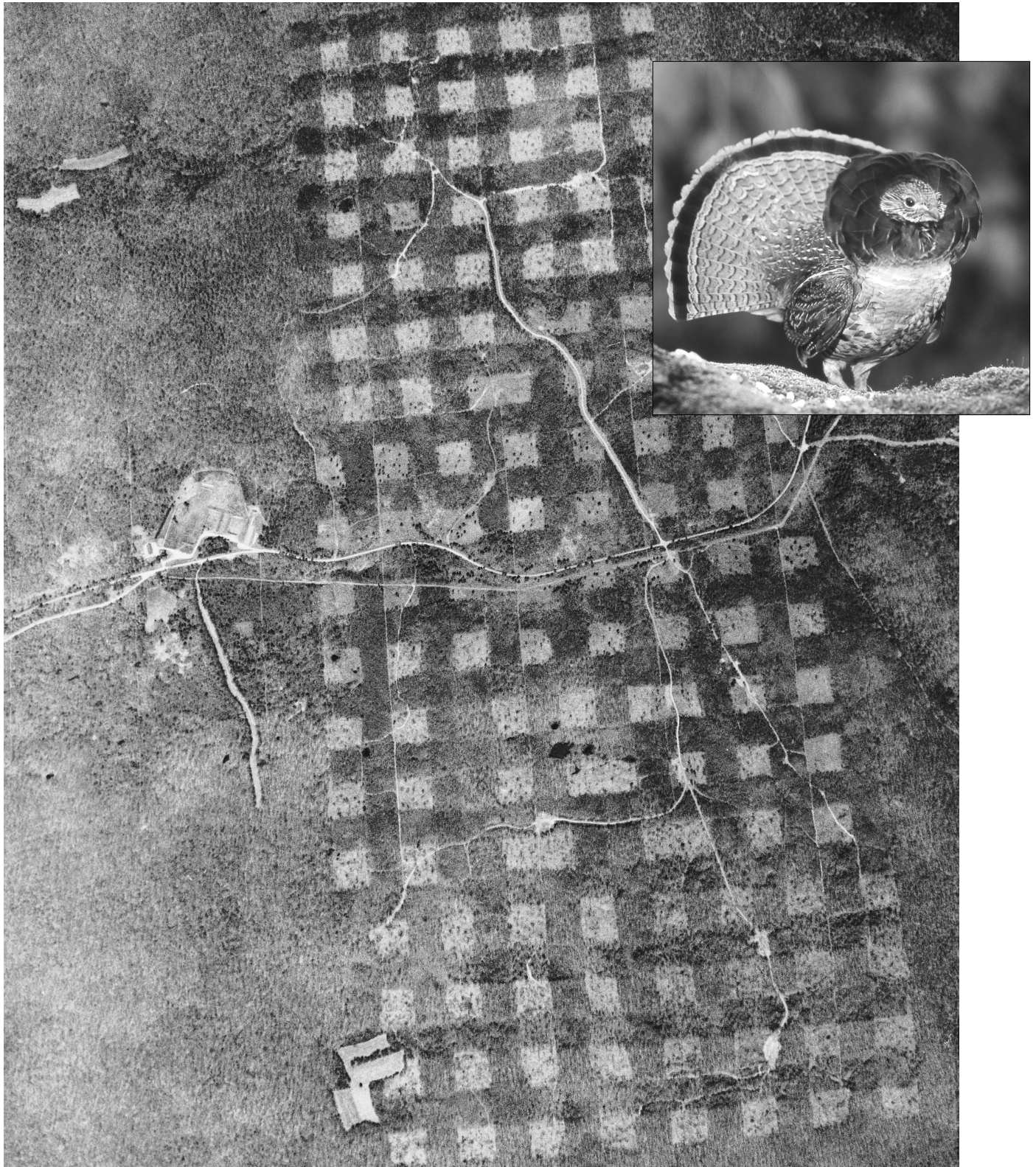

Ruffed Grouse Responses to Management of Mixed Oak and Aspen Communities in Central Pennsylvania

Gerald L. Storm, William L. Palmer, and Duane R. Diefenbach



Abstract

In 1975, the Pennsylvania Game Commission initiated a long-term study to evaluate responses of ruffed grouse to intensive habitat management of a central Pennsylvania forest that contained mixed oak and aspen-scrub oak communities. From 1976–98, grouse numbers and behavior were documented for two forest types, along with describing plant communities, to formulate forest management recommendations to benefit grouse. The study area included 1,120 ha on State Game Lands 176. Approximately one half of the study area was treated with 1-ha patch clearcuts, while the untreated half served as a control for comparison. Flushing surveys in spring and fall and drumming male surveys in spring were used as indices to grouse population trends. Females with broods and males were radio-tagged to determine their habitat selection and home range size and location. Fall flushing rates were about 75% greater on the treated area (0.61 flushes/1.61 km) than on the control area (0.35/1.61 km), during 1990–98. Spring flushing rates were two times greater (0.61/1.61 km compared to 0.30) on the treated area during 1990–98. Numbers of drumming activity centers on the treated area increased from 9 in 1976 to 68 in 1994, while on the untreated area, activity centers increased from 10 to 44 for the same period. Dur-

ing 1993–96, drummer densities were 16.0, 16.4, and 25.6/100 ha of young stands (5–19 years old) total, mixed oak, and aspen-scrub oak, respectively. Drummers began to use both mixed oak and aspen-scrub oak patches 5–7 years following cutting. Both females with broods and males preferred >10-year-old cuts; stem densities at sites used by females averaged >21,000 stems/ha and 7,500 stems/ha for active drumming sites of males. The average summer home range was 59 ha for females with broods, whereas male home ranges averaged 6 ha during the spring breeding season and 11 ha during summer. Overall, mixed oak clearcuts resulted in numerical and behavioral responses of grouse that were like those in aspen clearcuts. Based on our study, we concluded that small patch cuts of 2 ha were cost effective for forest management and long-term maintenance of multi-age and interspersed habitat. Fifty percent of aspen would be maintained in a young forest stage (<20 years old) using a 4-patch block and cutting a 2-ha patch every 10 years. Mixed oak, because of longer cutting rotations (100 years), requires a larger block of 2-ha patches (20 ha) where cutting a patch every 10 years would keep 20% in young forest.

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Introduction

Management of forests with small (1-ha) clearcuts and short rotations that create multiple structured and diverse forest communities can provide suitable habitat for ruffed grouse (*Bonasa umbellus*) during all seasons (Gullion 1972, Gullion and Svoboda 1972, Gullion and Alm 1983). A density of one breeding pair of ruffed grouse per 4 ha has been reported for forests dominated by aspen (*Populus* spp.) in small clearcuts (Gullion 1977). A positive population response—increased numbers—by ruffed grouse to managed aspen has been demonstrated by several previous workers, particularly in the upper midwestern states (Svoboda and Gullion 1972, Robinson 1984). However, there is little information available on the effect of managed mixed oak (*Quercus* spp.) forests on ruffed grouse populations in the mid-Atlantic and southeastern states where mixed oak are much more prevalent than aspen.

In 1975, the Pennsylvania Game Commission (PGC)

initiated a long-term study to evaluate responses of ruffed grouse to intensive management of forests in central Pennsylvania that contained mixed oak, aspen, and scrub oak communities (Liscinsky 1980). Prior to this study, the feasibility of this style of management had not been documented for large (>500 ha) tracts of forest land. An important question for the PGC was whether intensive management (1-ha clearcuts) was cost-effective relative to commercial forestry practices to improve habitat for ruffed grouse. The objective of this study was to determine the response of (abundance of and habitat selection by) ruffed grouse in an area with a diversity of size classes of mixed oak and aspen-scrub oak stands created by 1-ha clearcuts. In this bulletin we report on the results, conclusions, and management implications based on the initial 22 years of research on ruffed grouse at the Barrens section of State Game Lands (SGL) 176 in central Pennsylvania.



Study Area

The study area included 1,120 ha of 2,500 ha on State Game Lands (SGL) 176 (4°50' N, 77°53' W) in Centre County, Pennsylvania, 8 km northwest of State College (Fig. 1). The area, locally known as the Barrens, is part of the Nittany Valley between Bald Eagle and Nittany Mountains in the Valley and Ridge Province (Keener and Park 1986). Topography varied from gentle to moderately rolling and elevation ranged from 360 to 450 m above sea level. The study area included a shallow central valley bounded by two low ridges. Most slopes were gradual, usually less than 15°. Soils were classified as a sandy porous type in the Morrison series (Braker 1981).

Braker (1981) characterized the climate as a mixture of the dry midwestern and the humid eastern seaboard types. Mean monthly temperatures range from -3.4 C in January to 21.9 C in July. The mean annual temperature was 9.6 C, and the mean annual precipitation was 95.6 cm during 1951–1981 (National Oceanic and Atmospheric Administration 1985).

Scrub oaks (*Quercus* spp.) and aspens (*Populus* spp.) occurred throughout lower elevations in the central portion of the study area (Hudgins et al. 1985). The dominant species were bear oak (*Q. ilicifolia*), chinquapin oak (*Q. prinoides*), large-toothed aspen (*P. grandidentata*), and quaking aspen (*P. tremuloides*). Other species present

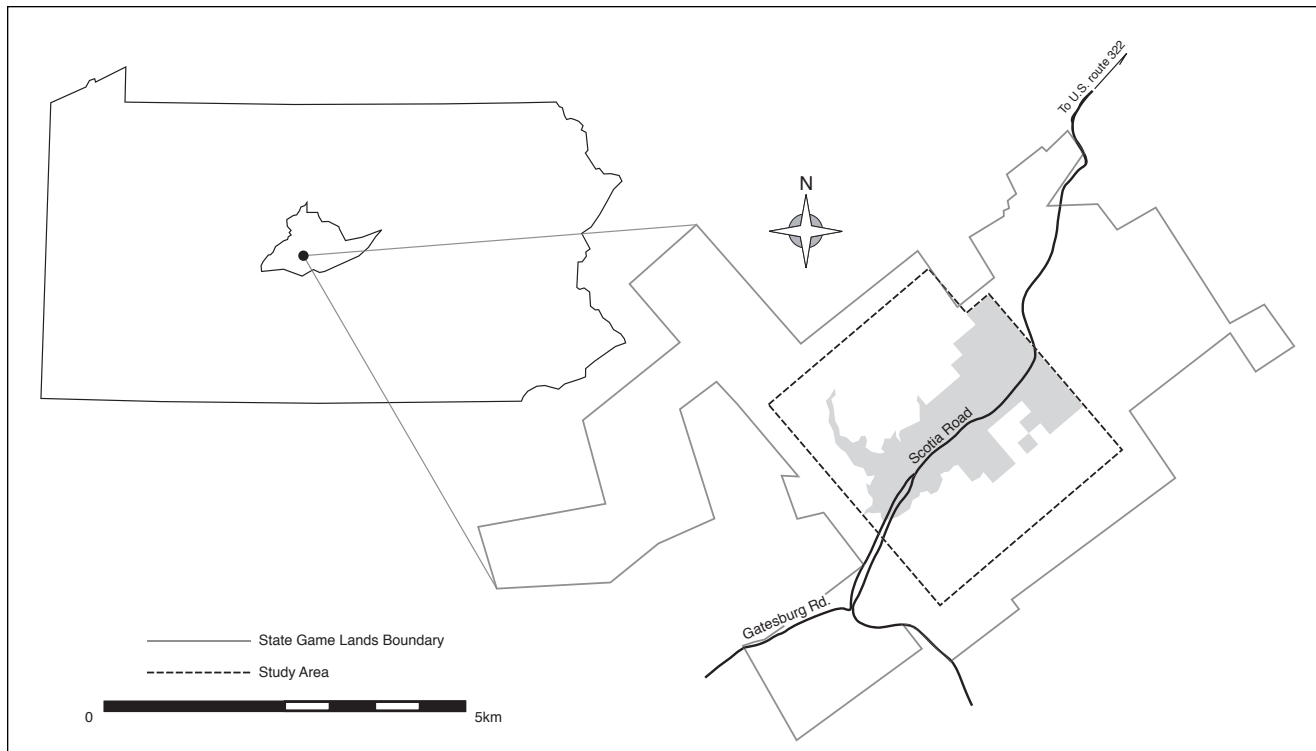
included pitch pine (*Pinus rigida*), black cherry (*Prunus serotina*), American hazelnut (*Corylus americana*), and gray dogwood (*Cornus racemosa*) (Clark 1946).

The ridges north and south of the central valley (Holderman 1978) were dominated by mixed oaks, including white oak (*Q. alba*), red oak (*Q. rubra*), chestnut oak (*Q. montana*), and scarlet oak (*Q. coccinea*). Black oak (*Q. velutina*), red maple (*Acer rubrum*), and hickories (*Carya* spp.) also were present in the overstory. The understory was usually poorly developed, often consisting of red maple, blueberry (*Vaccinium* spp.) and/or huckleberry (*Gaylussacia* spp.), and American hazelnut.

Sidelinger (1977) and Holderman (1978) provided vegetation maps and detailed descriptions of plant communities. Earlier descriptions of a portion of the study area indicated that the overall plant community during 1976–1998 was much more mature than during the 1940s, when studies of ruffed grouse were conducted on a 595-ha (1,470 acres) area. For example, Sharp (1957:8) reported that “The experimental grouse study area was located in a poletimber forest which had not replaced the brushfield stages of scrub oaks in the swales where frosts are more severe and frequent during the growing season.”

A survey reported by Liscinsky (1980) provided an

Figure 1. Location of the Barrens grouse habitat study area, Centre County, Pennsylvania.





Frost pocket associated with a plant community of aspen, scrub oak, and pitch pine at lower elevation.

inventory of the distribution of three predominant forest cover types—aspens, scrub oak, and mixed oak—prior to the initial treatments in 1976–77. These major types are not always distinct but blend into one another in many sections of the study area. After 1977, updated forest cover maps provided more detail on the plant communities that developed after cutting on the treated area. The original cover map depicting the distribution of timber

types was used primarily to establish the layout of cutting rotations by two major vegetation types: mixed oak and aspen-scrub oak. The more detailed maps prepared in 1982 by Williams (1986), in 1986–87 by Scott (1995), and in 1990–91 by McDonald (1993) were used primarily to assess responses of ruffed grouse to habitat management based on studies of home range and habitat selection.

Methods

FOREST MANAGEMENT AND PLANT COMMUNITY DEVELOPMENT

■ **Treatments and timber sales** — The area where the research was conducted encompassed 1,120 ha (2,768 acres). The treatment area consisted of 544 ha (Fig. 2). A 576-ha area adjacent to the treatment area was not intensively managed by clearcutting and was designated the untreated area.

The 544 ha on the treatment area were divided into 136 4-ha blocks. Sixty blocks were typed aspen-scrub oak and 76 blocks were typed mixed oak. Each block was subdivided into four square 1-ha patches and patches designated as either A = western, B = northern, C = eastern, or D = southern (Fig. 2).

The long-term goal was to cut 1-ha patches in each block at 10-year intervals in aspen-scrub oak (40-year rotation) and at 20-year intervals in mixed oak (80-year rotation) to provide a variety of habitat conditions suitable for ruffed grouse (Liscinsky 1980, Gullion 1984). The intent was to provide the annual resource requirements of a pair of breeding ruffed grouse on each 4 ha. Because most of the forest on the study area was approaching maturity, initial cutting intervals were reduced by five years in aspen-scrub oak and 10 years in mixed oak. Designated years for cutting the A, B, C and D patches, respectively, were 1976, 1981, 1986, and 1991 in aspen-scrub oak and 1976, 1986, 1996, and 2006 in mixed oak.

Clearcutting treatments were accomplished by using both commercial timber sales (income realized) and non-commercial operations, where money was paid to accomplish cutting. To establish the area for prospective sales, PGC forestry personnel blazed boundaries, marked log trees (100 percent tally of trees ≥ 27.9 cm diameter-at-breast-height [dbh], containing at least one log 2.43 m in length), and estimated pulp volume (three 10-factor prism plots/ha). These were standard procedures for commercial sales on SGLs in Pennsylvania. Prior to clearcutting of selected patches, the shrub and small aspen understory was machine-treated (Fig. 3). This mechanical chopping was planned to enhance the regeneration of the aspen and also to rejuvenate the relatively short-lived scrub oak.

In addition, special provisions were included with each sale to optimize habitat conditions for grouse. For the treatment of all A patches in 1976–77, and for the 60 B patches in aspen-scrub oak cut during 1980–81, species were reserved, including crabapple, hawthorn (*Crataegus* spp.), gray dogwood and flowering dogwood (*Cornus florida*), blackhaw (*Viburnum prunifolium*), and all pitch pine within 15 m of the gravel road. Special cutting

requirements included tree harvests restricted to the months of September through April; all trees > 5 cm dbh to be cut; all tree stems completely severed from trunk; stumps no higher than diameter of tree and never > 30.5 cm; all down trees and tops remaining to be lopped to within 0.9 m of ground; and reservation of larger vines > 5.1 cm in diameter.

Following the cutting scheduled for 1980–81, special provisions were the same with four exceptions. Reserved pitch pines included all within 46 m of the road and up to five trees on other patches where they existed. Two to four trees per patch, > 36.8 cm dbh, were left downed as potential drumming logs. If a corner tree were present, it was reserved to facilitate future boundary designations. For the B, C, and D mixed oak patches only, 10–12 of the larger long-lived den and/or good seed-producing trees, as evenly spaced as possible, were reserved.

Clearcutting in the D patches in aspen-scrub oak (scheduled for 1992) and C patches in mixed oak (originally scheduled for 1996) was delayed to maintain mature trees and a greater variety of size classes on the treatment area. These patches were expected to be cut before the end of year 2000. And, if the long-term goal of 40- and 80-year rotations is achieved, the second cutting of A patches would occur during year 2016 in the aspen-scrub oak type and during year 2056 in the mixed oak type.

Expenses incurred during treatments, as well as income from timber sales, were recorded to evaluate the economics of intensive forest management.

■ **Plant community descriptions** — To profile the plant communities on the treated area we conducted surveys before and after the cuts were made during 1985–88. During 1984–85 we described the species composition and structure of plant communities in C patches in aspen-scrub oak and B patches in mixed oak. Two to five sampling plots were established in 15 of the aspen-scrub oak and in 15 of the mixed oak patches, with the higher number of plots used in patches with more heterogeneous plant communities.

