime (*bottom graph*; based on data from Fulé and others 2003) in 1880.

1890s. Prior to 1880, frequent, low-intensity fires were routine on Kaibab Plateau (Fulé and others 2002, 2003). Reconstructions of fire history from fire-scarred trees within the adjacent Grand Canyon National Park indicate that fires burned on average every 4–8 years until 1880, when fires essentially ceased (Figure 8). The change in fire regime likely resulted from a reduction in fine fuels with the onset of livestock grazing (Fulé and others 2003). The timing of the cessation of fire corresponded to the ten-fold increase in number of aspens relative to the long-term trend. Although some authors have suggested that a reduction in fires would decrease aspen (Mitchell and Freeman 1993), this insight from infrequent, stand-replacing fires (Schier 1975) probably does not apply to the

frequent surface fires that were characteristic of the Kaibab Plateau. Aspen shoots less than 5 or 10 years old would have high mortality rates from surface fires. We expect that the proximal cause of the increase in aspen in the 1880s/1890s was the cessation of fires, and the ultimate cause was livestock grazing that altered the fire regime. The increase in small aspen stems would have dramatically increased the forage supply for deer as an indirect result of change in fire regime brought about by livestock grazing. Fires were absent from most of the plateau through the 20th century, so any of the later anomalies in the aspen age structure would not be driven by the fire regime.

Livestock Populations

Livestock herbivory appears to explain none of the anomalies in aspen numbers. Caughley (1970) suggested that an increase in the deer population in the early 1900s could have resulted from an increased availability of forage for deer following reductions in sheep numbers from 200,000 in 1889 to 5,000 in 1908, citing Russo (1964) as his source. Botkin (1990) cited Rasmussen (1941) and Caughley (1970) as stating that there were 200,000 sheep and 20,000 cattle on the plateau in 1889, with declines to 5,000 sheep and few cattle by 1908. The citation of these numbers was mistaken. Russo (1964; compare Mitchell and Freeman 1993) quoted the original source of these livestock estimates correctly: ''It is reported that in 1887 and 1889 at least 200,000 sheep and 20,000 cattle were using the range in the surrounding desert country and the Kaibab Mountain'' (Mann 1931, 1941). These values were regional estimates, not local numbers for the Kaibab Plateau. Mann (1931, 1941) also stated: ''The earliest indicated extensive use of the Kaibab Plateau for livestock is in 1885 and 1886 when about 2,000 cattle were placed there.''

No records are available of the number of livestock on the plateau from 1880 to 1906 (Bostick 1949). Cattle numbers increased from about 9,000 in 1906 to a peak of over 15,000 in 1913 (contrary to Botkin's characterization of ''few cattle'' after the turn of the century), declining to 7,000 to 10,000 through the mid-1920s, then dropping below 5,000 and remaining at that level (Mann 1941). Estimates of sheep numbers dropped from an initial 20,000 (''not very accurate,'' Mann 1941) to 5,000 by 1910, followed by a steady decline through the 1940s. In fact, sheep use was largely restricted to the northern end of the plateau by the early 1900s (Lang and Stewart 1910), below the

elevational range where most aspen are found. The classic story of the deer irruption (Figure 1) coincided with sustained high use of the plateau by cattle (the early phase of the deer irruption was accompanied by a 50% increase in cattle grazing) and with the elimination of sheep. The suggested period of high herbivory and competition between livestock (especially sheep) and deer (1880s and 1890s, Caughley 1970) coincided with a major increase in aspen numbers (and therefore food supply for deer). Although the livestock estimates are not precise or certain, substantial reductions in competition with livestock are unlikely to explain the irruption of deer, because the deer food supply was anomalously high during the pre-irruption period.