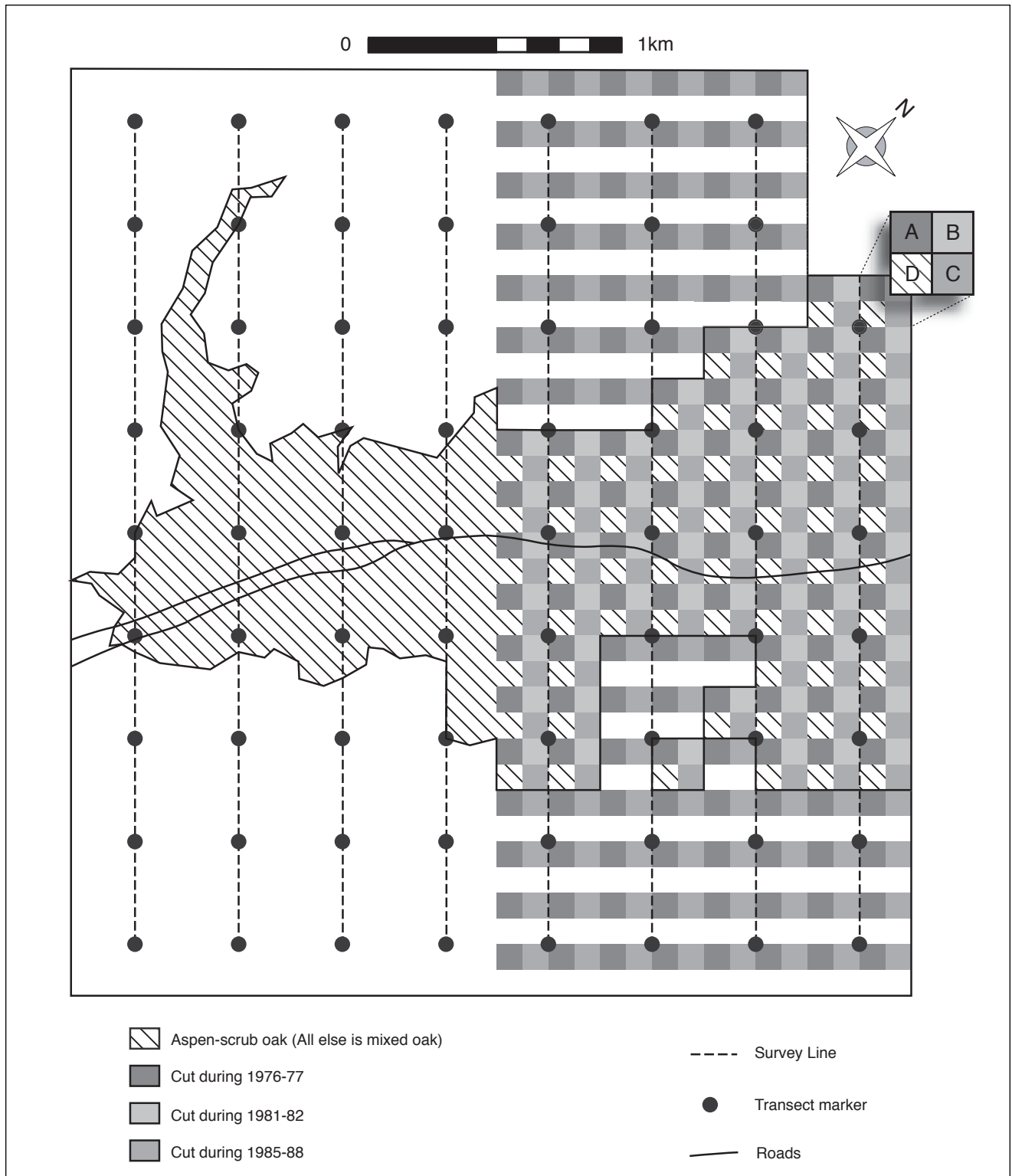
The location of each plot was determined by random selection of distance and direction from a patch corner to the center of the plot. Plots, each 400 m² in size, contained nested subplots to facilitate measuring of trees and shrubs (James and Shugart 1970). Diameter-at-breast-height (dbh) was measured for each tree (> 1.3 m in height) for each species. Relative abundance of seedlings (dbh < 2.54 cm, ht ≥ 0.3 m) and shrubs was estimated within five 10-m² subplots. Scrub oak stems were not included in shrub counts during 1984–85.

After the 1985–88 cuts, a survey of plant communities was conducted during 1993 in each of the aspen-scrub oak and mixed oak patches that were previously surveyed during 1984–85. The 1993 survey was intended to provide data on short-term plant community development after clearcutting, with emphasis on species-specific regeneration. The 1993 survey also provided background data for long-term monitoring of changes in the

structure and species composition of plant communities on the treated area.

Within each of the 30 patches, two sampling plots were established by using the same direction and distance measures used to locate plots during the 1984–85 survey. Each sampling plot consisted of a 20- x 20-m area (400 m²) that was subdivided into four 10- x 10-m sub-plots for measuring trees and shrubs (Storm and Ross

Figure 2. Barrens grouse habitat study area with cutting treatments, 1975–98.



1992). A 2- x 2-m subplot nested in the center of the plot was subdivided into four 1- x 1-m subplots.

In each 10- x 10-m subplot, species and dbh was recorded for tree stems >1.5 m in height and >1.0 cm dbh. Counts of tree and shrub seedlings (woody stems ≤ 1.5 m in height) were made in each 1-m² area of each central 2- x 2-m subplot. All tree seedlings were categorized in height by 25-cm increments. Shrub coverage was estimated in two of the 10- x 10-m subplots using the line intercept method (Hays et al. 1981). Due to layering and overlap of species, estimates of total shrub coverage could exceed 100 percent for any given subplot. Estimates of shrub coverage were based on all height classes of shrubs, including scrub oak coverage.

POPULATION RESPONSES

To monitor changes in the abundance of ruffed grouse, four permanent survey lines, each 3.2 km long, 1.5 m wide, and positioned 400 m apart, were established and maintained at each of the treated and untreated portions of the study area (Fig. 2). These lines provided the trails from which counts were made of flushed grouse and of drumming males (Hudgins et al. 1999).

Nine stakes, each marked with a unique identification number, were positioned at 400-m intervals along each of the eight survey lines. The 400-m spacing between survey lines and between stakes was used to provide maximum survey coverage and to minimize the chances of recording the location of the same breeding (drumming) male from more than one line and from more than two stakes on the same line. Previous research has suggested that drumming males could be heard from 200 m (Petraborg et al. 1953, Archibald 1975). The 72 numbered stakes served as reference during spring and fall flush counts and surveys of drumming males during spring.

Access to the study area by motorized vehicles was provided by one gravel-surfaced road that crossed at about the mid-point of each survey line (Fig. 2). The eight points where survey lines intersected the gravel road served as start and end points during each survey.

■ **Abundance — spring and fall flush counts** — Counts of ruffed grouse observed and/or heard after being flushed on or near survey lines were conducted during spring (15 March–15 April) and fall (15 September–15 October). Three counts were conducted annually during spring of 1978 and 1979, and a minimum of 10 counts were conducted annually during spring of 1980 through 1998. In fall, 10 counts were conducted annually from 1979 through 1998, except for 1988, when only six counts were completed.

Each of four persons surveyed two survey lines and two crossover lines between 0630 and 0930 hours. Survey personnel marked the location of each grouse by recording the following information: (1) the identification number of the stake encountered before the grouse was flushed and the identification number encountered after the flush; (2) the perpendicular distance (m) from the survey line to where the grouse flushed; and (3) the direction where the grouse flushed relative to the survey line, recorded as east or west on survey lines and north or south on crossover lines.

Flush counts were not conducted during days with heavy precipitation, high winds (>15 km/hr), or low temperatures (>10 degrees C below average temperature). Each survey person recorded weather conditions prevailing midway through the survey, and any discrepancies among survey personnel were resolved by the survey coordinator.

■ **Abundance — breeding male counts (activity centers)** — Ten counts of drumming males were conducted annually between 15 April and 15 May during 1976 through 1998. Each of eight persons surveyed one-half of each of two survey lines and one crossover line (Fig. 2) between 0500 and 0700 hours, so that the entire study area was surveyed simultaneously during a two-hour period. Each observer recorded the following information to indicate the presence and general location of drumming males heard from the survey lines: (1) the position of the observer on the survey line; (2) a compass bearing from the survey line to the drumming grouse; and (3) the identification number of the stake encountered before hearing the male and the number of the next stake encountered along the survey route.

The following procedure was used during May and June to locate areas that were consistently used by drumming males. Two or three personnel returned to the sur-

Figure 3. Hydro-axe used to treat areas with a dense understory in order to enhance regeneration of aspen at the Barrens grouse habitat study area.



vey lines and followed the compass bearings directed at the general location of potential drumming sites as indicated during the surveys for the current year. Within the general location, personnel examined each suitable log, rock, or stump for fresh fecal material (droppings). Logs or other objects with >30 droppings and other signs (e.g., fresh marks on bark of logs made by feet and wings of grouse) were considered active activity centers for the current year's breeding season. An activity center was defined (Gullion 1967) as an area of intensive activity in the proximity of one or more drumming logs used by a single male grouse.

Once an active drumming log was located, searches were made for other logs in the vicinity that showed evidence of being active. Any log with fresh sign of activity and located ≤ 100 m from another active drumming log was considered part of the same activity center.

Each log was marked with an aluminum tag with a unique number and the year the log was first located. The location was plotted on a field map, and new compass bearings to the activity center were determined from two stakes along the survey line closest to the activity center.

After the initial survey in 1976, activity centers used in the previous year or previous two years of the current survey were revisited even if drumming activity was not detected during the current year's survey. Known activity centers with no current sign of use by ruffed grouse were classified as inactive during the survey year.

BEHAVIORAL RESPONSES

■ **Onset and use of cut patches by breeding males** — The year of first occupancy of cut patches by breeding males was determined from annual survey records. The year when patches became suitable as activity centers was recorded by habitat type (aspen-scrub oak and mixed oak).

■ **Drumming site attributes** — We described the drumming sites used by males by measuring physical dimensions of the drumming platforms in activity centers examined each spring during 1976–1997. These records consisted of the year the drumming site was first located, the type of drumming platform (i.e., fallen log, tree stump, rock), height of drumming stage above ground, and the length and diameter of drumming logs and stumps.

We also measured drumming logs, shrub cover, canopy cover, and woody stem density associated with activity centers that were used by breeding males in 1998 on the untreated area, in both mixed oak and aspen-scrub oak cover types. Height of drumming platform and the diameter and length of the logs were recorded. Counts of woody stems were made within a 10- x 10-m plot centered at the base of the drumming log.

■ **Alternate drumming sites** — Drumming sites within

activity centers were mapped, digitized, and attributed in a geographic information system (ARC/INFO, Environmental Resources Research Institute, Redlands, California, USA) to facilitate spatial analyses. We used drumming site coordinates to calculate distances between alternate sites and primary sites. If multiple alternate sites were present within an activity center, we estimated a measure of circular dispersion (Zar 1984), ranging from 0 (circular uniformity) to 1 (no dispersion), to describe the spatial arrangement of alternate sites relative to the primary. We used the Kuiper Chi-square test (Zar 1984) to detect directional tendencies in the placement of alternate logs throughout the study area and relative to the position of the nearest neighboring activity center. Standard deviations of directional data were calculated according to Mardia (1972). Analysis of variance (ANOVA) was used to compare log characteristics between primary and alternate sites, and Kruskal-Wallis procedures were used to test for differences if non-normal distributions were observed.

DISTRIBUTION OF FLUSHES AND ACTIVITY CENTERS RELATIVE TO HABITAT TYPES

The locations of flushes and activity centers were summarized for each 4-ha block and for specified time intervals. Spring flushes were totaled for the interval 1982–98, fall flushes were totaled for the interval 1981–98, and activity centers were totaled for the period of 1976–98 and for the individual years of 1981, 1991, and 1997. These block totals were overlaid with cover type maps of the area to examine general relationships between the locations of grouse and the timber cover types in the study area. Correlation coefficients were calculated to measure the relationship among these three variables.

HOME RANGE AND HABITAT USE

■ **Adult females and broods** — Adult females were captured using modified shorebird traps (Liscinsky and Bailey 1955, Gullion 1965) or in a mist net in conjunction with a taped distress call of a 16-day-old chick (Lyons 1981). Age and sex were determined at the time of capture (Bump et al. 1947). Adult female grouse were marked with a numbered leg band and fitted with a radio transmitter attached with a poncho-style collar (14–19 g) (Amstrup 1980) or a backpack harness (25–27 g) (Brander 1968).

Home range: During 1986 and 1987, radio-tagged adult females were located once per day from the time of capture until 9 August, five times per week, separated by at least one day, from 10 August to 9 September, and two to four times per month from 10 September to 24 November (Scott et al. 1998). Each grouse was located at a random time between 0600 and 2000 hours. An effort was made to sample all grouse equally. Locations were estimated from direct observations, approaching to within 50 m of the grouse with the use of a hand-held yagi antenna, and triangulation from points of known



Survey line with 22-year-old stand on the left and 12-year-old stand on the right, in aspen-scrub oak type.

coordinates. Direct observation by flushing was conducted at least once every 14 days, to confirm that broods were with radio-tagged females. Accurate counts of brood size were not possible. Locations on the treated area also were recorded by block number and patch type. Locations were assigned a quality code (high, low) based on the method of location and its estimated accuracy. High quality locations were those that could be mapped confidently within a 0.25-ha area. These included most locations determined from flushing or observing the grouse and some locations determined by triangulation. Only high quality locations were used for analysis of home range and habitat use.

The size of summer home ranges of grouse with broods was estimated between the time of capture and 9 September of 1986 and 1987. September was considered the onset of brood break-up and dispersal (Chambers and Sharp 1958, Godfrey and Marshall 1969). Home range size was estimated by harmonic mean 95 percent contour (Dixon and Chapman 1980) and minimum convex polygon methods (Mohr 1947) for comparison to previous research. Home range size of grouse on the treated and control areas was compared using one-way analysis of variance.

We examined patterns of habitat selection by females and broods at three levels: cover-type composition, patch type relative to time of cutting, and micro-

habitat characteristics. Estimates of cover-type selection were based on dominant overstory vegetation at treated and untreated areas, whereas estimates of patch selection were limited to the treated area. Descriptions of microhabitats were made at treated and untreated areas.

Macrohabitat: A cover map, which identified eight cover types based on vegetation and land use (Williams 1986), was updated during 1986 and 1987 (Scott 1995) using aerial photography and field reconnaissance to account for ongoing clearcutting activities in the 1-ha patches. Use of cover types and patches was estimated by the number of times grouse were located in each category. Uses of cover types and patches were compared to their availability using Chi-square goodness-of-fit tests and Bonferroni 95 percent confidence intervals (Neu et al. 1974). These tests were conducted with pooled data for all grouse.

Microhabitat: Sixteen vegetative and physiographic variables were measured at sites used by ruffed grouse with broods and randomly located sites to estimate microhabitat selection and to assess changes in microhabitat due to forest management. Variables were measured at 120 sites (60 each on the treated and untreated areas) used by radio-tagged grouse and at 60 random sites (30 each on the treated and untreated areas). Used sites were randomly selected from weekly sets of radio locations from each grouse, obtained during 5 June

through 7 August of 1986 and 1987. A location was selected only if it was of high quality, if there was no known disturbance to the grouse prior to estimating the location, and if the location was >12 m from any previously selected site. Random sites were selected by randomly generating coordinates within the study area. Random sites located on gravel roads, buildings, standing water, and mowed grass fields were rejected.

Basal area and density of tree species (≥ 7.5 -cm dbh) were determined by total stem counts within a 0.04-ha circular plot centered on each site (James and Shugart 1970). Height and percent overhead cover also were determined from within the 0.04-ha plot. Density of small woody stems (2.5- to 7.5-cm dbh) was estimated using two crossing 1- x 20-m belt transects centered on each site. Percent cover of ground and understory vegetation was estimated using the point intercept method at 1-m intervals along belt transects (Hays et al. 1981). Slope was measured with an Abney level at the circular plots and distance variables were determined with the use of aerial photographs of the study area.

Microhabitat data were analyzed with multivariate analysis of variance using the Statistical Analysis System (Helwig and Council 1985). Variables were compared between used sites and random sites on the entire study area, and between random sites on the treated and untreated areas. Significant differences between used and random sites throughout the entire study area suggested microhabitat selection by brood-rearing grouse, whereas differences between random sites on the treated and untreated areas indicated effects of habitat management on microhabitat composition.

■ **Adult males** — Adult males were captured during spring 1990–1991 with mirror traps (Bowers 1948) set on drumming logs. We determined sex and age of captured grouse using procedures described by Davis (1969) and Roussel and Ouellet (1975), and weighed each grouse with spring scales to the nearest g. Each grouse was fitted with a 11–17 g wire harness or poncho style (Small and Rusch 1985) radio transmitter (Advanced Telemetry Systems, Isanti, MN). Transmitter packages were <3 percent body weight of each grouse. Each grouse was banded with a numbered aluminum leg band (National Band and Tag Co., Newport, KY) on each leg.

Home range: We located each grouse once daily from time of capture until 31 August, unless transmitter failure occurred or the bird died, with a portable radio receiver and a handheld, three-element, yagi antenna. On the untreated area, grouse were circled and their position fixed by pacing along a perpendicular bearing to the nearest survey transects with the numbered stations (McDonald et al. 1994). On the treated area, the cut and uncut patches and the transects enabled us to accurately locate grouse within an area <0.25 ha. Locations were plotted on 1:5000 scale maps and recorded as Universal Transverse Mercator coordinates to the nearest 10 m. Grouse were purposely flushed approximately every 10 days to verify that the individual was still alive.

We also flushed grouse if they did not appear to change location for two days or if they moved an unusually great distance (>200 m) between consecutive locations.

Tracking days were divided into four four-hour periods: 0501–0900, 0901–1300, 1301–1700, and 1701–2100. We located each grouse approximately an equal number of times during each period each month.

Seasons were defined as breeding (capture date–31 May) and summer (1 June–31 August or loss of contact prior to 31 August). We used the McPaal computer program (M. Stuwe, Nat. Zool. Park, Front Royal, VA, unpub. manual) to calculate seasonal and monthly home ranges based on the minimum convex polygon (Mohr 1947) and harmonic mean (Dixon and Chapman 1980) methods. We calculated 95 percent harmonic mean home ranges using 10 grid cell divisions (121 intersections). We calculated breeding season home ranges only for grouse that survived ≥ 21 days after capture. We compared home range area estimates between the treated and untreated areas using t-tests.

Macrohabitat: We used color aerial photographs taken in 1990 and 1991 (scale=1:2800) to delineate 11 habitat types on the study area. Forest stands were delineated according to dominant species and dbh (sapling, 2.5–12.5 cm dbh; pole-timber, 12.6–27.9 cm; sawtimber, ≥ 28.0 cm). Stands of the same dbh were pooled within species groups, regardless of stem density, with the exception of sparse (40–50 percent canopy cover) sapling stands.

We calculated the total area of each of 11 habitat types to determine habitat availability separately for the treated and untreated areas. Because the treated and untreated areas were adjacent, and grouse could move between them, we included a 200-m buffer zone of each area (treated, untreated) in the availability calculations (McDonald et al. 1994).

We used a chi-square goodness-of-fit test (Neu et al. 1974) to assess grouse use of habitats. We used Bonferroni confidence interval estimation (Neu et al. 1974), with a family-wide error rate of $P = 0.05$, to determine preference of habitat types.

Microhabitat: In 1990, we measured microhabitat conditions associated with activity centers that were active ≥ 3 years during 1987 through 1990 and sites that were inactive during 1988 through 1990 but had been active ≥ 3 years during 1976–1987. We also chose 30 random points by selecting random numbers referenced to Universal Transverse Mercator system coordinates.

The drumming stage (Gullion and Marshall 1968) served as the plot center for active or inactive sites. The random point served as the plot center at random sites. Two nested circular plots (0.04-ha [radius (r) = 11.28m] and 0.002-ha [r = 2.52m]) were established at each location to sample and describe habitat attributes.

All large woody stems >12.6 cm dbh and >1.8 m in height were tallied and their dbh measured to the nearest 0.1 cm in the 0.04-ha plot. Crown position was recorded for each large woody stem in one of four cate-

gories: dominant, co-dominant, intermediate, suppressed (Smith 1986). Five co-dominant trees closest to the plot center were used to measure height to top of tree crown (upper canopy height), and height to bottom of tree crown (lower canopy height). Heights were measured with a clinometer or a meter tape. Small woody stem (<12.6 cm dbh) densities in four size categories were estimated by total stem counts in the 0.002-ha plots.

Variables were examined for normality by examining skewness and kurtosis (Snedecor and Cochran 1989) and conformity to a normal probability plot (Neter et al. 1990). Non-normal variables were transformed with either logarithmic (base 10), square root, or arcsine (for percentage variables) transformations.

Means of normal variables were compared among active, inactive, and random sites with single factor analysis of variance (ANOVA). Differences were declared significant if $P \leq 0.05$. The Tukey Multiple Comparisons (TMC) procedure (Neter et al. 1990) was used to detect differences between pairs of site categories if ANOVA resulted in a significant result. The family-wide alpha level was controlled at 0.05 for the TMC procedure.

Variables that could not be transformed to approximate a normal distribution were analyzed with the Kruskal-Wallis test (Neter et al. 1990). Percent grapevine canopy cover was tested with a median test as it was a categorical variable. Differences were declared significant at the $P = 0.05$ level.

Data analysis was performed in two stages. Initially, the data were combined for the treated and untreated areas; the three site categories (active, inactive, and random) were then separated into treated and untreated area groups. The same procedures were used on these groups as on the combined data set to assess differences among site categories.

Because of the differences in habitat between the treated and untreated areas due to management of these areas, analysis of the data by treated and untreated area groups was important. Differences among site categories on one area may have masked a lack of difference or an opposite result on the other area.

Linear discriminant function analysis (DFA) (Tabachnick and Fidell 1983) was used to classify sites as active or inactive. The difference between active and inactive sites was of most interest; therefore, random sites were not considered in these analyses. Variables chosen for inclusion in the models met three criteria: (1) conformity to a normal distribution, (2) significant difference between active and inactive groups as noted in ANOVA and TMC, and (3) stepwise selection from this subset of variables (Tabachnick and Fidell 1983).