Deer Populations

The high estimates of deer population in the 1920s and late 1940s/early 1950s (Figure 1) coincided with periods of very low numbers of aspen. Estimates of the actual size of deer populations in the 1920s were highly variable, but the presence of very high numbers of deer in the 1920s was uniformly endorsed (Mann 1931, 1941; Rasmussen 1941; Young 2002). The Kaibab Forest Supervisor, Walter Mann, thought that the estimates improved from 1930 onward, and he revised earlier Forest Service estimates from their maximum values of 30,000 deer to ''probably more than 100,000 deer during 6 six years'' (1921–1926). A second irruption was reported in the late 1940s, when the deer population increased from 21,000 in 1945 to 57,000 in 1949 (Kimball and Watkins 1951, cited in Russo 1964). Russo's (1964) population estimates began with just 17,000 deer in 1950 [only one-third of the estimate by Kimball and Watkins [1951], although no mention is made of any major die-off], rising to 27,000 in 1953–1954 and followed by a die-off during the winter of 1954–1955 that reduced the herd to fewer than 10,000. Later population estimates reached a low of 5,000 in the late 1970s (Barlow and McCulloch 1984), with upper limits of 20,000 in the mid 1980s.

Did deer herbivory play a role in the development of the age structure of aspen on the Kaibab Plateau? The order-of-magnitude drop in aspen numbers for the 1920s coincided with the classic story of the first deer irruption. The paucity of aspen supports the idea of the deer irruption, but it does not directly confirm it. Our confidence in a causal connection is increased by the age distributions we found around the site of the Quaking Aspen Ranger Station (where hunting dogs were said to keep deer away) and in the exclosures
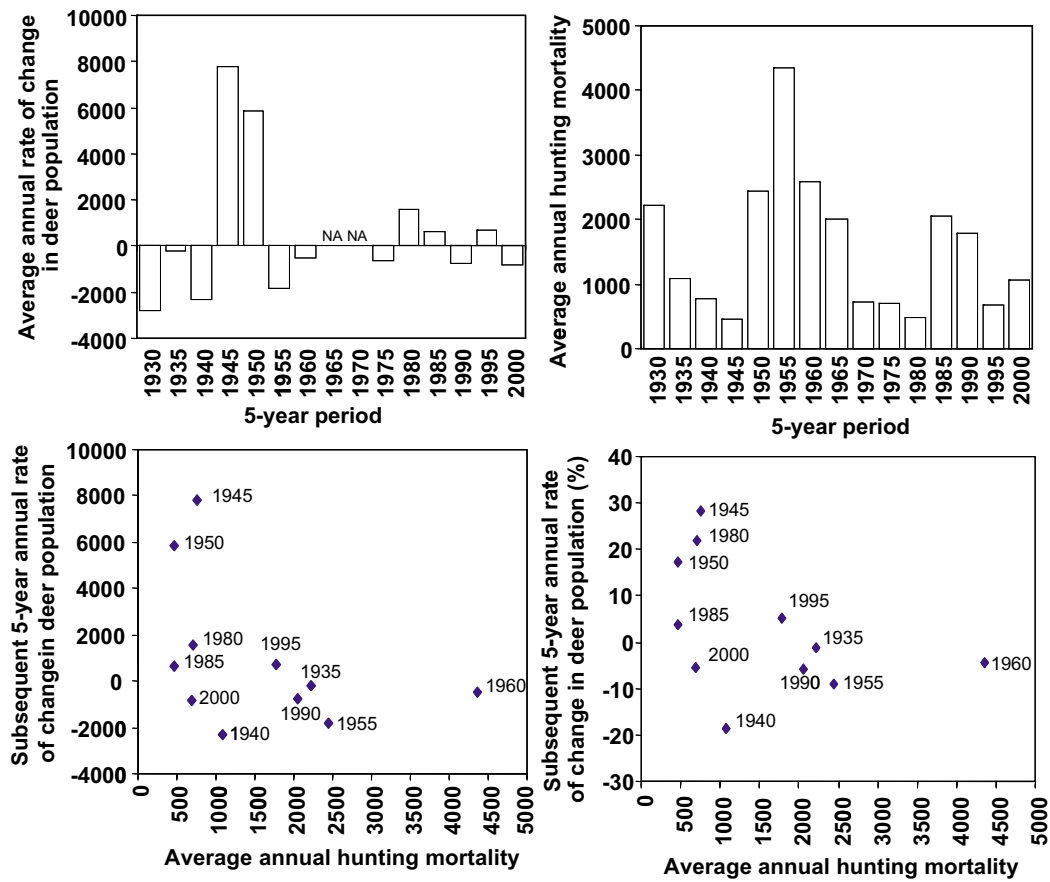
Figure 9. The second irruption of the deer population in the late 1940s (*top left*) followed a period of sustained predator control and low hunting (*top right*). The average rates of increase in deer populations exceeded 5,000/y (*bottom left*) and 15%/y (*bottom right*) only in periods following low deer mortality from hunting. Not all periods with low hunting were followed by rapid increases in deer population (Russo 1964; J. Goodwin, personal communication).

established in 1927. The near-absence of aspen in the 1950s after the second deer irruption was again consistent with the major role of deer herbivory in regulating aspen regeneration.

The abundance of aspen recruitment in the 1880s and 1890s is strong evidence that the deer population was not limited by food (bottom-up control of the food web). The near-absence of aspen recruitment in the 1920s (and into the 1930s) would be consistent with a food limitation when deer populations were high. Was the deer irruption in the 1920s driven by a reduction in predation (release from top-down control)? The combined absence of hunting by humans and the active predator control program were unprecedented, and the shift into a food-limited condition is consistent with this idea. We note that aspen recruitment was also lower than expected inside the adjacent national park during this period (Fulé and others 2002, 2003) (Figure 9), even though predators were not intentionally controlled within the park

(Young 2002). However, hunting by humans was prohibited for deer, but continued for predators; predator hunters ventured regularly into the park into the 1930s (J. Vaughn and D. Lund, personal communication). The irruption of deer within the National Forest may also have spilled over into the park, swamping the capacity of the remaining predators to control the deer population (as noted by Thompson 1934).

Was the food-production capacity of the plateau reduced in the aftermath of the deer irruption in the 1920s? Reports from the USDA Forest Service clearly indicate that recovery began rapidly in the 1930s. Typical excerpts from the annual range condition reports (summarized in Mann 1941) include:

1926: Browse on west side made very little growth.
1927: Favorable conditions for plant growth. . . . Damage to all conifer reproduction and aspen cliff rose [*Purshia mexicana* (D. Don) Henrickson], and all other browse plants is extensive.
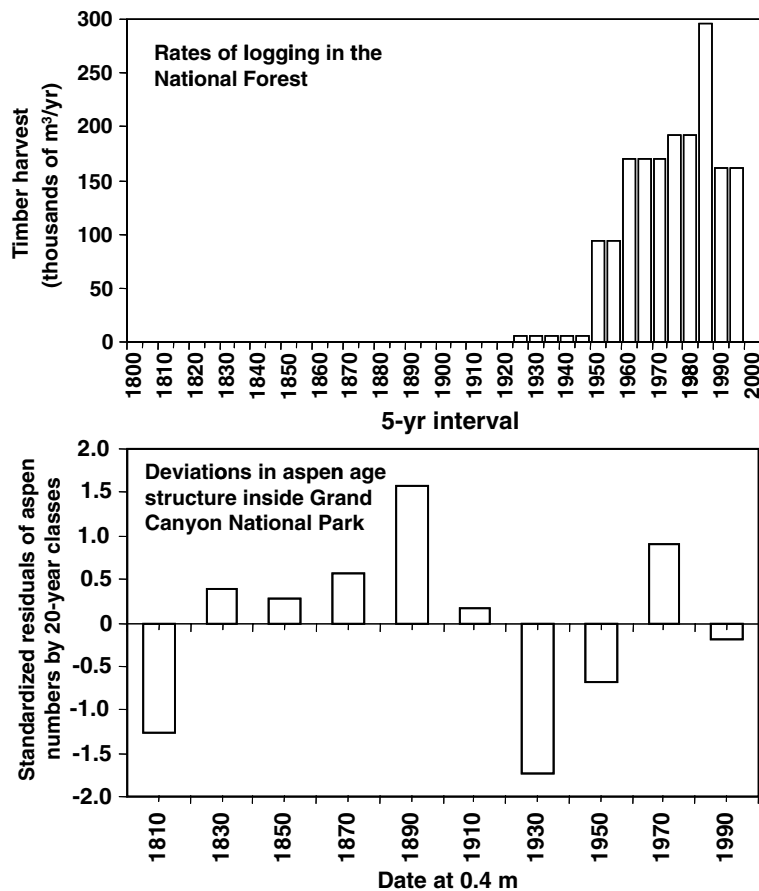
Figure 10. The massive increase in logging in the mid-1960s (*top*) [Sesnie and Bailey 2003] corresponded with the order-of-magnitude increase in aspen (Figure 8). No logging occurred in the national park during this period, and the number of aspen for 1960–1980 was just 75% greater than the long-term average (Fulé and others 2003), in contrast to more than an order-of-magnitude increase inside the National Forest.