DFA was performed using the Statistical Analysis System (SAS) (SAS Institute, Cary, NC) to examine correlation of variables and test for homogeneity of covariance matrices. SPSS (SPSS Inc., Chicago, IL) was used to calculate the standardized discriminant function.

Longevity of use of activity centers: The longevity of use of activity centers by breeding males was estimated

by calculating the proportion of activity centers in each of the four patch types (A, B, C, D) for each forest type (aspen-scrub oak, mixed oak). The data were summed for years beginning with 1977 and ending at three years (1987, 1993, and 1998), approximately 10 years following each of the cutting periods. The changes in the proportion of activity centers within patch types during the three eras provided a prediction of the length of time the habitats provided the best conditions for breeding males.

During 1990–1991, 13–14 years after the A patches were cut, we estimated stem densities at two groups of activity centers with a history of being active and inactive. One group consisted of eight sites that were active at least three years prior to 1987, but were inactive during 1987–1990; this was the inactive group. The second group consisted of 13 sites that were active during 1987–1990; this was labeled the active group. Fourteen of the sites (4 in the inactive group and 10 in the active group) were located in the A patches cut during 1976.

Results

FOREST MANAGEMENT AND PLANT COMMUNITY DEVELOPMENT

■ **Treatments and timber sales** — In 1975 PGC land management personnel established the survey line trails. Boundaries were laid out for the 136 4-ha blocks and 1-ha A patches, and A patches were cruised for the timber sale. During February and March 1976, two A patches were cut by sportsmen volunteers prior to bidding the timber sale. This was a demonstration, to illustrate for prospective bidders the appearance of a finished 1-ha patch.

Several treatment methods were employed during the fall of 1976 and winter 1976–77 to accomplish the clearcutting of 136 patches (25 percent of the total treatment area), 60 in aspen-scrub oak and 76 in mixed oak. A hydro-axe was contracted to mechanically chop the small trees and brush on 36 patches. An operator was contracted for clearcutting of 56 patches and cutting the remaining trees on the machine-treated patches. The remaining 42 patches were clearcut via a commercial timber sale. An additional three patches were burned in 1977, following clearcutting. The first round of treatments in 1976–77 resulted in \$56,403 invested in timber sale preparation and non-commercial cutting, while the timber income was \$6,536. Because most of the forest on the study area was approaching maturity, initial cutting intervals were reduced by five years in aspen-scrub oak and 10 years in mixed oak. Therefore, the 60 B patches in aspen-scrub oak were cut during 1980–81, and the 60 C patches in aspen-scrub oak and the 76 B patches in mixed oak were cut during 1985–88.

In the fall of 1980, 48 patches were hydro-axed. This was followed by a commercial timber sale for the 60 total patches, which were cut in the winter of 1981–82. These patches constituted 11 percent of the total treatment area. For this second round of treatments, costs were \$47,675 with income of \$5,500.

During the period of fall 1985 through winter 1988, the next 136 patches (76 mixed oak B patches and 60 aspen-scrub oak C patches) were clearcut. Prior to cutting, 24 patches were hydro-axed and 26 were cleared by a Royer cutter. The machine treatment was applied to 24 patches in 1985, 11 patches in 1986, and 15 patches in 1987. The overstory was removed from 24 patches in the fall of 1986. The remaining 112 patches were cut during 1987 and 1988. The habitat management for this period showed \$77,421 invested and \$79,981 in timber sale income, the first cutting cycle during which income exceeded investment.

By 1988, 75 percent of the aspen-scrub oak and 50 percent of the mixed oak patches had been cut on the

544-ha treatment area (Table 1). Cost/benefit improved over time, primarily due to changes in costs of machine treatments and in timber values (Table 2). Although D patches in aspen-scrub oak and C and D patches in mixed oak were not cut by 1998, preliminary figures on economics were available (J. Byerly, personal communication, PGC).

■ **Plant community descriptions** — Descriptions of the woody stems prior to clearcutting in 1985–88 were based on attributes of overstory (pole and sawtimber, ≥ 12.7 cm dbh), saplings (2.54–12.6 cm dbh), and seedling (0–1.25 m height) strata recorded during 1984–85.

In the mixed oak (B patches) we recorded 12 species of overstory trees with more than one stem in the 15 patches. The estimated density of overstory trees in the mixed oak type was 3.1 stems per 100 m² (125 stems per 0.4 ha or per square mile). The most common species were white oak, black oak, scarlet oak, and chestnut oak (Fig. 4). Red maple, hickories, and sassafras (*Sassafras*

Table 1. The number and cumulative percent of patches clearcut on the treated^a area at the Barrens grouse habitat study area, 1976–1988.

Year(s) Of Cutting	Aspen-scrub oak (240) ^b			Mixed oak (304) ^b		
	Patch Code	Number Cut	Cumulative Percent Cut	Patch Code	Number Cut	Cumulative Percent Cut
1976–77	A	60	25	A	76	25
1981–82	B	60	50		0	25
1985–88	C	60	75	B	76	50
	D	0		C, D	0	
Total		180	75		152	50

^a The treated area consists of 136 4-ha (10-acre) blocks (60 in aspen-scrub oak and 76 in mixed oak); each block consists of 4 patches.

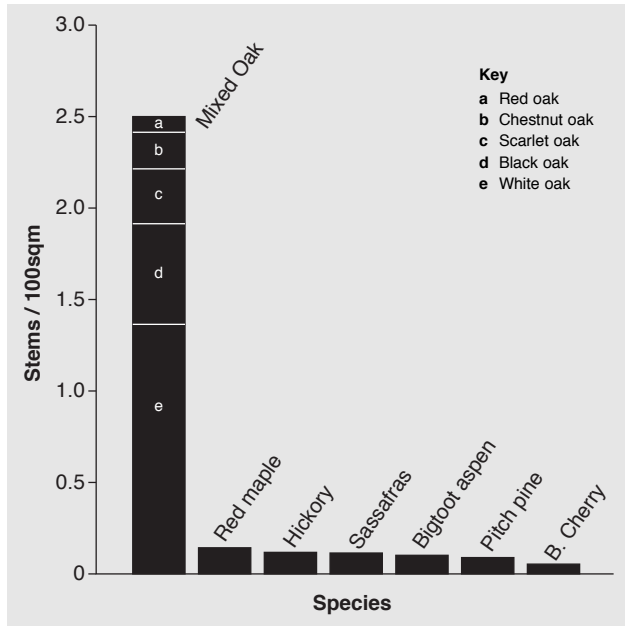
^b The number in parentheses is the total number of patches per forest type.

^c Within each 4-ha (10-acre) block, the four 1-ha (2.5-acre) patches are labeled A, B, C, and D; see Fig 2.

Table 2. Cost-benefit of intensive forest management at the Barrens grouse habitat study area, 1975–2000.

Year(s)	# Patches	Investment		Income Sale Price
		Treatment	Site Preparation	
1975–77	2	Sportsmen Volunteers	\$500	–
	36	\$13,950 (hydro-axe)	\$13,950	–
	56	\$2,950 (non-commercial cut)	\$14,263	–
	42	–	\$10,790	\$6,536
1980–81	48	\$29,880 (hydro-axe)	–	–
	60 (includes 48 above)	–	\$17,795	\$5,500
1985–88	24	\$22,000 (hydro-axe)	–	–
	26	\$5,500 (Royer)	–	–
	136 (includes 50 above)	–	\$49,921	\$79,981
Totals	332	\$74,280	\$91,657	\$92,017
(2000 projections)	(136)	[\$17,000–Royer (64 patches)]	(\$72,000)	(\$300,000)
(Grand totals projected)	(468)	(\$91,280)	(\$163,657)	(\$392,017)

Figure 4. Pre-cut density of overstory trees, ≥ 12.70 cm dbh, in mixed oak B patches at the Barrens grouse habitat study area, 1984–85.



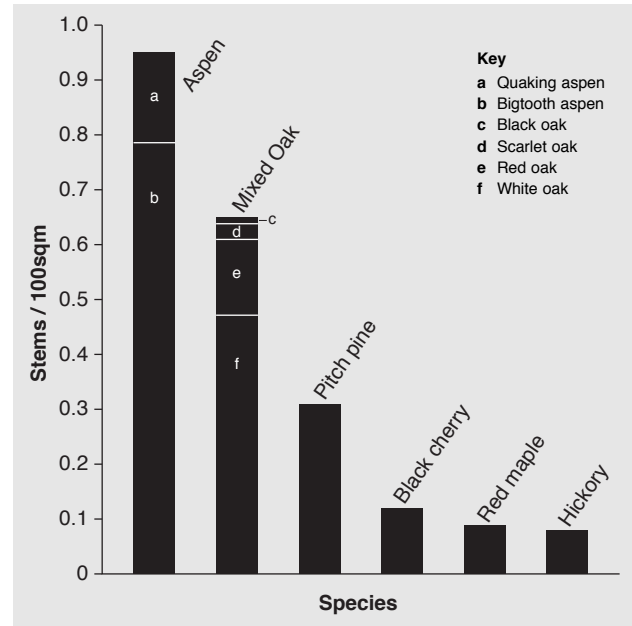
albidum) also were common species in the mixed oak patches prior to the 1985–88 cuts. Dbh averaged 23, 33, and 35 cm for white oak, black oak, and scarlet oak, respectively. The dbh of white oak, the most dominant tree species in the mixed oak patches, ranged from 12.7 to 51.3 cm (5.0 to 20.2 inches).

In the aspen-scrub oak (C patches) we recorded 11 species of overstory trees with more than one stem in the sample of 15 patches. The estimated density of overstory trees was 2.2 stems per 100 m² (89 stems per 0.4 ha). The most common species were bigtooth aspen and white oak (Fig. 5). Pitch pine, quaking aspen, red oak, black cherry, red maple, and hickories also were present in the aspen-scrub oak patches prior to the 1985–88 cuts. Dbh averaged 21 and 24 cm for bigtooth aspen and white oak, respectively. The dbh of bigtooth aspen, the most dominant species in the aspen-scrub oak patches, ranged from 12.7 to 47.0 cm (5 to 18.5 inches). Based on counts of annual rings, we estimated that the largest aspen were 68–70 years old.

A total of 11 species of trees in the sapling (2.54–12.6 cm dbh) stage occurred in the mixed oak type during the 1984–85 survey. The number of species averaged 3.3 per patch in the 15 mixed oak patches. The most common species were red maple and white oak (Fig. 6). Other species present included hickories, sassafras, black cherry, bigtooth aspen, and other oaks. Saplings in the mixed oak patches averaged 7.5 cm dbh and ranged from 4.6 to 10.8 cm.

The mean density of saplings for the 15 mixed oak patches averaged 3.9 stems per 100 m² (157 stems per 0.4 ha) (Fig. 6). This relatively low density of saplings coupled with the lack of scrub oak (only one stem recorded in one of the 15 patches) indicated the relatively sparse understory in the mixed oak patches prior to clearcut-

Figure 5. Pre-cut density of overstory trees, ≥ 12.70 cm dbh, in aspen-scrub oak C patches at the Barrens grouse habitat study area, 1984–85.



ting the B patches in 1985–88.

A total of 10 species of trees in the sapling stage were recorded for the aspen-scrub patches (Fig. 7). The number of species in the sapling stage in the aspen-scrub oak patches averaged 4.7 per patch prior to the 1985–88 clearcuts. The most common species were aspens, black cherry, mixed oaks, and red maple. Saplings in the aspen-scrub oak patches averaged 6.7 cm dbh and ranged from 4.1 to 10.7 cm.

The mean density of saplings for the 15 aspen-scrub oak patches averaged 7.5 stems per 100 m² (299 stems per 0.4 ha) prior to clearcutting (Fig. 7). This density was more than two times greater than the density of saplings in the mixed oak patches. Furthermore, 13 of the 15 aspen-scrub oak patches had a prominent scrub oak component in the understory.

In 1993, six to eight years after the 1985–88 cutting, saplings dominated the B patches in the mixed oak. A total of 14 tree species were recorded in the mixed oak patches, and the number of tree species in the sapling stage averaged 6.0 per patch. Scrub oaks were not included in the sapling category during the 1993 survey, but were measured as part of the shrub strata. The most common tree species were red maple, black cherry, and oaks (Fig. 8). The high abundance of black cherry and chestnut oak in the post-cut period was in marked contrast to the lower abundance of these two species in the pre-cut years. Saplings in the mixed oak patches averaged 3.5 cm dbh. The density of saplings during the 1993 survey averaged 15.2 stems per 100 m² (608 stems per 0.4 ha) in the mixed oak patches. As expected, the stem density was significantly greater than the mean density (157 stems per 0.4 ha) during the pre-cut period.

A total of 12 tree species were recorded as saplings in the aspen-scrub oak patches, and the number of species

Figure 6. Pre-cut density of tree saplings, 2.54–27.69 cm dbh, in mixed oak B patches at the Barrens grouse habitat study area, 1984–85.

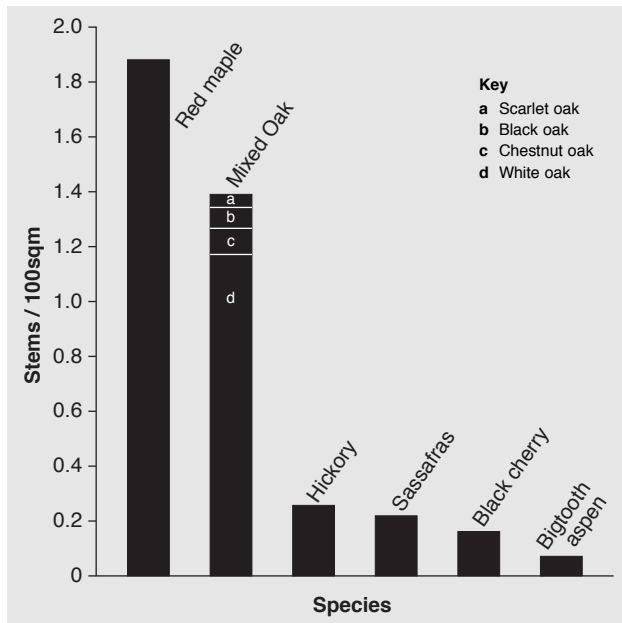


Figure 7. Pre-cut density of tree saplings, 2.54–27.69 cm dbh, in aspen-scrub oak C patches at the Barrens grouse habitat study area, 1984–85.

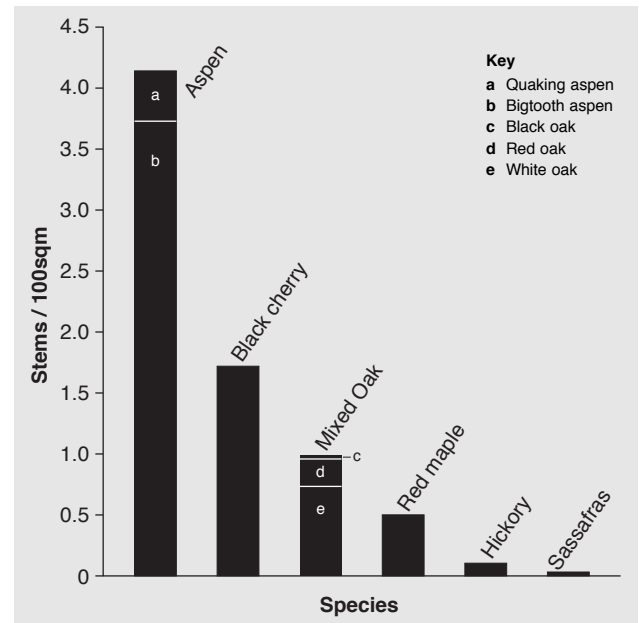


Figure 8. Post-cut density of tree saplings, 2.54–27.69 cm dbh, in mixed oak B patches at the Barrens grouse habitat study area, 1993.

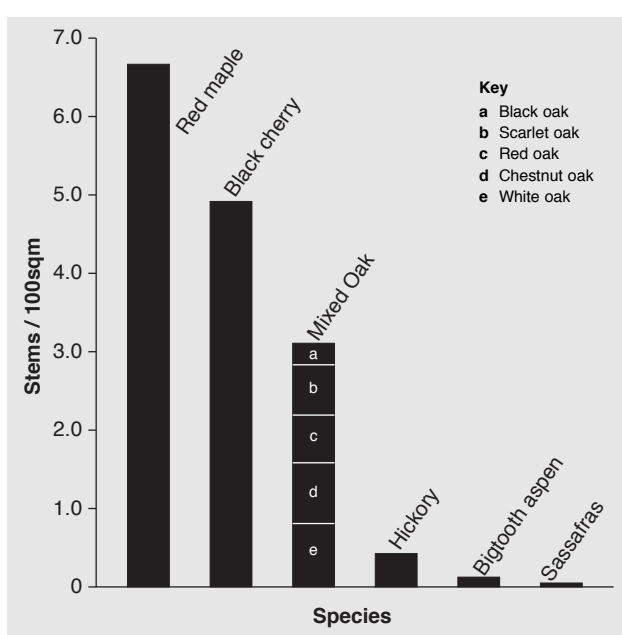
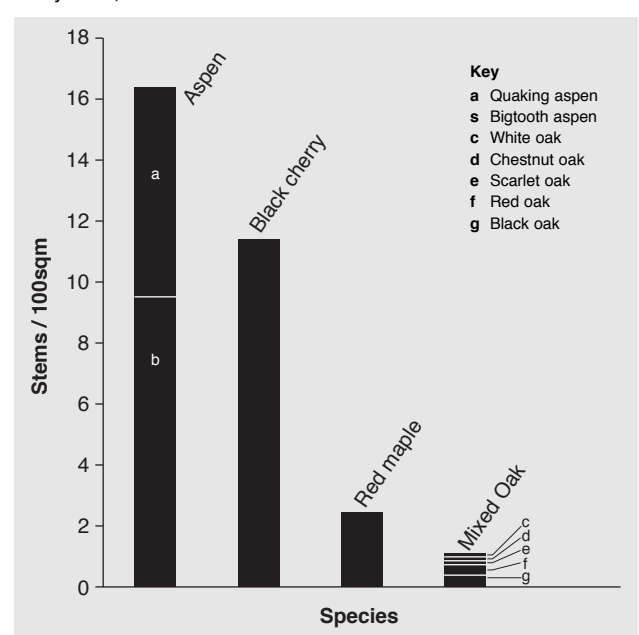


Figure 9. Post-cut density of tree saplings, 2.54–27.69 cm dbh, in aspen-scrub oak C patches at the Barrens grouse habitat study area, 1993.



per patch averaged 6.0 during the post-cut survey in 1993. The most common species were aspens, black cherry, and red maple (Fig. 9). The density of chestnut oak, 0.1 stems per 100 m² (4.0 stems per 0.4 ha), in 1993 was greater than during the pre-cut period, when chestnut oak was absent in the patches sampled. Saplings in the aspen-scrub oak patches averaged 5.1 cm dbh, which was greater than the 3.5 cm dbh for the mixed oak patches in the post-cut period. The post-cut density of saplings averaged 31.1 stems per 100 m² (1,242 stems per 0.4 ha) in the aspen-scrub oak patches (Fig. 9).

Red maple, sassafras, mixed oaks, and black cherry were the dominant species of tree seedlings in the mixed oak patches prior to cutting (Fig. 10). Aspen seedlings were present in only six of the 15 patches sampled and made up a minor component of the seedling population in the mixed oak type during the pre-cut sample in 1984–85.

Red maple and black cherry were the most common tree seedlings in the aspen-scrub oak patches prior to the cuttings in 1985–88 (Fig. 11). Quaking aspen ranked ninth in abundance with 13.3 stems per 100 m² (532

Figure 10. Pre-cut density of tree seedlings, <2.54 cm dbh and >0.30 m in height, in mixed oak B patches at the Barrens grouse habitat study area, 1984–85.