1929: West side range is so extensively killed out as to browse that it does not make a good growth even in favorable years.
1931: Aspen sprouts not eaten as closely as formerly. On the west side one inch of annual growth of cliff rose had been left uneaten, in some places 2 inches.
1932: Cliff rose made wonderful growth.
1933: Aspen sprouts were more vigorous than ever before and were showing recovery. All brush plants recovering. Deer fat at hunting time.

The dramatic turnaround in 1931 was attributed to a 50% die-off of the deer herd in the winter of 1930–1931. By 1935, the condition of the range appeared to have improved so much that the Forest Service increased the number of cattle permitted on the plateau (Bostick 1949). The notations about the survival of aspen sprouts in the 1930s were corroborated by the subsequent recruitment of aspen stems (more than 1.4 m tall) in the 1940s. Given that no major erosion followed the high grazing (only some back-cutting of gullies was noted, Bostick 1949), and that the vegetation recovery in

the 1930s was rapid once the deer population dropped below 20,000, there is no evidence to support a long-term degradation of deer habitat or carrying capacity.

Did predation play a major role in the dynamics of the deer population after 1930? Predator control continued, including hunting of cougars (*Felis concolor*) and trapping of coyotes (*Canis latrans*) through the 1940s. Efforts intensified in the 1950s and 1960s, with widespread, repeated use of poison baits (Russo 1964, poisoned baits were used once in the 1920s, but discontinued after the deaths of several valuable hunting dogs). Hunting by humans removed an average of 1,600 deer/y after 1930, with a range from 250/y (450/y on a 5-year average basis, Figure 9) to 8,000/y (4,800/y on a 5-year average basis). The largest increase in deer population after 1930 was between 1943 and 1952, with growth rates exceeding 5,000 deer/y and 15%/y. One other period (1978–1983) had growth rates exceeding 15%/y for 5 years, but the actual rate of growth was relatively low (1,600 deer/y) owing to the low initial population at the beginning of the period. The 5-year periods of rapid increase in deer all followed 5-year periods of low hunting

mortality (one-quarter to one-half of the long-term average, Figure 9), consistent with the idea that low rates of predation (by humans in this case) enabled the deer population to irrupt. Two other periods also had low hunting mortality (1983–1988, 1998–2002) but no major increases in deer population; both of these periods occurred after the intensive predator control ceased and when the deer population was quite low. Overall, the two major irruptions of the deer population in the 20th century followed periods of major reductions in predation.

Logging

Minor logging occurred on the plateau from the late 1800s through World War II (Sesnie and Bailey 2003), followed by increasing commercial harvests through the late 1980s (Figure 10). Most of this logging was based on the selection of individual trees, typically greater than 50 cm in diameter (D. Lund, personal communication), and the extensive logging was supported by a dense network of roads (few areas of the plateau are more than 1 km from roads). As logging increased to more than 150,000 m^3/y in the 1960s, the use of seed-tree harvest regimes increased, and only a few large trees/ha were retained. The peak in logging occurred from 1983 through 1987, when almost 300,000 m^3/y were removed. Harvests dropped by about half into the early 1990s and then fell dramatically as the mill that processed most of the logs closed and logging was curtailed because of goshawk (*Accipiter gentilis*) habitat issues (Reynolds and others 1992).

The cutting of dominant conifer trees, as well as disturbance of the soil during logging, would be expected to increase the regeneration of aspen (Shepperd and others 2001). Aspen numbers were more than an order of magnitude above the long-term trend from 1963 through 1992 (Figure 4), likely as a result of logging. This inference is supported by the age structure of aspen across the boundary in Grand Canyon National Park, where logging did not occur and aspen numbers did not differ from the long-term expectation (Figure 10).

Remaining Uncertainties

Our aspen data and summary of historical documents show that many aspects of the classic Kaibab deer story remain uncertain. The overall trends in deer population were probably robust, although the actual magnitudes remain imprecise. The general trend of declining forage production (for both deer and cattle) through the 1920s was noted consistently among all observers at the time, as was the strong recovery in the 1930s. The dramatic change in fire regime in the 1880s was abrupt and widespread, leaving very little uncertainty about fire; however, the contribution of the absence of fire to the order-of-magnitude increase in aspen recruitment in the 1880s remains an inference rather than an experimental determination.

The available information also leaves gaps in the complete ecosystem story. For example, several of the historical reports make passing comments about the impacts of rodent grazing, such as this note from 1922 (in Bostick 1949):

> There are no extensive areas infested with rodents but it has been noted that pocket gophers [*Thomomys talpoides*] and ground squirrels [*Spermophilus lateralis*] are on the increase in V.T. Park and other parks along the highway. . . If allowed to increase, these rodents will seriously affect the amount of forage in these parks.

Another note from the 1930s stated: ''The ground squirrel, especially, is abundant at the edge of meadows, enough so as to exercise considerable pressure on plant growth'' (in Rasmussen 1941).

One might ask how much of the vegetation story on the plateau was influenced by the dynamics in populations of rodents, and what the impacts of predator control (especially coyotes and raptors) might have been on the rodent populations. However, unfortunately, no rodent exclosure studies were undertaken, and we do not know if rodents substantially affected long-term vegetation patterns.

Conclusions

The classic story of the Kaibab deer popularized by Aldo Leopold in the 1940s was criticized in the 1970s for making selective use of the available information (compare Caughley 1970; Burk 1973; Colinvaux 1973). Unfortunately, these critiques did not take advantage of the rich vein of information available from vegetation surveys, fenced exclosures, and revised deer population estimates. Although population estimates were crude and variable, the broad range of evidence was consistent with a major deer irruption in the late 1910s through the 1920s. The age structure of aspen adds another line of convergent evidence that supports the deer irruption. However, the rapid recovery of aspen recruitment after the deer population dropped below 20,000 in 1930 did not provide evidence for any general, long-term habitat degradation due to the irruption.

We conclude that Caughley's (1970) hypothesis about the reduction of livestock/deer competition as a driver of the irruption is refuted, based on the misquotation of livestock numbers and the unlikely food limitation when aspen recruitment increased more than an order of magnitude above background rates.

This aspen increase in the late 19th century coincided with the cessation of frequent surface fires across the Kaibab Plateau (Fulé and others 2002, 2003), and we expect the lack of fire greatly enhanced the survival of aspen shoots. The dramatic increase in aspen recruitment in the late 20th century probably resulted from widespread logging on the plateau. These patterns and processes may have two important implications for the future. Restoring this historic surface fire regime would likely reduce aspen recruitment. Similarly, 50-years of logging in the late 20th century led to a ten-fold increase in aspen recruitment, and lower rates of logging in the future would likely promote less aspen recruitment than in the late 20th century. The combination of more frequent fire and low rates of logging could dramatically decrease aspen recruitment, but this reduction may represent a return to historic levels rather than an unprecedented loss of aspen.