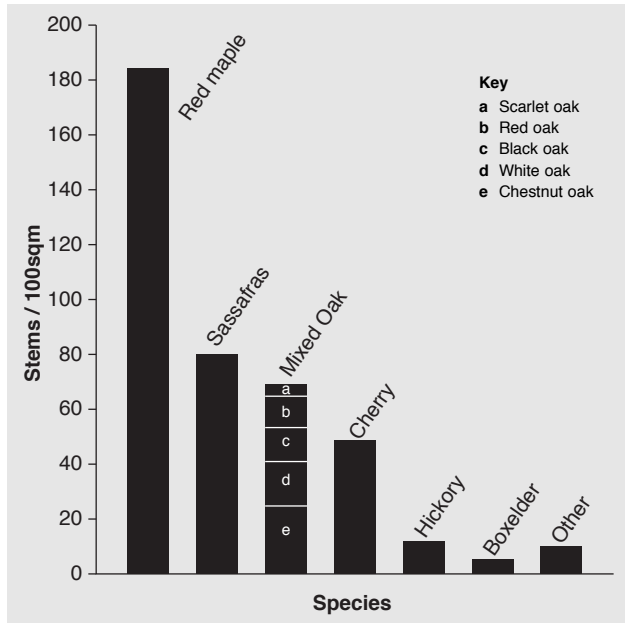


Figure 11. Pre-cut density of tree seedlings, <2.54 cm dbh and >0.30 m in height, in aspen-scrub oak C patches at the Barrens grouse habitat study area, 1984–85.

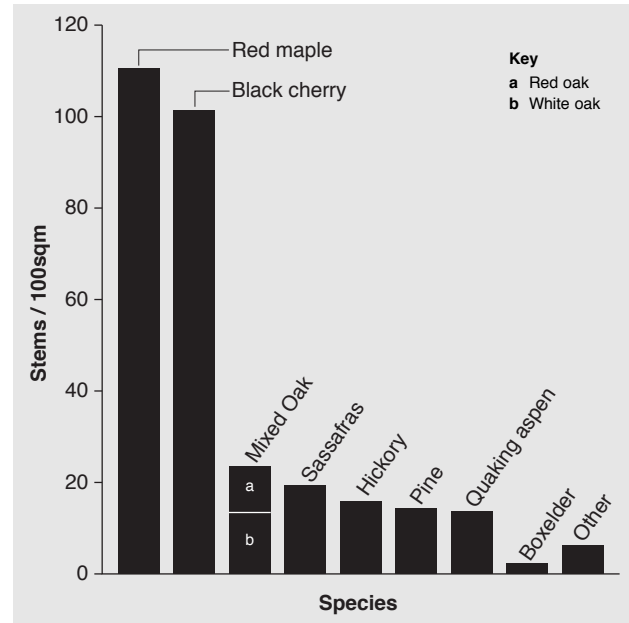


Figure 12. Post-cut density of tree seedlings, <2.54 cm dbh and >0.30 m in height, in mixed oak B patches at the Barrens grouse habitat study area, 1993.

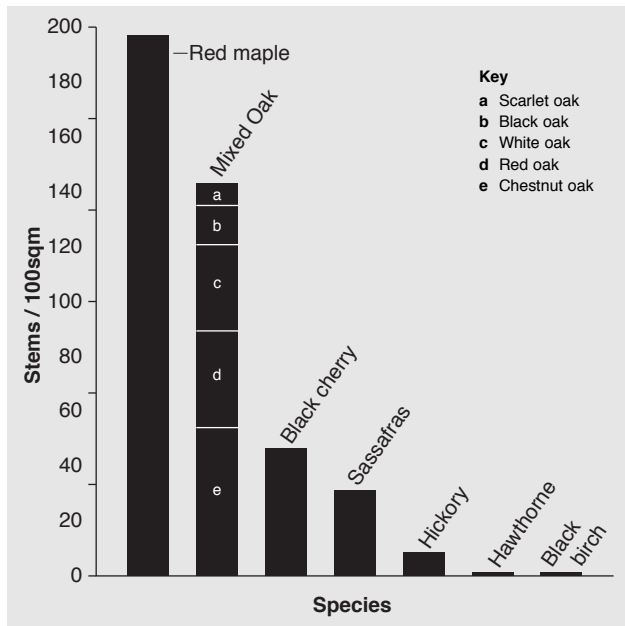
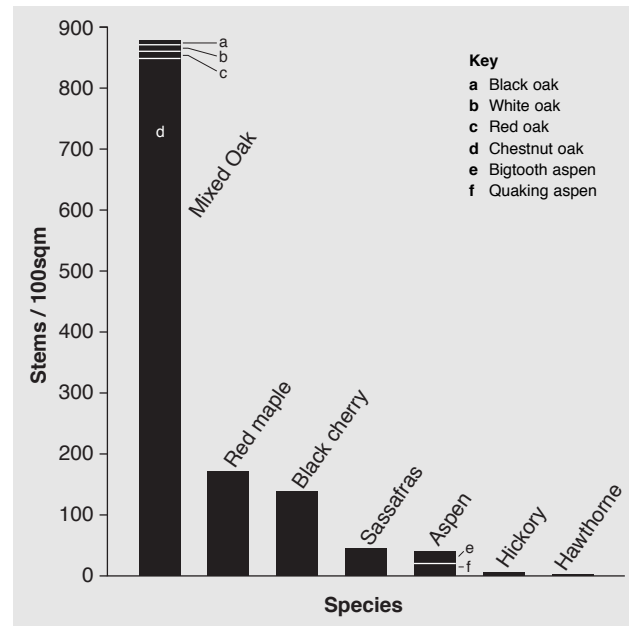


Figure 13. Post-cut density of tree seedlings, <2.54 cm dbh and >0.30 m in height, in aspen-scrub oak C patches at the Barrens grouse habitat study area, 1993.



stems per 0.4 ha) and outnumbered bigtooth aspen (53 stems per 0.4 ha).

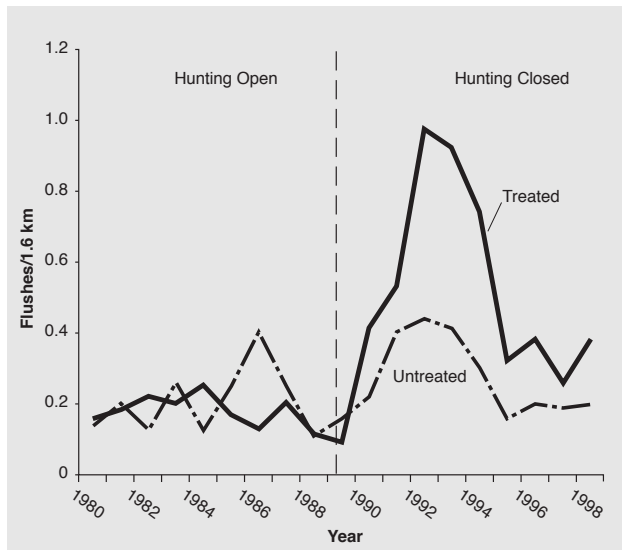
Red maple and mixed oaks were the most common tree seedlings in the mixed oak patches post-cut in 1993 (Fig. 12). Mixed oak species went from 68.1 stems per 100 m² (2,724 stems per 0.4 ha) pre-cut (ranked fourth among all seedlings) to 143.1 stems per 100 m² (5,724 per 0.4 ha) post-cut (ranked second). Chestnut oak seedlings doubled, from 952 per 0.4 ha during the pre-cut to 2,132 per 0.4 ha in the post-cut period.

In the aspen-scrub oak in 1993, mixed oaks were the

dominant tree seedlings (Fig. 13). Red maple and black cherry, with one fifth and one sixth, respectively, the number of oak seedlings, were next for tree seedlings in the aspen-scrub oak type. The number of chestnut oak seedlings increased from <40 stems per 0.4 ha to more than 33,000 per 0.4 ha.

We recorded 21 species of shrubs (excluding scrub oak) during 1984–85, 18 in mixed oak and 13 in aspen-scrub oak. Blueberry comprised >75 percent of the shrub stems in both forest types and was present in each of the 30 patches sampled. *Rubus spp.* comprised 13 per-

Figure 14. Number of grouse flushed per 1.61 km during spring flush counts (n=10) on treated and untreated areas at the Barrens grouse habitat study area, 1980–98.



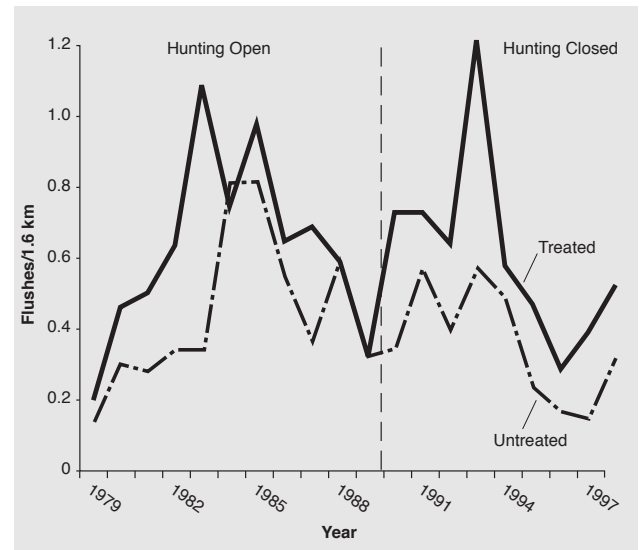
cent and 15 percent of the stems in mixed oak and aspen-scrub oak, respectively. Sweet fern (*Comptonia peregrina*) comprised 3 percent of the stems in aspen-scrub oak and 4 percent in mixed oak. All other shrubs comprised <1 percent of total stems counted.

Nine species of shrubs (excluding scrub oak) were recorded during 1993. Eight of these were present in the pre-cut sample, while autumn-olive (*Elaeagnus umbellata*) was not. Scrub oak was tallied in 14 of 15 aspen-scrub oak plots and in nine of 15 mixed oak plots. Coverage for scrub oak was 53 percent in aspen-scrub oak and 18 percent in mixed oak. Blueberry was present in every patch sampled, and the percent coverage was 65 percent in mixed oak and 55 percent in aspen-scrub oak. Blackberry (*Rubus allegheniensis*) was found in 87 percent of mixed oak plots and 67 percent of aspen-scrub oak plots. The percent coverage of blackberry was 43 percent in mixed oak and 12 percent in aspen-scrub oak. All other shrubs were present in 5 percent or fewer of the plots and had correspondingly low coverages.

POPULATION RESPONSES

■ **Abundance — spring and fall flush counts** — During spring, the average number of grouse flushed during 1980 through 1989 (the first year grouse hunting was not permitted on the study area) was 13 (range 7–19) and 16 (range 9–32) for the treated and untreated areas, respectively. The maximum number (32 flushes) occurred on the untreated area in 1986. During 1980–1989, the average number of spring grouse flushes/1.61 km (Fig. 14) was 0.17 and 0.20 for the treated and untreated areas, respectively. After 1989, the average number of flushes during 1990–1996 was 46 (range 24–74) and 24 (range 13–35) for the treated and untreated areas, respectively. During each year after 1989, the number of flushes on the treated area exceeded that of the untreated area by >8 flushes and by as many as 39 in 1992. During

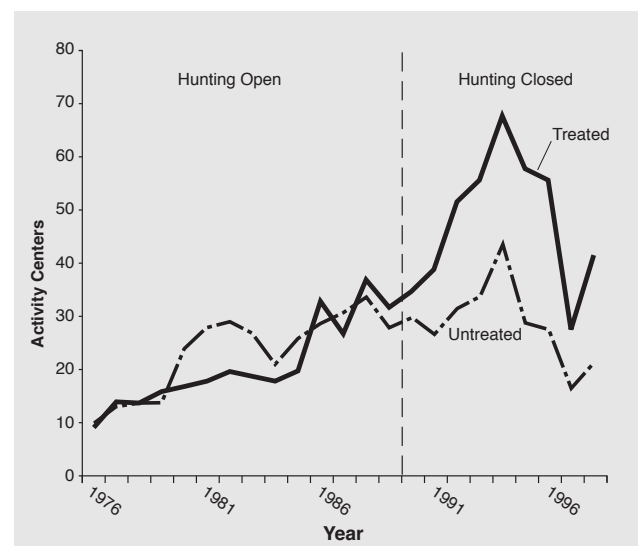
Figure 15. Number of grouse flushed per 1.61 km during fall flush counts (n=10) on treated and untreated areas at the Barrens grouse habitat study area, 1979–98.



1990–1996 the average number of grouse flushed/1.61 km was 0.61 and 0.30 for the treated and untreated areas, respectively.

During fall, the average number of grouse flushed during 1979 through 1989 was 47 (range 15–82) and 34 (range 12–65) for the treated and untreated areas, respectively. The maximum number flushed on the untreated area was the 65 recorded during each of 1984 and 1985. During 1979–1989, the average number of flushes/1.61 km (Fig. 15) was 0.62 and 0.43 for the treated and untreated areas, respectively. After 1989, the average number flushed during 1990–1998 was 46 (range 21–91) and 34 (range 11–45) for the treated and untreated areas, respectively. During each year following 1989 the number flushed on the treated area exceeded that of the untreated area by >5 flushes and by as many

Figure 16. Number of activity centers used by drumming grouse on the treated and untreated areas at the Barrens grouse habitat study area, 1976–98.



as 46 in 1993. During 1990–1998, the average number of grouse flushed/1.61 km was 0.61 and 0.35 for the treated and untreated areas, respectively.

■ Abundance — breeding male counts — The number of activity centers occupied by drumming males in the treated area increased from nine in 1976 to 68 in 1994 (Fig. 16). In the untreated area, the number of activity centers increased from 10 in 1976 to 44 in 1994. During 1980 through 1985 the number of activity centers in the untreated area was higher than in the treated area. This trend was reversed in 1988 and in subsequent years when the number of activity centers on the treated area exceeded the number on the untreated area (Fig. 16). During the last 11 years (1988–1998), the number of activity centers on the untreated area averaged 30 (range 17–44), compared to an average of 46 (range 26–68) on the treated area.

The relative high number of activity centers on the treated area became more pronounced in 1991, which was two years after the entire study area was closed to hunting for ruffed grouse. By 1994 and continuing through 1996, the number of activity centers on the

treated area was two times greater than on the untreated area.

BEHAVIORAL RESPONSES

■ Onset and use of cut patches by breeding males — Activity centers in the aspen-scrub oak patches cut during 1976–77 were first established by male ruffed grouse in 1981, which was five years post-treatment (Fig. 17). By 1985 (nine years after cutting), the density of activity centers in the A aspen-scrub oak patches was 10 per 100 ha, and reached 25 per 100 ha in 1993, near a peak of the grouse population, then dropped to 10 per 100 ha in 1997.

The first use of the mixed oak A patches occurred in 1983, seven years after cutting (Fig. 17). The density of activity centers in these A patches was eight per 100 ha by 1985, reached 33 per 100 ha at the grouse population peak in 1994, and dropped to nine per 100 ha by 1997.

Except for 1986, use of A patches in the aspen-scrub oak type was more pronounced than in the A patches in mixed oak until 1987. However, from 1988 through 1998, the density of drumming males in mixed oak A patches equaled or exceeded the density of those in the aspen-

Figure 17. Density of drumming grouse activity centers by year of cut in mixed oak and in aspen-scrub oak on the treated area at the Barrens grouse habitat study area, 1976–98.

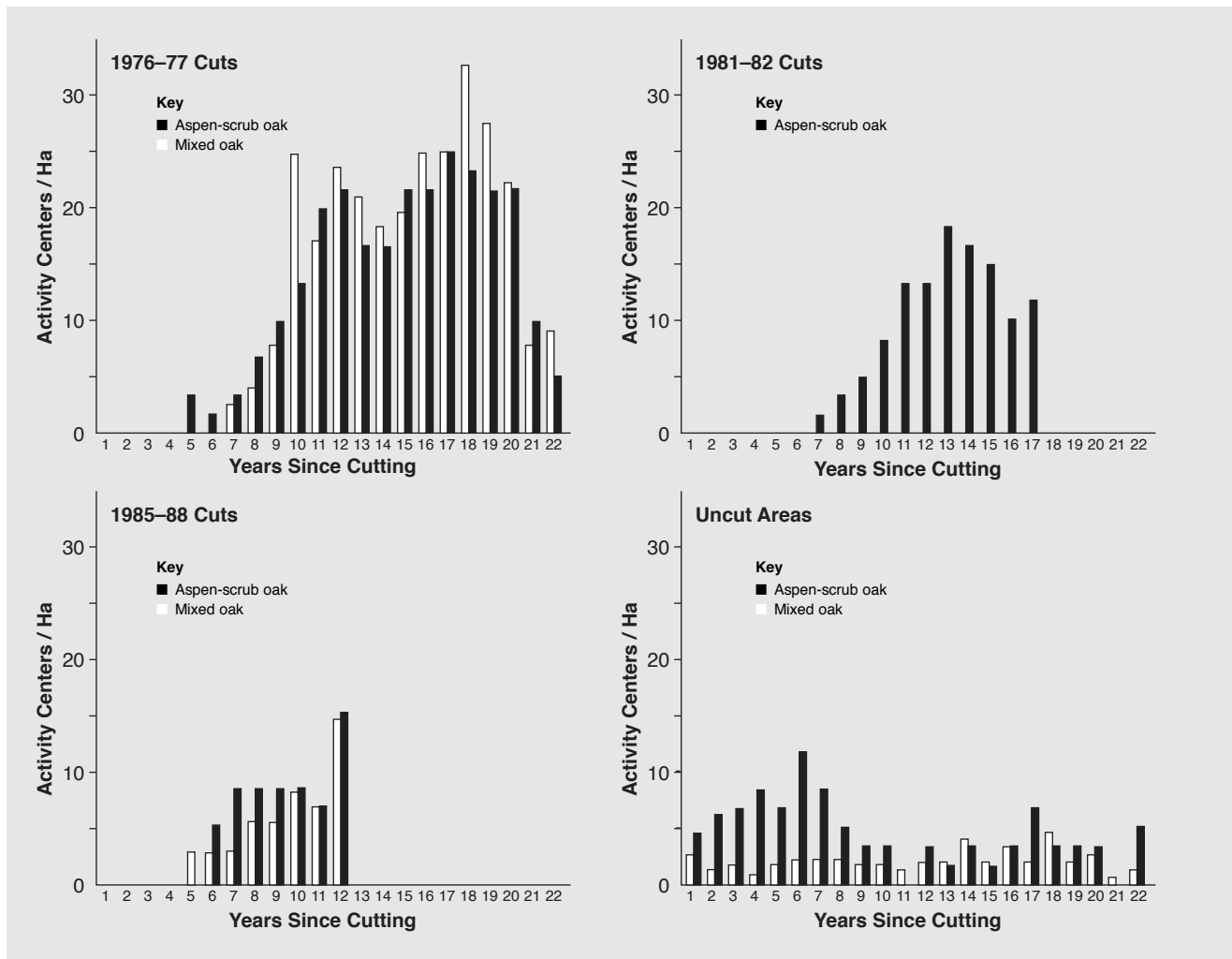


Table 3. Attributes of primary and alternative drumming logs used by grouse during 1976–97, and attributes of active and inactive logs on the untreated area in 1998, at the Barrens grouse habitat study area.

Site	Height of platform				Log diameter			Log length		
	n	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range
Primary	259	30.7	9.6	5–65	38.5	25.2	6–155	9.6	4.5	1–21
Alternate	92	31.0	10.1	10–64	38.6	24.6	11–125	10.0	6.2	1–41
Primary and alternate	64	30.7	9.2	5–10	36.2	24.2	10–120	10.0	4.7	1–20
All logs	415	30.8	9.6	5–65	39.0	30.6	6–155	9.7	4.9	1–41
1998 (untreated only)										
Active	17	36.1	11.0	20–60	53.8	30.3	20–110	11.0	4.0	4–16
Inactive	29	37.9	19.0	13–70	39.0	14.1	20–65	9.8	6.0	2–20

scrub oak A patches for eight of 11 years.

The first use of aspen-scrub oak B patches cut in 1981–82 occurred during 1988, seven years following cutting (Fig.17). The density of drummers trended upward and reached 18 per 100 ha during the grouse population peak in 1994, then dropped to 10 per 100 ha by 1997. This was similar to the 10 and nine drummers per 100 ha in A patches for aspen-scrub oak and mixed oak, respectively, in 1997.

The C patches in aspen-scrub oak and B patches in mixed oak were cut during 1985–1988. Activity centers became established in mixed oak in 1991, six years following cutting, and in 1992, seven years after cutting, in aspen-scrub oak (Fig. 17). By the grouse population peak in 1994 the densities of drummers were five and eight per 100 ha for mixed oak and aspen-scrub oak, respectively. In 1998 the density of drummers was seven per 100 ha in these mixed oak patches and nine in aspen-scrub oak. For the patches cut in 1985–1988, after the initial year in mixed oak, the density of drummers was greater in every year for the aspen-scrub oak.