The complexity of this story demonstrates the challenge of identifying controls on food webs at a scale of 1,000 km^2 and 10–100 years. Historical evidence may enable some potential driving factors to be excluded. Year-to-year variations in precipitation had short-term effects on plant production (as noted in historical documents), and years with large (and early) snowpacks tended to have high rates of deer mortality, but climate showed no clear influence on the recruitment of aspen. Similarly, large increases in aspen recruitment in the 1880s refuted the idea that competition with livestock would have kept deer populations artificially low. Available evidence may support the importance of driving factors, but uncertainty about causality remains. The evidence for deer irruptions following periods of reduced predation was consistent for both the 1920s and the 1940s, supporting the idea that predation limits the density of low deer populations, and food limits deer populations (and the absence of aspen recruitment) at high populations. However, this consistent pattern cannot prove which factors control the food web. Our results combine with other case studies (for example, Gasaway and others 1992; Krebs and others 2003; Ripple and Beschta 2003, 2004) to indicate that top-down control of food webs is probably not unusual in terrestrial ecosystems.

As with many case studies of ecology, wildlife, and land management, the Kaibab deer story did not end when Leopold popularized his version. The fire regime remained outside the range of historical variation, predator control continued (and intensified with the use of poison baits), and hunting by humans became a major mortality factor for deer. The second irruption of deer in the 1940s followed a period of low predation (hunting) by humans, consistent with the predation mechanism in the earlier story. Some uncertainty remains concerning some of the details of the classic story, but this level of ambiguity is common in almost all cases involving population ecology, land management, and people (Young 2000, 2002). We suggest that this uncertainty is an asset in educating students about the nature of case studies as tests of ecological ideas and propose that the complete Kaibab deer story (and the history of the story) be reinstated in ecology textbooks.

ACKNOWLEDGEMENTS

REFERENCES

Adams CC. 1925. The conservation of predatory mammals. J Mammal 6:83–96.

Avery TC, Burkhart H. 2002. Forest measurements. New York: McGraw-Hill.

Barlow J, McCulloch CY. 1984. Recent dynamics and mortality rates of the Kaibab deer herd. Can J Zool 62:1805–12.

Bostick VB. 1949. North Kaibab deer–livestock forage relationship study. Progress report (15 September, 1949), USDA Forest Services, Fredonia, Arizona.

Botkin D. 1990. Discordant harmonies: a new ecology for the twenty-first century. New York: Oxford University Press.

Burk JC. 1973. The Kaibab deer incident: a long persisting myth. BioScience 9:43–7.

Carson R. 1962. Silent spring. Boston: Houghton-Mifflin.

Caughley G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51:53–71.

Colinvaux P. 1973, 1986. Introduction to ecology. New York: Wiley.

Cook ER, Meko DM, Stahle DW, Cleaveland MK. 1999. Drought reconstructions for the continental United States. J Clim 12:1145–62.

Dasman RF. 1964. Wildlife biology. New York: Wiley.

Dunlap TR. 1988. That Kaibab myth. J For Hist 31:60–8.

Elton C. 1927. Animal ecology. New York: Macmillan.

Fulé PZ, Covington WW, Moore MM, Heinlein TA, Waltz AEM. 2002. Natural variability in forests of the Grand Canyon, USA. J Biogeogr 29:21–47.

Fulé PZ, Crouse JE, Heinlein TA, Moore MM, Covington WW, Verkamp G. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. Landscape Ecol 18:465–86.

Gasaway WC, Boertje RD, Grangaard DV, Kelleyhouse DG, Stephenson RO, Larsen DG. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monogr 120:1–59.

Grey Z. 1924. The deer stalker. New York: Harper.

Hungerford CR. 1970. Response of Kaibab mule deer to management of summer range. J Wildlife Manage 34:852–62.

Joy SM. 2002. Northern goshawk habitat on the Kaibab National Forest in Arizona: factors affecting nest locations and territory quality [dissertation]. Fort Collins (CO): Colorado State University.

Kimball TL, Watkins AG. 1951. The Kaibab North cooperative deer–livestock forage relationship study. Phoenix (AZ): Arizona Game and Fish Commission.

Kormandy EJ. 1969. Concepts of ecology. Englewood Cliffs (MJ): Prentice-Hall.