For all cut patches, drumming males established activity centers five to seven years following cutting. Drumming densities in the A patches, cut in 1976–77, peaked in 1993–94, and some of these patches were still being used in 1998, 22 years after they were cut. The aspen-scrub oak patches and the mixed oak patches provided drumming habitat for ≥ 18 and 17 years, respectively. The number of drummers in aspen-scrub B patches also peaked in 1994, and in 1998 was similar to the A patches in drummer densities. The number of drummers in mixed oak B patches and aspen-scrub C patches (both cut in 1985–88) dropped after the grouse population peak in 1994, but in 1998 had both rebounded to their greatest densities to-date.

■ **Drumming site attributes** — During 1976 through 1997 we examined 472 drumming sites within 316 activity centers, and measured the physical dimensions of the drumming platforms at 415 sites. Ninety-nine percent of the drumming site platforms in the untreated area were on logs, whereas the platforms in the treated area were more diverse (81 percent logs, 14 percent stumps, 5 percent rocks).

Drumming logs located throughout the entire study area during 1976 through 1997 were associated with pri-

mary, alternate, or a combination of primary and alternate sites (Table 3). For all logs combined the mean height of the drumming platform was 31 cm, mean diameter of the logs was 39 cm, and mean length of drumming logs was 10 meters. The physical

dimensions of logs measured at active and inactive sites during 1998 on the untreated area were like those measured during 1976 through 1997. As well, there was no difference in the structure of logs between active and inactive sites (Table 3).

For the 1998 logs, shrub cover at active sites was 5.6 percent, similar to the 5.5 percent at inactive sites. Percent canopy cover was also similar, with 88 percent at active sites and 83 percent at inactive sites.

In 1998, the mean density of saplings at active sites ($n = 17$) for the combined mixed oak and aspen-scrub oak types was 109 per 100 m² compared to 108 per 100 m² at inactive sites ($n = 29$). However, sites in only the mixed oak showed a difference in stem density of seedlings and saplings between active and inactive sites (Table 4). The mean stem density at active sites was greater for all stem height categories compared to that of inactive sites, and the total stem density averaged 99 stems per 100 m² at the active sites and 51 stems per 100 m² at the inactive sites.

■ **Alternate drumming sites** — We identified 316 activity centers used 1,256 times during 1976–1997. During this time, the density of grouse ranged from 1.6 males per km² to 12.5 males per km² on the treated area and from 1.7 males per km² to 7.6 males per km² on the untreated area. Density estimates in the treated and untreated areas were highly correlated ($r = 0.75$, $P < 0.001$).

The percentage of males using at least one alternate display site within an activity center was highly correlated ($r = 0.873$, $P < 0.001$) with the density of drumming males on the entire study area (Table 5). The percentage of males using alternate sites on the study area ranged from 2.4 percent when the density of males was 3.7 per km² to 42.9 percent when the density of males exceeded seven males per km². The same relationship was evident for

Table 4. Mean density (stems/100 m²) of seedlings, <2.54 cm dbh and >0.30 m height, and saplings, 2.54–12.45 cm dbh, at active logs in mixed oak on the untreated area at the Barrens grouse habitat study area, 1998.

Log type	n	Stem height (m)			Total ^a
		> 0.3–1.0	> 1.0–1.5	> 1.5	
Active	9	12.0	19.3	67.9	99.2
Inactive	10	4.0	5.2	41.9	51.1

Table 5. Number of drumming male grouse and percent using alternate drumming sites on the Barrens grouse habitat study area, 1976–1997.

Year	Treated Area			Untreated Area		
	Drumming males (n)	Males with alternate sites (n)	(%)	Drumming males (n)	Males with alternate sites (n)	(%)
1976	10	0	0.0	9	0	0.0
1977	13	0	0.0	14	0	0.0
1978	14	0	0.0	14	0	0.0
1979	14	0	0.0	16	0	0.0
1980	24	1	4.2	17	0	0.0
1981	28	2	7.1	18	0	0.0
1982	29	3	10.3	20	0	0.0
1983	27	4	14.8	19	0	0.0
1984	21	2	9.5	18	2	11.1
1985	26	6	23.1	20	6	30.0
1986	29	8	27.6	33	11	33.3
1987	31	7	22.6	27	8	29.6
1988	34	8	23.5	37	10	27.0
1989	28	4	14.3	32	8	25.0
1990	30	9	30.0	35	8	22.9
1991	27	13	48.1	39	6	15.4
1992	33	9	27.3	52	11	21.2
1993	34	13	38.2	56	21	37.5
1994	44	16	36.4	68	32	47.1
1995	29	13	44.8	58	25	43.1
1996	28	5	17.9	56	16	28.6
1997	17	2	11.8	28	9	32.1

drumming males on both treated and untreated areas.

Sixty-six percent ($n = 211$) of the activity centers contained only primary drumming sites, whereas 6 percent always contained a primary and one or more alternate sites. The remaining 87 activity centers (28 percent) showed variable annual inclusion of alternate drumming sites. The persistence (number of years used) of activity centers was similar between those that contained only primary logs (median = 2 years) and those that always contained alternate logs (median = 2.5 years) ($P = 0.973$). Centers that had variable inclusion of alternate sites persisted longer (median = 6 years) than other cen-

ters ($P < 0.001$). We observed one activity center on the untreated area that was used for 17 years. There was no difference between persistence of use of centers on the untreated and treated areas ($P = 0.151$).

We observed 73 activity centers with more than one alternate drumming site. The number of alternate drumming sites used by individual grouse within activity centers increased with grouse density and with the proportion of males using alternate sites within activity centers (Fig. 18). The greatest number of alternate sites used within an activity center was five (four logs, one stump) observed in the treated area during 1994, a year of high density. More primary sites were located on logs (92 percent) than alternate sites (79 percent), whereas alternate sites were located more frequently on stumps (20 percent of alternate sites versus 5 percent of primary sites).

The majority (97 percent) of alternate sites were located within 90 m of the primary site (Fig. 19). Distances between primary and alternate sites were not normally distributed ($P < 0.01$). Median distance between alternate and primary sites during all years was greater ($P = 0.009$) in the untreated (31.8 m) than the treated area (26.5 m). There was no correlation between primary to alternate site distance within activity centers and annual density of drumming males in the untreated ($r = 0.05$, $P = 0.517$) and treated ($r = -0.02$, $P = 0.779$) areas.

We detected strong directional fidelity among alternate sites relative to their associated primary site within an activity center. There were no differences among median measures of circular dispersion for activity centers that contained two, three, or four alternate sites in a given year ($P = 0.211$) or between activity centers in the treated and untreated areas ($P = 0.837$). There was no overall directional trend in the orientation of alternate sites relative to their respective primary sites throughout the study area ($P = 0.998$). We did not detect a directional relationship between the spatial arrangement of

Figure 18. Number of alternate drumming sites used by individual grouse and density of activity centers at the Barrens grouse habitat study area, 1980–97.

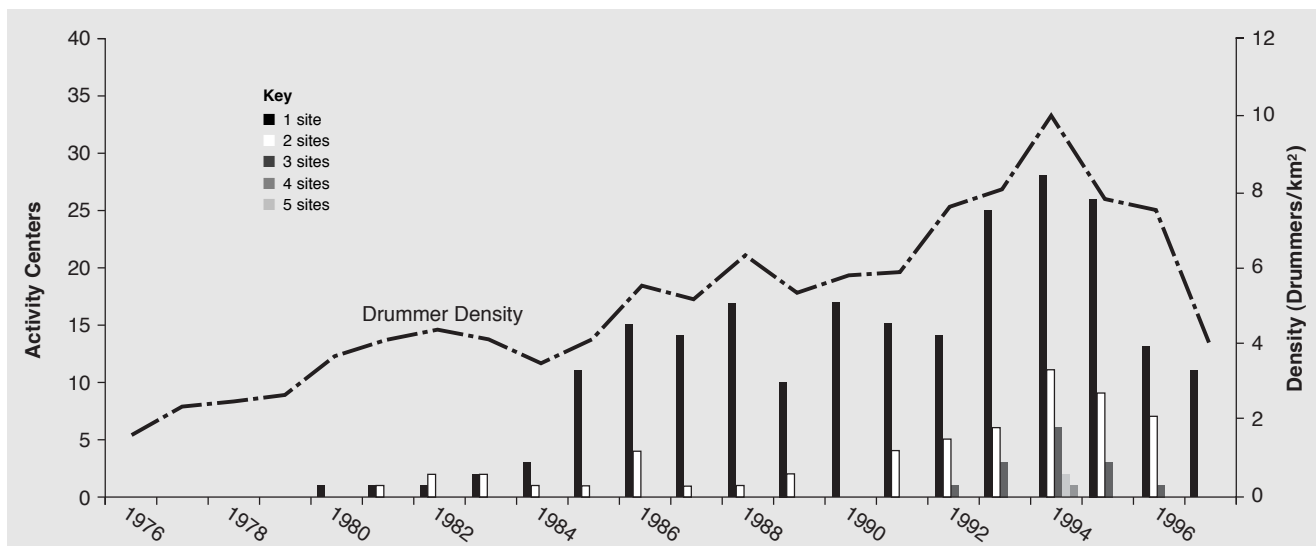
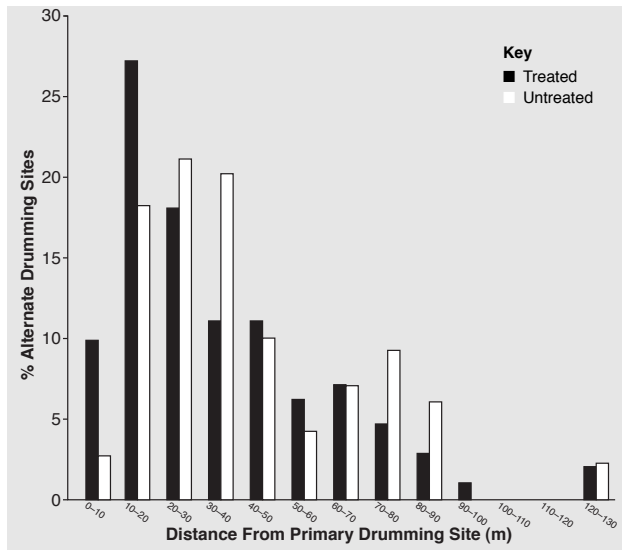


Figure 19. Frequency of alternate-to-primary drumming site distances on the treated ($n = 235$) and untreated ($n = 153$) areas at the Barrens grouse habitat study area, 1980–97.



alternate drumming sites within an activity center and direction of the nearest neighboring activity center ($P = 0.945$).

DISTRIBUTION OF FLUSHES AND ACTIVITY CENTERS RELATIVE TO HABITAT TYPES

Spring and fall flush counts indicated individual areas of habitat with relatively high grouse numbers (Figs. 20 and 21) across the entire study area. At the same time, there were blocks throughout the treated area that had zero flushes over the time intervals shown. This situation reflected the diversity of habitat structure, and the preferences of grouse for specific habitats.

The same blocks did not always have the greater number of flushes for both seasons. There was a relatively low correlation ($r = 0.51$) between spring and fall flushes. Of the 41 blocks with relatively high spring flushes (≥ 7), 16 (39 percent) were not the blocks with the greater number (≥ 10) of flushes in the fall. Of the 49 blocks with greater fall flushing rates, 21 (43 percent) were also ranked with relatively high spring flushes. On average, one half of the blocks for either season had relatively high flushes for both seasons. There were zero flush blocks for both spring and fall that had flushes in the contrasting season.

For the entire study area, higher spring and fall flush counts tended to be on the slopes and upper elevations, away from the low-lying areas adjacent to the main road (Figs. 20 and 21). On the untreated area, lower numbers of flushes were recorded in the southern sector, compared to the northern sector, where flushes were concentrated in areas with a shrubby understory. The southern sector of the untreated area had more extensive stands of mature mixed oak compared to the northern sector. The northern sector had diverse habitat with scrub oak, and other shrubs, that mimicked the treated

Figure 20. Location of spring grouse flushes by 4-ha blocks at the Barrens grouse habitat study area, 1982–98.

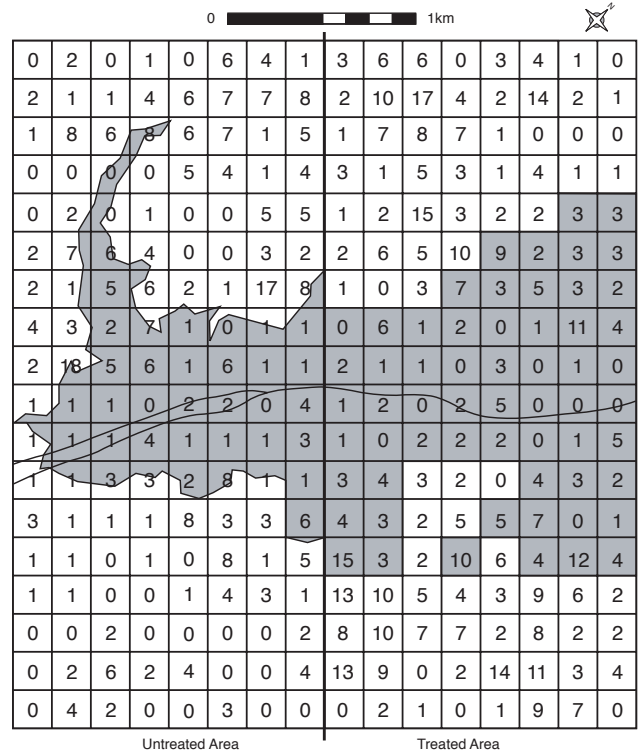
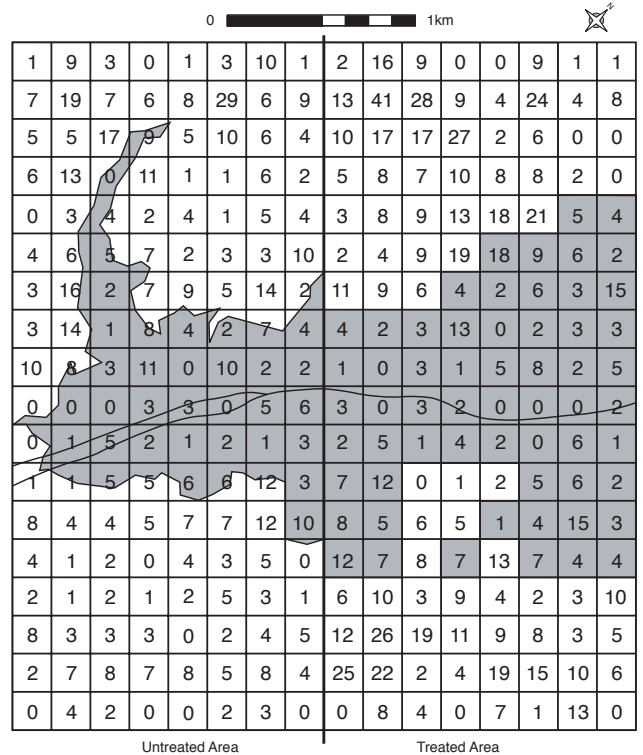
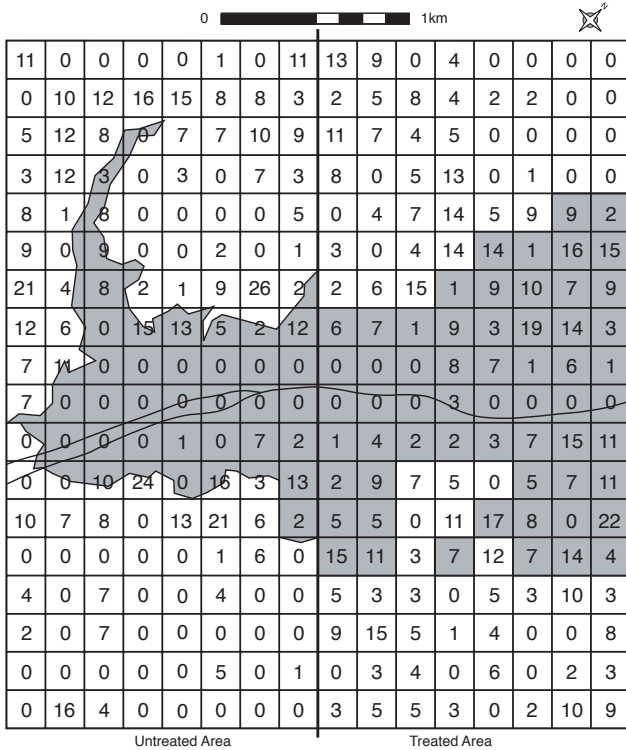


Figure 21. Location of fall grouse flushes by 4-ha blocks at the Barrens grouse habitat study area, 1981–98.



area in some ways. In the treated area, both spring and fall flush counts indicated relatively higher use by ruffed grouse in the mixed oak cover type compared to in the aspen-scrub oak. The density of flushes, for both seasons combined,

Figure 22. Location of drumming activity centers by 4-ha blocks at the Barrens grouse habitat study area, 1976–98.



in the mixed oak was double that in the aspen-scrub oak. The aspen-scrub oak blocks with greater numbers of flushes tended to be concentrated in the transition zone, on the slopes where this cover type was changing to the mixed oak type. Many of the aspen-scrub oak blocks adjacent to the main road were in frost pockets and had more grassy areas and areas with low shrubs and few trees.

Grouse drumming activity centers, like the flushes, were distributed across the study area (Fig. 22). Some blocks had no activity centers, while other blocks had relatively high numbers of centers. This indicated again the diversity of the area, with some blocks providing good drumming habitat and others apparently not having suitable sites for drumming. For the study area as a whole, blocks with the greater number (≥ 7) of activity centers were not always the same as the blocks with relatively high numbers of flushes. There was little correlation between activity centers and either spring flushes ($r = 0.19$) or fall flushes ($r = 0.28$).

On the untreated area, blocks with greater numbers of flushes (spring or fall) were not always used as activity centers by breeding males (Fig. 20, 21, and 22). However, the blocks containing the greater number of activity centers tended to be in or near higher flushing blocks.

On the treated area, the number of activity centers was greater in the aspen-scrub oak type than in the mixed oak type (Fig. 22). For the mixed oak type the blocks with relatively greater numbers of flushes did not always have greater numbers of activity centers. However, the mixed oak blocks with greater numbers of activity

centers tended to be in or adjacent to blocks with high spring and/or fall flushes.

Activity centers in the aspen-scrub oak type were found both in the blocks with and those without relatively large numbers of spring/and or fall flushes (Figs. 20, 21, and 22). Also, blocks with relatively large numbers of centers did not necessarily have the greatest number of flushes for this cover type. Both young aspen patches and the scrub oak associated with all ages of aspen provided good drumming habitat.

Over time, there was a change in the distribution of drumming activity centers relative to habitat type. In 1976 most of the suitable drumming habitat was in the aspen-scrub oak type. As more cutting occurred in the treated area, there was a shift in the distribution of activity centers by cover type.

In 1981 there were 46 drumming activity centers on the study area, 28 in the untreated area, and 18 in the treated area (Fig. 23). On the treated area 14 of the 18 activity centers were in the aspen-scrub oak type. Ten years later in 1991, the number of activity centers increased to 66. The number on the untreated area was 27, similar to the 28 in 1981; the pattern or distribution of activity centers on the untreated area was very similar to that in 1981 (Figs. 23 and 24). Meanwhile, on the treated area the number of activity centers had increased by 117 percent to 39, and the proportion of centers in the mixed oak type went from the 22 percent in 1981 to 51 percent ($n = 20$) in 1991, a major shift in distribution (Figs. 23 and 24).

Following the grouse population peak in 1994, the 45 activity centers on the study area in 1997 was similar to the 46 in 1981. However, with 17 on the untreated area and 28 on the treated area, the division was almost the reverse of that found in 1981 (Figs. 23 and 25). Activity centers on the untreated area in 1997 were distributed in a pattern similar to the one in 1981. On the treated area in 1997, not only were there relatively more activity centers compared to the untreated area, but within the treated area the distribution of centers remained quite different from the pattern of centers in 1981, with 43 percent found in the mixed oak. During 1976–1997, the average distance between nearest-neighboring activity centers was 250 m ($SD = 83$, range = 171–436 m) for the untreated area and 260 m ($SD = 72$ m, range = 172–457 m) for the treated area.

HOME RANGE AND HABITAT USE

■ **Adult females and broods** — Twenty-three adult female ruffed grouse with broods were fitted with radio transmitters, 13 in 1986 and 10 in 1987. Of the radio-equipped hens, one moved 2,400 m from the boundary of the treated area within seven days of capture, and another was found dead 710 m from its capture location 20 days after capture. The 21 remaining birds stayed within the study area and survived at least 30 days from the time of capture. A total of 919 locations were used for analysis of habitat use, and an average of 44 usable loca-

Figure 23. Activity centers occupied (indicated by star) by drumming grouse at the Barrens grouse habitat study area in 1981.

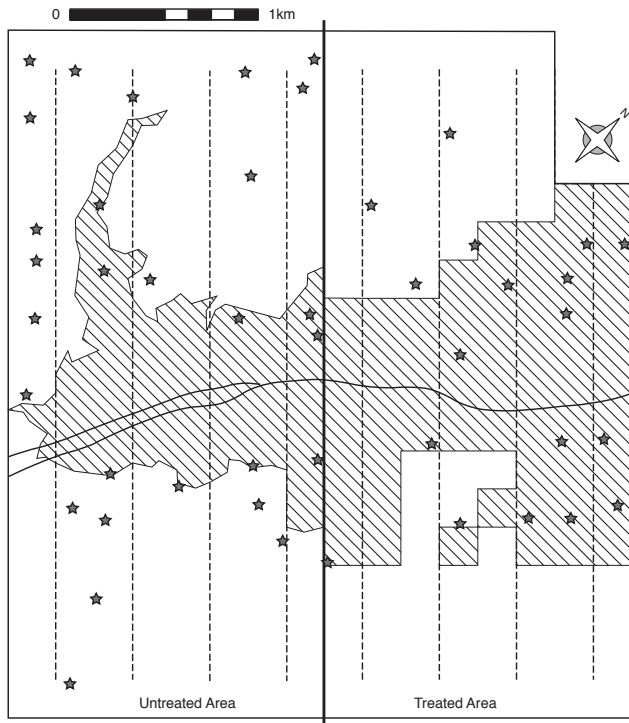
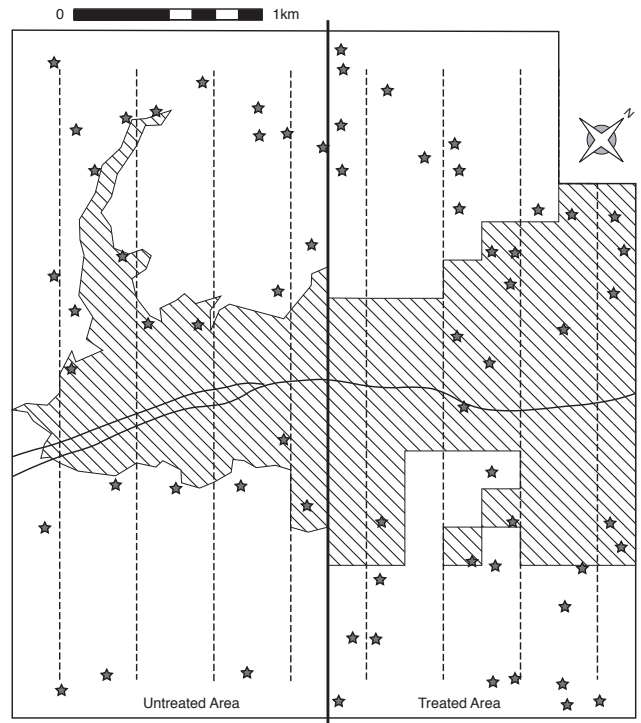


Figure 24. Activity centers occupied (indicated by star) by drumming grouse at the Barrens grouse habitat study area in 1991.



tions were recorded for each radio-tagged grouse.

Mean home range size of all adult females was 59.4 ha using the 95 percent harmonic mean method, and 84.4 ha using the minimum convex polygon method. Eight grouse stayed almost entirely (≥ 95 percent of locations) within the untreated area; six grouse stayed almost entirely within the treated area. The seven remaining grouse were located within both the untreated and treated areas. Mean home range of grouse that used both the untreated and treated areas was twice (89.9 ha) that of grouse using only the untreated (43.7 ha) or treated area (44.9 ha). Grouse were located uniformly throughout the treated area, whereas 67 percent of all grouse locations on the untreated area were within the northern half of the study area.

Macrohabitat: Based on use of the eight habitat types defined in 1986–87 (Table 6), the mixed oak-scrub oak type was selected, the herbaceous-clearcut and pine-scrub oak types were avoided, and the scrub oak, aspen, aspen-mixed oak, aspen-scrub oak, and mixed oak types were used in proportion to their availability (Table 7).

Some patches were used disproportionately to their availability on the treated area in both 1986 and 1987 ($P < 0.001$). The mixed oak-A patch type was selected in 1986, and was used in proportion to its availability in 1987. In 1986, all other

patch types were avoided. In 1987, aspen-A patches were selected, aspen-B, uncut mixed oak, and uncut aspen patch types were used in proportion to availability, and mixed oak-B and aspen-C patches were avoided (Table 8).

Microhabitat: Our analysis of microhabitats used by adult females and broods indicated differences ($P < 0.007$) between used and random sites throughout the entire study area for two vegetation variables and two distance variables (Table 9). Density of woody stems 2.5–7.5-cm dbh and percent cover of live vegetation < 2 m in height were greater at used sites than at random sites. Distance to nearest edge and distance to nearest opening were less at used sites than at random sites, suggesting that forest openings and habitat edges were important components.

Table 9. Microhabitat comparisons between sites used by female grouse with broods ($n = 120$) and random sites ($n = 60$) at the Barrens grouse habitat study area, 1986–87.

Variable	Used		Random		P
	\bar{x}	SE	\bar{x}	SE	
Canopy height (m)	14.1	0.9	16.7	1.2	0.092
Canopy cover (%)	77.7	2.0	79.3	2.8	0.257
Small stem density (/ha)	21,106	1,558	11,496	2130	<0.001
Large stem density (/ha)	294.2	32.4	429.2	85.1	0.075
Basal area (m ² /ha)	11.0	0.6	11.3	1.0	0.936
Woody species (no.)	4.0	0.2	4.9	0.4	0.283
Cover live veg <2 m (%)	78.4	1.5	65.5	3.1	0.001
Cover dead veg <2 m (%)	8.3	0.8	9.0	1.1	0.587
Distance to edge (m)	24.8	2.1	52.3	3.3	<0.001
Distance to opening (m)	40.4	7.1	70.1	13.5	0.006
Slope (%)	11.5	0.6	11.0	0.9	0.736
Ground cover					
Organic litter (%)	95.9	0.5	96.3	0.6	0.575
Bare ground (%)	0.6	0.1	1.3	0.4	0.027
Logs (%)	2.9	0.4	2.3	0.4	0.280
Moss and lichen (%)	1.0	0.3	0.6	0.2	0.498
Herbaceous (%)	24.8	2.0	27.5	3.7	0.492

Table 10. Microhabitat comparisons between random sites on the treated ($n = 30$) and the untreated ($n = 30$) areas at the Barrens grouse habitat study area, 1986–87.

Variable	Used		Random		P
	\bar{x}	SE	\bar{x}	SE	
Canopy height (m)	17.5	1.9	16.0	1.4	0.539
Canopy cover (%)	78.8	5.4	79.8	5.2	0.896
Small stem density (/ha)	12,479	3,771	10,513	2,044	0.648
Large stem density (/ha)	542.0	166	315.8	33.0	0.185
Basal area (m ² /ha)	11.3	1.5	11.3	1.5	0.961
Woody species (no.)	5.4	0.8	4.4	0.4	0.256
Cover live veg <2 m (%)	64.0	4.2	67.2	4.7	0.616
Cover dead veg <2 m (%)	9.0	1.84	8.9	1.32	0.965
Distance to edge (m)	28.1	3.3	76.5	17.3	0.008
Distance to opening (m)	54.1	19.9	86.1	18.1	0.239
Slope (%)	10.6	1.2	11.4	1.2	0.877
Ground cover					
Organic litter (%)	94.6	1.0	98.0	0.7	0.006
Bare ground (%)	1.8	0.7	0.8	0.4	0.214
Logs (%)	94.6	1.0	98.0	0.7	0.006
Moss and lichen (%)	1.8	0.7	0.8	0.4	0.213
Herbaceous (%)	27.2	4.2	27.8	6.1	0.940

stems were key attributes of high quality habitat for males during the breeding season. The density of stems > 12.5 cm dbh was greater ($P < 0.05$) at inactive sites than at active and random sites (Table 14). Conversely, the density of woody stems in the 2.6–12.5 cm dbh size class was higher ($P < 0.05$) at active sites compared to the inactive and random sites. Stem densities per ha in this size class ranged from 3,500 to 13,000 at active sites, 1,000 to 5,500 at inactive sites, and 0 to 5,500 at random sites. The majority of the active sites were in clearcut patches < 15 years old, whereas 50 percent of the inactive sites were in uncut patches.

The dominant woody stems > 12.5 cm dbh on the treated area were aspen, black cherry, and pitch pine at active sites. Aspen, black cherry, and mixed oaks were dominant at inactive sites, whereas mixed oak had the greatest importance values at random sites. For woody

Table 11. Seasonal minimum convex polygon (MCP) and 95% harmonic mean home range estimates (ha) for male grouse at the Barrens grouse habitat study area, 1990–91.

Season	n	Treated area				Untreated area				
		MCP		Harmonic Mean		MCP		Harmonic Mean		
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	
Breeding ^a	11	5.0	1.2	6.6	0.9	8	7.2	1.6	9.4	2.3
June	11	5.5	1.7	5.6	1.4	8	6.1	1.0	7.7	1.4
July	9	5.6	1.1	7.3	1.6	8	5.8	1.5	7.4	1.9
August	6	4.4	1.3	5.3	1.2	7	6.0	2.0	8.6	3.3
Summer ^b	11	11.3	2.8	11.6	2.4	8	12.2	2.1	13.6	2.3

^a Capture – May 31.

^b June 1 – August 31 or earlier loss of contact.

stems in the 2.6–12.5 cm size class, aspen, black cherry, red maple, and scrub oak were dominant at active sites. Black cherry, red maple, and aspen were dominant at inactive and random sites. Perhaps the most striking differences between active and inactive sites on the treated area were the presence of scrub oaks and the more uniform representation of aspen and black cherry in terms of density, dominance, and frequency at the active sites. The relatively high importance value of scrub oaks at active sites compared to inactive sites stood out as a significant difference in habitat structure between used and unused activity sites. For example, the importance value of scrub oak was 31.4 at active sites, compared to 12.0 at inactive sites for woody stems 2.6–12.5 cm dbh (McDonald 1993).

At the untreated area, the mean density and mean dbh were not different among active, inactive, and random sites for woody stems in both the > 12.5 cm and 2.6–12.5 cm size classes. In the > 12.5 cm size class, white oak had the greatest importance value at all three site types. The importance value of black cherry was greater at active sites than at inactive and random sites. For woody stems in the 2.6–12.5 cm size class, red maple,

Figure 26. Trends in the use of patches, by cover type and year of cut, on the treated area at the Barrens grouse habitat study area in 1987, 1993, and 1998.

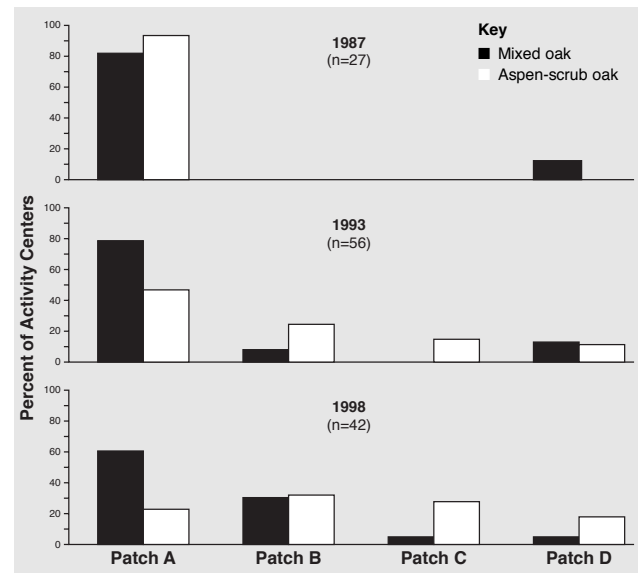


Table 12. Habitat use by male grouse during the breeding season (capture–May 31) and summer (June 1–August 31) relative to availability on the treated area at the Barrens grouse habitat study area, 1990–91.

Habitat type	Proportion of area	Breeding		June		July		August		Summer	
		Use	Pref. ^a	Use	Pref.	Use	Pref.	Use	Pref.	Use	Pref.
Grassy-open	0.04	0.02	0	0.01	-	0.03	0	0.01	-	0.02	-
Aspen-black cherry saplings	0.13	0.30	+	0.28	+	0.25	+	0.08	0	0.23	+
Aspen-black cherry sparse saplings	0.03	0.00	-	0.00	-	0.02	0	0.02	0	0.01	-
Aspen-black cherry poletimber	0.06	0.10	0	0.08	0	0.07	0	0.08	0	0.08	0
Aspen-black cherry sawtimber	0.01	0.00	-	0.01	0	0.00	-	0.00	-	<0.01	-
Scrub oak	0.04	0.02	0	0.04	0	0.06	0	0.01	-	0.04	0
Mixed oak saplings	0.10	0.30	+	0.17	+	0.20	+	0.13	0	0.17	+
Mixed oak sparse saplings	0.07	0.07	0	0.09	0	0.10	0	0.08	0	0.09	0
Mixed oak poletimber	0.02	0.08	+	0.11	+	0.06	+	0.23	+	0.11	+
Mixed oak sawtimber	0.47	0.12	-	0.21	-	0.22	-	0.38	0	0.24	-
Pine-mixed forest	0.03	0.01	-	0.01	-	0.00	-	0.01	0	0.01	-

^a 0, habitat used in proportion to availability ($P > 0.0023$); -, habitat used less than availability ($P < 0.0023$); +, habitat used more than availability ($P < 0.0023$).

Table 13. Habitat use by male grouse during the breeding season (capture–May 31) and summer (June 1–August 31) relative to availability on the untreated area at the Barrens grouse habitat study area, 1990–91.

Habitat type	Proportion of area	Breeding		June		July		August		Summer	
		Use	Pref. ^a	Use	Pref.	Use	Pref.	Use	Pref.	Use	Pref.
Grassy-open	0.04	0.01	-	0.02	0	0.01	-	0.02	0	0.02	-
Aspen-black cherry saplings	0.01	0.00	-	0.00	-	0.00	-	0.00	-	0.00	-
Aspen-black cherry sparse saplings	0.01	0.02	0	0.01	0	0.00	-	0.00	-	<0.01	-
Aspen-black cherry poletimber	0.14	0.42	+	0.36	+	0.39	+	0.37	+	0.37	+
Aspen-black cherry sawtimber	0.02	0.10	+	0.10	+	0.10	+	0.02	0	0.10	+
Scrub oak	0.05	0.05	0	0.02	-	0.01	-	0.01	-	0.01	-
Mixed oak saplings	0.01	0.00	-	0.00	-	0.00	-	0.00	-	0.00	-
Mixed oak sparse saplings	0.01	0.00	-	0.00	-	0.00	-	0.00	-	0.00	-
Mixed oak poletimber	0.01	0.02	0	0.04	0	0.01	-	0.01	0	0.02	0
Mixed oak sawtimber	0.62	0.28	-	0.29	-	0.31	-	0.46	-	0.34	-
Pine-mixed forest	0.08	0.10	0	0.11	0	0.17	+	0.11	0	0.13	+

^a 0, habitat used in proportion to availability ($P > 0.0023$); -, habitat used less than availability ($P < 0.0023$); +, habitat used more than availability ($P < 0.002$).

black cherry, and scrub oak had the highest importance values for all sites combined on the untreated area. However, scrub oaks were much less important at inactive than at active and random sites.

Longevity of use of activity centers: Trends in the use of patch types on the treated area throughout our 22-year study reflected the longevity of habitats used by males during the drumming season. The dynamics of use of cut and uncut patches on the treated area indicated high use of cut patches that were 10–21 years old in both the aspen-scrub and mixed oak types (Fig. 26).

Table 14. Woody stem attributes for active and inactive drumming sites and for random sites on the treated area at the Barrens grouse habitat study area, 1990.^a

Site	n	Mean Density (stems/ha)	Mean diameter-at-breast-height (cm)	Mean Basal Area (m ² /ha)
Woody stems > 12.5 cm dbh				
Active	13	65.4A	16.7A	3.5A
Inactive	8	281.3B	19.0A	10.2A
Random	14	126.8A	22.4A	10.6A
Woody stems 2.6–12.5 cm dbh				
Active	13	7,461.5A	4.3A	-
Inactive	8	3,312.5B	5.7A	-
Random	14	1,857.1B	4.5A	-

^a Means with a different letter differ ($P < 0.05$) within a column.

All but two of the activity centers located in 1987 ($n = 27$) were in the 10-year-old A patches cut during 1976 and 1977. The use of A patches in the aspen-scrub oak type, based on the percent of activity centers in each patch, declined from 100 percent in 1987 to 47 percent in 1993, and 23 percent in 1998. By 1998 there was a definite shift by drummers from A to B and C patches in aspen-scrub oak, which were 18 and 12 years old, respectively. Male ruffed grouse selected patches with younger and more dense stands of woody stems.

Use by breeding male grouse of A patches cut in 1976–77 in the mixed oak type also declined through 1987 and 1998. There also was a shift into the B patches, which were 12 years old in 1998. The percent of activity centers located in A patches during 1993 and 1998 was higher in the mixed oak than in the aspen-scrub oak type. Fifty percent of the mixed oak was still uncut, so the preferred habitat structure was more concentrated in the mixed oak type than in the aspen-scrub oak type.

Our counts of stem densities at activity centers during 1990–1991 indicated that suitable habitat for drumming activity in some A patches declined by 13–14 years after cutting. For example, density of saplings (2.6–12.5 cm dbh) at sites inactive during 1987–1990 were less ($P < 0.05$) than at active sites in those years. These findings indicated that stem density at some sites may have been too low to provide suitable breeding habitat. However, since 40 percent of the total activity centers in 1998 were still in A patches, other sites contained suitable drumming habitat 22 years after cutting.

The value of a shrub layer for promoting the longevity of activity centers was most evident on the untreated area (McDonald 1993:90). Activity centers with relatively low sapling densities (1,000/ha), but with a dense understory of scrub oaks or American hazel, were consistently active during multiple years of our study.

Discussion

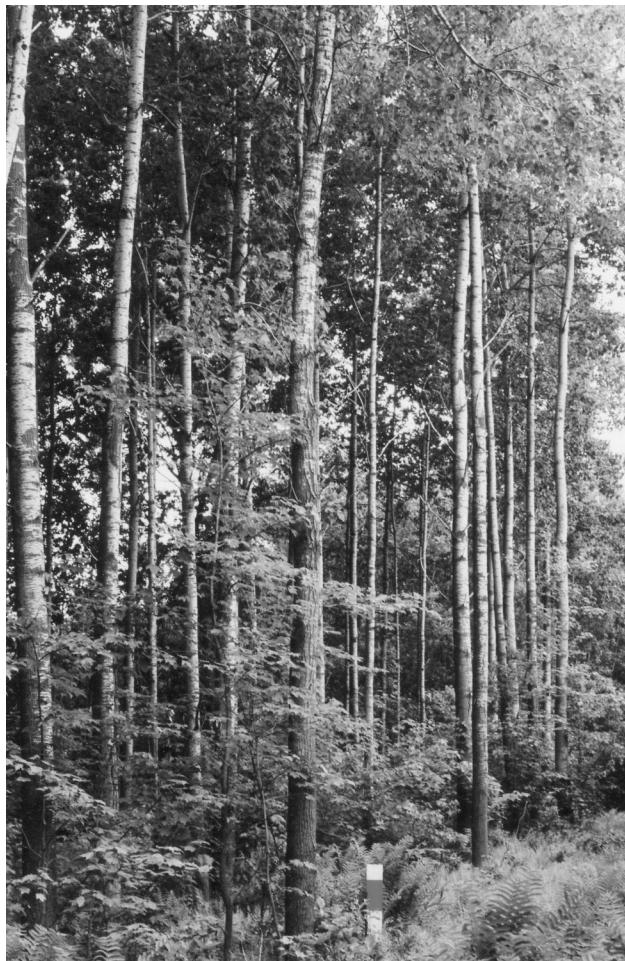
FOREST MANAGEMENT AND PLANT COMMUNITY DEVELOPMENT

■ **Treatments and timber sale** — Prior to this habitat management study, neither Game Commission foresters nor timber buyers were familiar with clearcutting 1-ha patches. Twenty acres was considered a “small” clearcut in Pennsylvania. Therefore, during February and March 1976, sportsmen volunteers cut trees on two 1-ha patches as an example of expectations from prospective timber sales.