Krebs CJ. 2001. Ecology: the experimental analysis of distribution and abundance. San Francisco: Benjamin Cummings.

Krebs CJ, Danell K, Angerbjorn A, Agrell J, Berteaux D, Brathen KA, Danell O, and others. 2003Terrestrial trophic dynamics in the Canadian ArcticCan J Zool8182743.

Lang DM, Stewart SS. 1910. Reconnaissance of the Kaibab National Forest. On file at North Kaibab Ranger District, Kaibab National Forest, Fredonia, Arizona.

Leopold A. 1943. Deer irruptions. Wisc Conserv Bull 8:3–11.

Mann WG. 1931, 1941. The Kaibab deer: a brief history and present plan of management. USDA Forest Service, Kaibab National Forest, Fredonia, Arizona (original 1931 report amended 1934 and 1941).

McHenry DE. 1935. Quaking aspen — its future in the park. Grand Canyon Nat Notes 9:361–5.

Merkle J. 1962. Plant communities of the Grand Canyon area, Arizona. Ecology 43:698–711.

Mitchell JE, Freeman DR. 1993. Wildlife-livestock-fire interactions on the North Kaibab: a historical overview. USDA Forest Service General Technical Report RM-222. Fort Collins (Co): USDA Forest Service.

Molles M Jr. 1999. Ecology: concepts and applications. Boston: McGraw-Hill.

Moore MM, Huffman D. 2004. Tree encroachment on meadows of North Rim, Grand Canyon National Park, Arizona, USA. Arctic Alpine Res 36:474–483.

National Research Council. 2002. Ecological dynamics on Yellowstone's northern range. Washington (DC): National Academy Press.

Owen OS. 1971. Natural resource conservation: an ecological approach. New York: Macmillan.

Paine RT. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities — how different are the structuring processes? J of Mammal 81:637–48.

Rasmussen DI. 1941. Biotic communities of the Kaibab Plateau, Arizona. Ecol Monogr 11:229–75.

Reynolds RT, Graham RT, Reiser MH, Bassett RL, Kennedy PL, Boyce DA Jr, Goodwin G, and others. 1992. Management recommendations for the northern goshawk in the southwestern United States. USDA Forest Service General. Technical. Report. RM-217. Fort Collins (CO): USDA Forest Service.

Ricklefs RE. 1973. Ecology. Newton (MA): Chrion Press.

Ricklefs RE. 2001. The economy of nature. New York: WH Freeman.

Ripple WJ, Beschta RL. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. For Ecol Manage 184:299–313.

Ripple WJ, Beschta RL. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755–66.

Ripple WJ, Beschta RL. 2005. Linking wolves and plants: Aldo Leopold on trophic cascades. BioScience 55:613–621.

Russo JP. 1964. The Kaibab deer herd: its history, problems, and management. Wildlife Bulletin No. 7. Phoenix (AZ): Arizona Game and Fish Department.

Schier GA. 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA Forest Service Report INT-170. Ogden (UT): USDA Forest Service.

Sesnie SE, Bailey J. 2003. Using history to plan the future of old-growth ponderosa pine. J For 101:40–7.

Shepperd WD, Binkley D, Bartos D, Stohlgren TJ, Eskew LG, Eds. 2001. Sustaining aspen in western landscapes. USDA Forest Service, Fort Collins, Colorado. General Technical Report RMRS-P-18. 460 p.

Smith RL, Smith TM. 2001. Ecology and field biology. San Francisco: Benjamin Cummings.

Stiling P. 2002. Ecology: theories and applications. Upper Saddle River (MJ): Prentice-Hall.

Thompson BH. 1934. National parks and wilderness use. In: Fauna of the national parks of the United States. Fauna Series No. 2. Washington (DC): National Park Service. p 47–55.

Young CC. 2000. A textbook history: use of the Kaibab lesson in teaching biology. Am Biol Teach 62:559–64.

Young CC. 2002. In the absence of predators: conservation and controversy on the Kaibab Plateau. Lincoln (NE): University of Nebraska Press.