Good aspen regeneration requires a relatively clean site. Because much of the study area had a scrub oak component, machine treatment of the understory was done to ensure good aspen regeneration and to maintain the aspen component of the overstory. A secondary beneficial result was rejuvenation of the scrub oak community, because scrub oaks are not long-lived species.

Although our study was not designed with financial gain from timber sales in mind, this may be considered important to other public and private landowners who

Border view of uncut aspen stand.



are managing their lands for ruffed grouse. Over time, the cost-benefit ratio improved with each sale. The timber sale in 1985–88 was the first one to result in a net profit. Projections for the treatments scheduled for the year 2000 were \$17,050 for machine treatments, \$71,950 for timber sale preparation, and \$299,411 income from sale of timber. Thus, the habitat management will be very cost-effective, with total income exceeding total investment by approximately \$137,000 (J. Byerly, personal communication, PGC).

In Pennsylvania, there has been no steady market for aspen, whereas the market for oak has steadily improved over the term of this study. For woodlands not requiring non-commercial treatments (e.g., no large scrub oak component), we believe that managing timber with small patch clearcuts is economically feasible. We also believe that today in Pennsylvania, small patch cuts are economically feasible even with the cost addition of some amount of non-commercial treatments.

■ **Plant community descriptions** — Following clearcutting in the mixed oak type, the regeneration was what we expected based on the pre-cut survey. The number of species present as post-cut saplings was similar to the number of species in pole- and sawtimber size classes prior to cutting. The major species also were present in the pre-cut stand as saplings and seedlings.

Red maple and black cherry, although not as abundant as oaks in the pre-cut overstory, were more abundant in the seedling and sapling categories. Their establishment in relatively greater numbers as post-cut saplings was what we expected following clearcutting in mixed oak stands in central Pennsylvania. However, oaks remained a major component in the sapling stand, with stem densities greater than what was present in the overstory during the pre-cut survey. The response of grouse use for the cuts in the mixed oak type demonstrated the suitability of these patches for both breeding activities and brood habitats.

The relatively greater numbers of aspen saplings in the post-cut aspen-scrub oak patches reflected the presence of aspen in the pre-cut overstory, even though aspen was a minor component of the pre-cut seedlings. This was expected because aspen regenerates, following cutting, by suckering from the lateral root system of the larger trees. Black cherry and red maple increased their presence in the post-cut aspen-scrub oak patches when compared to mixed oaks. Oaks had a greater stem density in the pre-cut overstory than cherry and maple combined. However, maple and cherry had far greater numbers of stems than did oaks in the seedling category and therefore responded better than oaks in the regen-

erating patches for the aspen-scrub oak type.

The number of shrub species present declined by 57 percent following clearcutting. Scrub oak, blueberry, and *Rubus* species predominated both pre- and post-cut. Before cutting, dogwood (*Cornus spp.*) was recorded in 10 of 15 patches in aspen-scrub oak, but in only one patch in mixed oak. Dogwood was found in one patch of each type in the post-cut sample. For post-cut, sweet fern (*Comptonia peregrina*) was present only in the mixed oak, whereas it was present in 11 of 15 aspen-scrub oak patches pre-cut. It appeared that many of the shrub species did not regenerate following the cutting treatments. This may have been due in part to competition from regenerating tree seedlings. Overall, the stem densities of trees and shrubs combined were much greater following cutting.

The majority (14 of 15) aspen-scrub oak patches sampled had a conspicuous scrub oak component in the understory. Pre-cut stem densities of scrub oak seedlings were 75.6 and 720.0/100 m² for mixed oak and aspen, respectively. During the period before the cut patches became attractive to grouse, the more complex understory (e.g., scrub oak) in the aspen-scrub oak type provided more suitable habitat for grouse, especially for breeding males. However, as the plant communities developed in the regenerating mixed oak type, the density of drumming grouse was equivalent to that in the aspen-scrub oak type.

POPULATION RESPONSES

■ **Abundance — spring and fall flush counts** — Spring flushing rates were relatively low until the grouse hunting closure on the study area in 1989. The one substantial increase prior to that time occurred on the untreated area only in 1987. This coincided with a peak in statewide grouse hunter flushing rates, when grouse numbers had risen in all regions in Pennsylvania (Grouse Project Annual Job Report 06291, PGC 1998).

Mature uncut stand in mixed oak type.



Spring flushing rates increased steadily from 1989 to a peak in 1992 and 1993, when the treated area had more than double the rate of the untreated area. Consistently higher flushing rates on the treated area after 1989 reflected the response of grouse to the habitat management.

During the 1980s, fall flushing rates were higher on the treated area than on the untreated area. Fall numbers showed an increase on both areas in 1983–85, at the same time that statewide hunter flushing rates were increasing. When spring grouse indices did not show continued increases at this time, we became concerned about the impact of heavy hunting pressure on the grouse populations. The treated area had higher fall flushing rates after 1989. The peak fall flushing rate was in 1993, when the rate on the treated area was double that on the untreated area.

While both spring and fall flushing rates were consistently higher on the treated area, compared to the untreated area, since the mid-1980s, the relative fall grouse populations were similar on both areas for both the 1980s and 1990s. We believe this reflects the redistribution, prior to fall flushing counts, of the grouse production on the study area as a whole. Both spring indices—flushes and drumming activity centers—indicated generally greater grouse populations in the 1990s, with the treated area having more birds by both indices. By the fall flushing survey, many of the broods had broken up and emigrated.

Although the grouse flushes did not increase greatly on the untreated area, it still had favorable habitat due the scrub oak and other shrub component. This was evidenced by the locations of drumming grouse and both spring and fall flushes.

■ **Abundance — breeding male counts (activity centers)** —When our study began in 1976, the drumming grouse population was small. From 1976–79, we located an average of 26 drumming activity centers

(2.3/100 ha) per year for the entire 1,120-ha study area (treated and untreated). The only previous estimate of grouse abundance on our study area was reported by Bowers and Tanner (1947), who estimated 2.9 drummers/100 ha on a 587-ha portion of the Barrens study area in 1946. During the 1940s, the overall woody plant communities were in an earlier-successional stage compared to 1976, which may have provided more suitable habitat than that at the start of our study. Stands of scrub oak and pitch pine were dominant in the lower elevations, and stands of aspen were more scattered over the area during the 1940s.

Densities of drummers were

similar on both the treated and untreated areas in the mid-70s. From 1980 through 1984 during an increase in the grouse population, the higher densities on the untreated area, at this time, may have been due in part to the fact that 25 percent of the treated area had been removed from drumming habitat by the initial clearcuts. As these patches, and subsequent cuts, developed structure more suitable for drumming activity, the numbers on the treated area increased dramatically. During the grouse population peak in 1994, the density of drummers on the treated area had increased to 12.5 per 100 ha, up by 522 percent from levels in 1976. For the same year on the untreated area, the density of drummers was 7.6 per 100 ha.

The drumming grouse populations on the treated area from 1977–80 (during a population low, with 25 percent of the area clearcut), averaged 2.8/100 ha. These levels were much lower than those reported for more northern latitudes, but were more like those reported for southeastern states (Servello and Kirkpatrick 1988) near the southern boundary of the geographic range of ruffed grouse. During the years 1993–96, when the grouse populations on the study area were relatively high, the density of drummers on the treated area averaged 10.9/100 ha. This was still lower than the 15.8 reported for a three-year period of 1979–81 on a managed study area in Wisconsin (Kubisiak 1985).

For young (5–15 years) aspen stands, drummer densities reported in Wisconsin during a grouse population high in 1988–90 were 20.5/100 ha (McCaffery 1996) and for similar habitats in Minnesota, 19.8–37.8/100 ha (Gullion 1990). When we consider only the young stands on our study area, during 1993–96, the drummer densities were 16.0, 16.4, and 15.6/100 ha of young stand total, mixed oak only, and aspen-scrub oak only, respectively. While not up to the highest grouse number densities reported in the Lake States, our peak year in 1994 on the treated area approached those densities, with 20.5 drumming activity centers/100 ha of young mixed oak and aspen-scrub oak stands combined.

We did not estimate clutch size, brood survival, or survival rates of adult grouse during our study. Therefore, we do not know if these life history attributes of the grouse on our study area were like those reported in the literature. However, if we apply an extension factor (Kubisiak 1984) to our 1994 spring density of 12.5 activity centers/100 ha, the estimated fall population would be 80 grouse/100 ha, or 207/square mile.

Reported densities of drumming males are presented in Table 15. Grouse population fluctuations make it somewhat tenuous to make specific year comparisons between states over different years. Still, it appears that the maximum densities we observed during our study in central Pennsylvania fall between reported densities in southeastern states and those in the Lake States. It appears that most of the maximum reported densities have been associated with 10–15-year-old aspen stands. However, our data indicated that the response in drum-

Table 15. Maximum density of drumming grouse during spring in different regions of eastern United States and Canada, 1930–1996.

Region	Year	Density (no./100 ha)	References
Pennsylvania, central	1993–96	10.9	Present study
Pennsylvania, central	1993–96	16.0*	Present study
Pennsylvania, central	1946	3.1	Bowers and Tanner (1947)
Alberta	1971	10.0	Boag 1976
Georgia	1982	4.4–6.4	Hale et al. 1982
Minnesota	1980–89	19.8–37.8*	Gullion 1990
New York	1935	17.4	Bump et al. 1994
New York, southern	1930–42	9.1	Bump et al. 1994
New York, northern	1930–42	4.3	Bump et al. 1994
Wisconsin, central	1979–81	15.8	Kubisiak 1985
Wisconsin, northcentral	1988–89	20.5*	McCaffery et al. 1996

*Per 100 ha of young forest only.

ming grouse to mixed oak stands was equal to that of aspen stands. Whether the mixed oak forests in Pennsylvania can be managed to create more suitable grouse habitats over a wide region remains unknown.

BEHAVIORAL RESPONSES

In our study, grouse behavioral response was influenced by our habitat management treatments. Habitat use by grouse was a function of the treatment type and timing, removal of material (e.g., machine treatment, logs left or removed), distance between patch and nearest suitable habitat, availability of suitable ground cover, and structure (size and density) of woody stems.

■ **Onset of use of cut patches by breeding males** — Grouse established drumming activity centers as a function of what species of trees existed on a site and vegetative growth rate. Vertical growth, high stem densities, and an open ground layer were key factors.

In our study, grouse began drumming in cut patches at about seven years of age. This was followed by increases in the three different age classes through the grouse population peak in 1994. The density of drumming males in the patches cut during the 1980s was not as great as in the 1976–77 cuts. This difference may have been because young plant communities were more abundant and widely distributed after three cuttings, compared to the years following the initial cutting.

The time span between cutting and initial use by drumming males was similar to what other research had found in the Midwest. At the Mille Lacs study area in Minnesota, grouse began drumming in aspen stands four to six years following cutting (Gullion 1983). Also in Minnesota, at the Cloquet study area, few new stands were occupied prior to 10 years after clearcutting (Gullion 1984). In central Wisconsin, new grouse drumming sites were established with highest frequency in 6- to 10-year-old aspen (Kubisiak 1985). Drumming grouse began using clearcuts in Missouri's oak-hickory forests when the new growth was seven to 10 years old (Barber et al. 1989). On a northern Wisconsin study area, drummers reoccupied young aspen stands when regrowth was five to 10 years old (McCaffery et al. 1996).

Also in our study, we saw a similar grouse drumming response to habitat treatments in both aspen-scrub oak and mixed oak. This was different from what studies had shown in the oak-hickory type in Missouri. Generally, the response to patch cuts in the oak was a new activity, while the activity centers in aspen-scrub oak were re-establishments; this was a profound shift because while there had been very few drummers in the mixed oak, the aspen-scrub oak had held drumming males because of the higher stem densities due to scrub oak, hazelnut, and other shrubs.

■ **Drumming site attributes** — Many grouse studies have described the characteristics of drumming activity centers (Palmer 1963, Gullion 1970, Stoll et al. 1979, Hale et al. 1982, McCaffery et al. 1996). Researchers agree that drumming male grouse select sites with high stem densities, for protection from avian predators, and with a relatively clear view near ground level, to see both ground predators and other grouse (Gullion 1970 and 1977). The physical dimensions of drumming logs and the structure of woody stems with active drumming logs in our study were in agreement with previous studies.

We found a difference in stem density between active sites and inactive (formerly active) sites for the mixed oak type on the untreated area. This also was consistent with other studies (Thompson and Fritzell 1989).

The higher number of alternative objects used for drumming platforms on the treated area was expected as a result of the patch cuttings. While fallen logs are commonly available in many forests, with the timber harvests on the study area, most of the trees were removed. Many good drumming habitats created did not have a suitable log present, but the grouse chose alternative objects such as stumps, dirt mounds, rocks, etc., for the drumming platform. This reaffirmed that what is most important to the drummer is not the object itself, but some stage that elevates him so he can view the surrounding area.

■ **Alternate drumming sites** — We assumed that all drumming sites located within the proximity (e.g., <100 m) of a primary drumming site were used by the same individual

grouse and that these sites comprised an activity center as described by Gullion (1967). Reports of distances between activity centers of neighboring males vary with habitats, topography, and population density. Kubisiak (1989) reported that, during most years, males occupying the best habitats in central Wisconsin were at least 200 m apart, and, in isolated habitats, males were up to 800 m apart. We believe the spacing between activity centers (the averages for nearest-neighboring centers were 260 m for the untreated and 250 m for the treated) was sufficient to allow us to differentiate between adjacent activity centers. Also, the median distance between alternate and primary sites was less than 32 m in both the treated and untreated areas.

We detected strong directional fidelity among alternate sites within an activity center. The lack of a directional relationship between the orientation of alternate drumming sites within an activity center and the direc-

Twenty-two-year-old stand in mixed oak type



Twenty-two-year-old stand in aspen-scrub oak type.



tion to the nearest neighboring activity center suggests that the use of alternate drumming sites was not directed toward the nearest resident male drummer. Use of alternate sites may have been directed toward other individuals. We could not determine if the behavior was directed toward females. It is possible that the use of alternate sites may have been directed toward males that did not occupy static activity centers or silent males in the population.

Ruffed grouse in our study area used up to five alternate and one primary site within an activity center. Our finding of up to five alternate drumming sites was consistent with Aubin (1972), who reported ruffed grouse in Alberta used up to six sites (including the primary site). Our study also was in agreement with other studies concerning the proportion of the male population using alternate sites. Annually, a maximum of 44 percent of the activity centers we examined contained alternate drumming sites during periods of relatively high density. Gullion (1967) reported 44 percent of 168 males, observed during years of varying density in northern Minnesota, used multiple display sites. Similarly, 52 percent of 106 grouse observed from 1972 to 1975 in Alberta used alternate drumming sites within their home range (Boag 1976). Neither of these two studies reported annual variation in the use of alternate sites relative to grouse density, but it seems that, in general, up to 50 percent of the male population may use alternate drumming sites in high density populations.

Distances between alternate sites and primary sites were greater in the unmanaged forest than in the managed forest but were not correlated to annual drumming male density. Gullion (1967) reported several males expanded their activity centers during years of low density in Minnesota. We believe the differences in primary-to-alternate site distance in the managed and unmanaged forests reflected differences in vegetative characteristics of these areas, rather than a response to male density.

DISTRIBUTION OF FLUSHES AND ACTIVITY CENTERS RELATIVE TO HABITAT TYPES

In our study we did not examine the distribution of flushes for individual years, but as a total for a 17-year period for spring flushes and an 18-year period for fall flushes. The location of flushes obviously reflected the diversity in habitat structure and species composition present on the study area. The survey line intervals with recently cut patches also influenced the distribution of flushes. However, the following patterns emerged.

Both spring and fall flushes were heavily distributed toward the treated area. This was the expected response to habitat management. The difference between treated and untreated areas was greater in spring than in fall, in part because fall flushing surveys were subsequent to the beginning of brood breakup and fall dispersal of juvenile birds. For both spring and fall flushes, the distribution weighted toward the treated area was most evident fol-

lowing the closure of the study area to grouse hunting. Because hunting pressure and kill were two to three times greater on the treated area, differences in flushing indices may have been suppressed prior to the closure.

On both the treated and untreated areas, the patches with the highest flush counts indicated relatively greater use of the mixed oak type and the transition zone between the aspen-scrub oak and mixed oak. The mixed oak on the treated area was desirable because of the regeneration following patch cuts, while selected mixed oak sites on the untreated area had a shrubby understory, consisting of predominantly scrub oak and hazelnut.

The relatively low number of flushes adjacent to the road, on both areas, was because these blocks had numerous frost pockets that were occupied with grasses and low-growing shrubs. In the southern sector of the untreated area, the low number of flushes was related to the much narrower band of aspen-scrub oak and more extensive stands of mixed oak with a sparse understory.

Visual inspection of habitat adjacent to survey lines with high numbers of flushes showed relatively high diversity of structure and plant species. A high stem density was usually evident, often associated with grape vines and small openings that provided clusters of ferns, grasses, and other herbaceous species. Overall, flushes were associated with edges containing young plant communities. Of course, survey lines followed edges of the patch cuts; we do not know whether grouse on the edge of, or within, the more contiguous younger habitats created by the treatments were more or less vulnerable to flushes since we surveyed only edges.

We feel that the selection for drumming activity centers also reflected the variety of structure and diversity present on the entire study area. That blocks with high numbers of flushes were not necessarily those with high numbers of activity centers was not surprising. As stated earlier, flushes were sampled only close to survey lines. Activity centers also reflected habitat between survey lines and provided complete censuses throughout the blocks.

The distribution of activity centers between the treated and untreated areas clearly showed the response of drummers to the habitat management. Prior to 1989, the numbers were weighted toward the untreated side, but by the late 1980s, the response of drummers to the initial patch cuttings resulted in a greater number of activity centers on the treated area.

During the early years of our study, on the treated area, the aspen-scrub oak type had more drummers than the mixed oak because the understory was more complex in the aspen-scrub oak, with the scrub oak component providing adequate drumming habitat. Over time, both mixed oak and aspen-scrub regeneration provided suitable habitat for drummers. These conditions resulted in a greater response of grouse populations on the treated area, and within the treated area the redistribution of activity centers into mixed oak showed drummer

densities equal to those in aspen-scrub oak. We feel that in our study, the new distribution of activity centers into the mixed oak illustrated the most dramatic response of ruffed grouse to habitat management. The resultant high densities compared to the aspen-scrub oak clearly show the suitability of small patch cuts in mixed oak for drumming habitat.

HOME RANGE AND HABITAT USE

■ **Adult females and broods** — The mean home range of female grouse rearing broods in our study (59.4 ha) was greater than reported in previous studies. Godfrey (1975) collected 509 locations from six broods in Minnesota, and estimated an average home range size of 12.0 ha. Other estimates of home range size of broods or female grouse with broods ranged from 12.0 to 16.5 ha (Bump et al. 1947, Archibald 1975, Godfrey 1975, Maxson 1978). The expansive home ranges we observed may

have been due in part to larger sample sizes (telemetry locations) relative to other studies. Home range estimators in general, particularly the minimum convex polygon technique, can be strongly influenced by sample size (Boulanger and White 1990). Large home ranges estimated in our study also may have been because broods were monitored into September and may have ranged greater distances just prior to breakup and dispersal. The areas used by females with broods on the treated area were similar in size to those in the untreated area, suggesting suitable habitat components for broods were available and perhaps distributed similarly on both the treated and the northern section of the untreated area.

Macrohabitat: The types preferred by females with broods differed somewhat between looking at the study areas as a whole (eight habitat types) and evaluating only use of patch types (six total). Overall, females preferred dense stands, such as 10-year-old clearcuts, and avoided open areas such as recent clearcuts. Mixed habitats generally were used similar to availability.

For the study area as a whole, our observations that female grouse used habitat types with an aspen component (aspen, aspen-mixed oak, aspen-scrub) in proportion to their availability agreed with results of Maxson (1978) and Porath and Vohs (1972), which documented preferential use of oaks or mixed hardwoods in areas with both aspen and mixed oak or mixed hardwoods habitats. Other research from the Midwest suggests preferential use of aspen habitat by ruffed grouse broods (Berner and Gysel 1969, Rusch and Keith 1971, Gullion and Svoboda 1972). Avoidance of the herbaceous-clearcut habitat type was consistent with findings by Maxson (1978) and Porath and Vohs (1972), who reported that grouse avoided large openings. Selection of the mixed oak-scrub oak habitat type was expected because this type had a relatively open overstory and dense understory/shrub layer, and contained the 10-year-old A patches in the mixed oak blocks on the treated area.

The results of patch use differed between years, but only A patches were preferred in either year. In 1986, selection of 10-year-old mixed oak (A patches) and avoidance of all other untreated mixed oak patches by radio-tagged females concurs with reported

Twelve-year-old stand in mixed oak type.



Twelve-year-old stand in aspen-scrub oak type.



greater use of young-aged, mixed oak forests stands by females with broods (Bump et al. 1947, Sharp 1963, Berner and Gysel 1969, Porath and Vohs 1972). Selection of the 10-year-old aspen-scrub oak patches during 1987 in our study agrees with previous studies, which have documented preferential use of young aspen (Gullion 1970, Gullion and Svoboda 1972, Kubisiak 1978).

Microhabitat: Our assessment of microhabitats indicated that suitable densities of woody stems were available throughout the treated area by 1985. The mean density (21,400 stems per ha) of woody stems > 2.5 cm dbh at sites used by adult females in our study was greater than the 5,000 stems/ha considered the minimum density suitable for grouse cover, and within the 12,400–29,000 stems/ha considered optimal brood habitat in aspen forests in Minnesota (Gullion 1970, 1977). We also saw a positive effect on brood microhabitat suitability because of the lesser distance to edge on the treated area.

■ **Adult males** — Cumulative summer home range sizes of adult radio-tagged males were larger than individual monthly home ranges, although the differences were not significant. Male ruffed grouse shifted their home range location throughout the summer. The shifting of location was likely because of the pattern of availability of summer foods (e.g., *Rubus* and *Vaccinium* spp.). The home ranges of males in our study were similar to the 6.7 ha reported by (Archibald 1975) during the breeding season in Minnesota. Breeding and summer home ranges on our study area were much smaller than the 45 to 68 ha reported by Thompson and Fritzell (1989) in Missouri, the 72 ha reported by Gudlin and Dimmick (1984) for transplanted grouse in Tennessee, and the 38 ha reported by Epperson (1988) in Tennessee.

Mean home range size tended to be larger on the untreated area than the treated area for each month and season, although the differences were not significant. Movement between the treated and untreated areas by radio-collared male grouse was not observed during our study.

Macrohabitat: A significant portion of the available habitat was affected during 1976–77, when the A patches were cut in the 136 blocks throughout the treated area. These patches were unsuitable to grouse during the first few years after cutting, and activity centers during these years were relegated to the uncut portions of the treated area. The decreases in movement of drummers into uncut patches, following successive cuttings, was expected because 75 percent of the aspen-scrub oak and 50 percent of the mixed oak had been converted to early-successional plant communities by 1988.

Our annual surveys of breeding males indicated that males were more evenly distributed across the treated area than the untreated area. Most males on the untreated area were in aspen-black cherry stands and made much less use of the mixed oak. Only 3 percent of the untreated area was in sapling and poletimber mixed

oak, compared to 19 percent in the treated area. Wiggers et al. (1992) reported that grouse densities in predominantly oak forests in Missouri were positively correlated with the amount of early-successional forest in the surrounding landscape.

The understory of aspen-black cherry stands on the untreated area was usually scrub oaks or American hazel, which provided suitable structure for breeding habitat despite the presence of some large overstory trees. Much of the aspen-black cherry overstory had a thin canopy that allowed the maintenance of a dense understory that compensated for the lack of sapling-sized stands. Therefore, we were not surprised by the preference male grouse showed for the aspen-black cherry poletimber and sawtimber, in almost all months.

With the absence of a dense understory, oak sawtimber had limited usefulness to male ruffed grouse until blueberries began to ripen. However, birds on both areas tended to use oak sawtimber with increasing intensity as the summer progressed. Mixed oak sawtimber stands had large amounts of blueberry that ripened during August, and the ripe fruits may have caused grouse to increase their use of mixed oak sawtimber. Heavy fall use of acorns by grouse, as reported by Servello and Kirkpatrick (1988), also points out the importance of a sawtimber component in mixed oak forests.

Microhabitat: Our finding of active drumming sites having greater stem densities compared to inactive and random sites was in agreement with Stoll et al. (1979). Narahaara (1987) examined drumming site dynamics in Vermont and found active drumming sites to be in areas with higher understory stem densities than previously active or unused sites. The high densities (3,500 to 13,000 per ha) of stems in the 2.6–12.5 cm dbh at active drumming sites was not surprising because 77 percent of the active sites were in 14-year-old cut patches. High stem densities were characteristic of regenerating patches, whether mixed oak or aspen-scrub oak. Stem densities in our study were within the range of what was considered adequate for drummer habitat in Ohio (Stoll et al. 1979), Wisconsin (Kubisiak 1985, McCaffery et al. 1996), and Minnesota (Gullion 1984).

While high stem densities result from regenerating hardwoods, drumming habitat can also be provided by low dense cover from evergreens, shrubs, or small trees. This was evident on the untreated area where the presence of an understory shrub layer in forest stands allowed drumming grouse more secure cover. On the untreated area, sites with only 1,000 saplings per ha remained active due to the presence of a dense persistent vegetative understory, consisting primarily of scrub oak and hazel. Kubisiak (1985) noted much higher densities of drumming males in a Wisconsin forest in areas with a dense alder understory. Thompson and Fritzell (1989) found higher densities of small (≤ 15 cm dbh) eastern red cedar (*Juniperus virginiana*) at perennial drumming sites than transient or unused sites in Missouri.

Although we found stems of red maple, black

cherry, and scrub oak all had high importance values for all sites in the untreated area, scrub oak was less important at the inactive sites. For suitable drumming habitat, scrub oak formed a more persistent vegetative cover than did red maple and black cherry, which are transient species affecting the structure of the shrubby layer.

Longevity of use of activity centers: Our findings indicated that perennially active drumming sites had higher densities of small woody stems and lower densities of large woody stems than abandoned drumming sites. These results supported the findings of previous studies (Gullion and Marshall 1968, Stoll et al. 1979, Kubisiak 1985, Thompson and Fritzell 1989, Wiggers et al. 1992), which suggest the value of young plant communities to drumming males. On the treated area, dense sapling regeneration provided suitable drumming habitat. Most of the drumming sites in the untreated area were with a dense scrub oak layer under a usually sparse canopy of aspen, oak, and black cherry.

Boag (1976) demonstrated that the shrub layer was critical in maintenance of perennial drumming sites. He removed shrubs from a sample of drumming sites with known use histories and compared subsequent use by residents and recruitment of new grouse at these sites to a control group. Use and recruitment at manipulated sites were much lower. Claffey (1980) and Williams (1986) each noted the importance of shrub cover, particularly scrub oak, at drumming sites on our study area.

On our study area, the sites with persistent shrub cover provided relatively long-term habitat suitable for drumming activity. Other sites, with dense sapling regeneration and few shrubs, also provided suitable drumming habitat but may decline somewhat in quality after a period of 15 years. Overall, the habitat management of patch clearcutting resulted in a dramatic gain in drumming sites where, prior to cutting, none to few existed. Even with decline of quality, sapling stands still provided suitable drumming habitat 21 years following cutting, as evidenced by containing almost half of all drummers in 1998. Bramble (1973) reported that after 25 years, aspen stands have gone beyond the best quality habitat for ruffed grouse. With the subsequent patch cuts, habitat was created that provided for a net gain in perennial use of activity centers for treated areas as a whole.

The longevity of activity centers use appeared to be greater in mixed oak than in aspen-scrub oak. Without the presence of a shrub component, the faster-growing aspen may not hold as many drummers for as long as mixed oaks. However, grouse in the aspen-scrub oak still had more habitat choices due to having 50 percent greater cut (more age classes), more interspersion of habitats, and more of a shrub component (e.g., scrub oak) than in mixed oak.

Management Implications

This study has clearly shown the benefits of small patch cuts, on a landscape scale, to ruffed grouse. The maximum grouse densities achieved approached standards for aspen habitats in the northern midwestern U.S. Patch cutting resulted in maximum long-term interspersion of young and older stands, or in optimum habitat conditions for grouse. The study reconfirmed the value of aspen to grouse and also demonstrated that young mixed oak can produce equivalent numbers of birds. The key ingredient for grouse production with both habitat types was maintaining a young community of woody stems five to 20 years old.

Our patch cuts were relatively small, but total acreage cut at intervals was up to 25 percent of the total area. Due to the intensity of treatments on the area, profits realized may not have met some landowners' objectives. While in the early stages of the study, investments exceeded income, the future sale will result in the habitat management being cost-effective for 1-ha patches. Because our situation of a combination of aspen and mixed oak was cost-effective, intensive management of mixed oak stands in general would be cost-effective (higher timber value of oaks and no need to treat understory). The market for aspen has been quite variable in Pennsylvania, but where and when it exists, the patch cut model should also be suitable. At the current costs for cutting and current value of aspen, cutting of 1-ha patches on public lands under a 40-year-rotation would meet the objective of creating high quality habitat for grouse and provide an economic return from the aspen harvested. Larger cuts would decrease the expense of establishing timber sales and increase income.

We assume that 2 ha is a reasonable patch size for timber sales of aspen. Therefore, aspen can be managed on a 40-year-rotation in 8-ha blocks containing four 2-ha patch cuts. This would maintain 50 percent of the aspen in the zero-to-20-year age category, while providing a continuous supply of young aspen distributed over the landscape. Thus, grouse would have access to optimum habitat within a range of 100 m.

Managing mixed oak stands for grouse presents more of a challenge. Our study has shown mixed oak, managed with small patch cuts in close proximity, to be as productive as aspen managed in the same style. Grouse will benefit from increased interspersion of habitat ages in a mixed oak forest. However, mixed oak, due to longer rotations necessary for trees to reach saleable size, will require more patches and therefore larger blocks to maintain a constant supply in the young age class. Cutting 2-ha patches every 10 years, using a 100-year rotation, requires 20-ha blocks. This pattern would

keep 20 percent of the oak in the zero-to-20-year age category. All grouse would be within 290 m of optimum habitat, a distance well within the home range of breeding males and adult females with broods.

Intensive habitat management can improve conditions for grouse and other species of birds that use early-successional forests. Currently only 16% of forested habitats in Pennsylvania are in the seedling/sapling size. This study has shown that patch cutting results in high grouse densities. Intensive habitat management on selected areas will result in not only better interspersion of desired habitats, but more forests in early-successional stages under conditions that can be maintained over long periods of time (indefinitely). Both aspen and mixed oak can be managed in this style, while sustaining sound timber rotations and yields.

This is in contrast to the conventional practice of larger cuts, where habitat conditions for grouse in one area are improved for a relatively short period of time, followed by longer periods of time without suitable habitat in that area. With conventional cutting, interspersion of habitats is minimized. A long-term plan of smaller cuts, within the context of the landscape, ensures availability of early-successional habitat, critical to ruffed grouse and many other species.

Summary

In 1975 the Pennsylvania Game Commission initiated a long-term study to evaluate the response of ruffed grouse populations to intensive management of forests in central Pennsylvania. This bulletin looks at grouse numbers through 1998. While monitoring grouse population trends was the primary objective of the study, we also looked at economic cost/benefit of timber harvests for small patch cuts; plant community response; habitat selection and use by both adult males and adult females with broods; and drumming sites.

The study area included 1,120 ha of 2,500 ha on State Game Lands 176 in Centre County, Pennsylvania. The treatment area was 544 ha and a 576-ha adjacent area served as a control for comparison. The 544-ha treatment area was divided into 136 4-ha blocks, with each block subdivided into four 1-ha patches. Sixty blocks were designated as an aspen-scrub oak type and 76 blocks were typed mixed oak.

In 1976–77 the initial patch in both types was cut, using both commercial timber sales and non-commercial cutting. Prior to overstory removal, the dense understory in 36 patches was cleared by brush-cutting heavy equipment. In 1980–81 the second patch in the aspen-scrub oak was cut, with 48 of these patches first receiving understory brush treatment. During 1985–88, the second patch in mixed oak and the third patch in aspen-scrub oak were cut (50 patches received understory removal). At this time, 50 percent of the mixed oak had been cut along with 75 percent of the aspen-scrub oak; a total of 322 ha (59 percent) of the 544-ha treated area was in early-successional stage of forest.

Grouse population trends were monitored by flushing surveys in spring and fall and drumming male surveys in the spring. In the beginning of the study, grouse numbers were similar as measured by all surveys. Over time, grouse responded to the habitat treatments and, again for all surveys, showed numbers $\geq 2X$ higher for the managed area. From 1980 through 1989, the numbers of birds flushed in spring were similar for the treated (0.17/1.61 km) and untreated (0.20/1.61 km) areas. During 1990–1996, the average number of grouse flushed per 1.61 km was 0.61 and 0.30 for the treated and untreated areas, respectively. Numbers of drummers for both areas followed the same general pattern as spring flushes. In the beginning the numbers were similar, although the treatment area exceeded the untreated area as drummers began to use the 1976–77 cuts. After 1988 the number of drummers on the treated areas was always higher, almost double for many years. These differences were impressive because, for periods of almost 10 years, up to 25 percent of the treated area habitat was unsuitable for drummers. For fall season flushes from

1980–1989, the averages per 1.61 km were 0.64 for the treated area and 0.43 for the untreated area. After 1989, the average numbers flushed during 1990–1996 were 0.65 and 0.39 for the treated and untreated areas, respectively. Location of flushes on the treated area showed relatively greater use of the mixed oak type and the transition zone between aspen-scrub oak and mixed oak.

Initial drummer use of cut patches, for both the aspen-scrub oak and mixed oak, occurred between five and seven years following clearcutting. Drumming increased in the three different age classes of cut patches through a grouse population peak in 1994. For the treated area as a whole, the density of drummers in 1994 was 12.5 pr 100 ha. When only the young stands on the area are considered during 1993–1996, drummer densities were 16.0, 16.4, and 15.6/100 ha of total, mixed oak only, and aspen-scrub oak only, respectively. In the 1994 peak year, there were 20.5 drumming activity centers per 100 ha of young stands combined. While a similar grouse drumming response to habitat treatments occurred in aspen-scrub oak and mixed oak, the response to patch cuts in the oak was a new activity. The aspen-scrub oak had historically held drumming males because of the higher stem densities due to scrub oak, hazelnut, and other shrubs.

Even with large investments in non-commercial cutting treatments and poor markets for aspen during most of this study, the cost-benefit ratio improved over this time. By the completion of logging in the winter of 2000–2001, the income in the study was projected to exceed investment by \$137,000.00, or a factor of 1.5. Cutting of 1-ha patches on a landscape scale met the objective of high quality habitat for ruffed grouse and provided an economic return for timber.

This study has shown the benefits of small patch cuts on a landscape scale to ruffed grouse. This style of intensive forest management results in long-term interspersion of various age classes, and is recommended. Larger patch cuts would decrease timber sale layout expenses and therefore increase income. This study has also shown that mixed oak cuts in Pennsylvania result in grouse response similar to that for aspen. Because mixed oak requires a longer cutting rotation than aspen, it is not possible to have as large a proportion in early-successional stages as with aspen. Using a patch size of 2 ha and a block size of 20 ha allows a patch cutting every 10 years, allowing mixed oak to be managed on a 100-year rotation. This would result in 20 percent of the oak in the young forest stage (compared to 50 percent of aspen) and provide optimum habitat within the home range of grouse.

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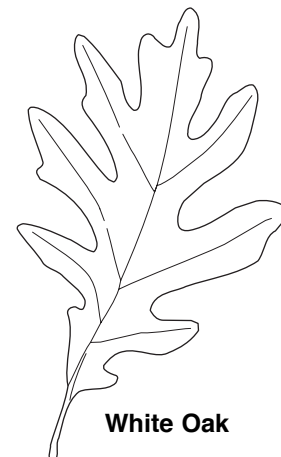
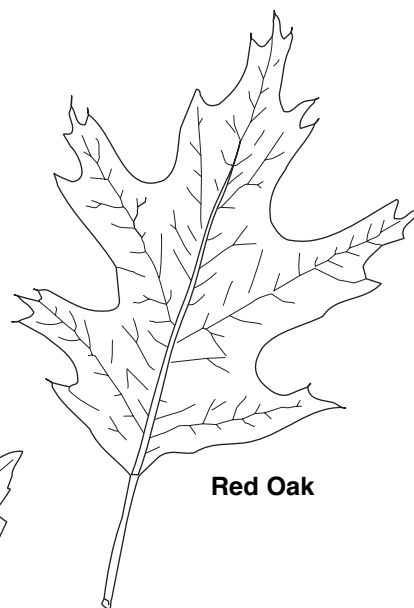
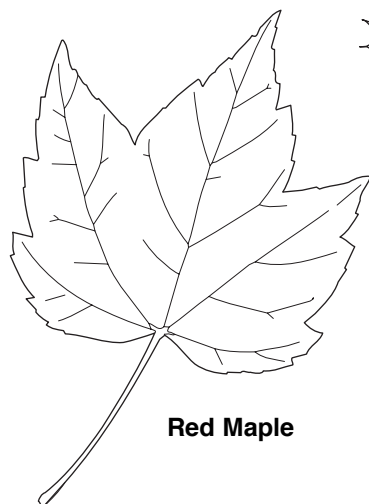
the project and cut the initial two patches. We thank James S. Lindzey for coordinating activities during the beginning years of the study, and we greatly appreciate the help of James E. Hudgins for coordinating field surveys and fine-tuning data management protocols. Numerous volunteers, students, and part-time employees assisted in managing and conducting field surveys. In particular, we thank the graduate students, J. E. Schmaltz, M. P. Claffey, G. D. Therres, S. A. Williams, J. G. Scott, and J. E. McDonald, who conducted research on ruffed grouse on the study area. We especially thank graduate student M. J. Lovallo for his contributions in writing the section on alternate drumming logs and for his assistance with early drafts of several figures.

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Appendix

Scientific Names of Plants Cited (Rhoads and Klein 1993)

Aspen	<i>Populus spp.</i>	Hazelnut, American	<i>Corylus americana</i> Walt.
Aspen, bigtooth	<i>P. grandidentata</i> Michx.	Hickory	<i>Carya spp.</i>
Aspen, quaking	<i>P. tremuloides</i> Michx.	Huckleberry	<i>Gaylussacia spp.</i>
Autumn-olive	<i>Elaeagnus umbellata</i> Thunb.	Maple, red	<i>A. rubrum</i> L. var. <i>rubrum</i>
Birch, black	<i>B. lenta</i> L.	Oak	<i>Quercus spp.</i>
Blackberry	<i>Rubus spp.</i>	Oak, black	<i>Q. velutina</i> Lam.
Blackberry	<i>Rubus allegheniensis</i> Porter	Oak, chestnut	<i>Q. montana</i> Willd.
Blueberry	<i>Vaccinium spp.</i>	Oak, dwarf chestnut	<i>Q. prinoides</i> Willd.
Box Elder	<i>Acer negundo</i> L.	Oak, northern red	<i>Q. rubra</i> L.
Cherry	<i>Prunus spp.</i>	Oak, scarlet	<i>Q. coccinea</i> Muenchh.
Cherry, black	<i>P. serotina</i> Ehrh.	Oak, scrub	<i>Q. ilicifolia</i> Wang.
Devils-walking-stick	<i>Aralia spinosa</i> L.	Oak, white	<i>Q. alba</i> L.
Dewberry	<i>Rubus spp.</i>	Pine, pitch	<i>P. rigida</i> P. Mill.
Dogwood	<i>Cornus spp.</i>	Raspberry	<i>Rubus spp.</i>
Dogwood, gray	<i>C. racemosa</i> Lam.	Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees
Hawthorn	<i>Crateagus spp.</i>	Sweet-fern	<i>Comptonia peregrina</i> L.



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