动物学报 52(Supplement): 697–701, 2006
Acta Zoologica Sinica

S39-5 Ecological forestry, old growth, and birds in the longleaf pine (*Pinus palustris*) ecosystem

R. Todd ENGSTROM[1,2], Richard N. CONNER[3]
1. Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, Florida 32312-9712, USA; engstrom@ttrs.org
2. Current address: The Nature Conservancy, Greenwood Program, P.O. Box 890, Thomasville, Georgia 31799, USA; tengstrom@tnc.org
3. Southern Research Station, 506 Hayter Street, Nacogdoches, Texas 75965-3556, USA; c_connerrn@tital.sfasu.edu

Abstract Renewed awareness of the longleaf-pine ecosystem and a legal mandate to provide suitable habitat for the endangered red-cockaded woodpecker (*Picoides borealis*) have generated interest in alternative forms of silviculture in the southeastern United States. Of 110–120 species of birds that occur in longleaf pine woodlands, 26 species (including three that are federally ranked) require special management attention. Over 80% of the extant ecosystem occurs on government-owned or privately-owned nonindustrial property, and constitutes potential sites for ecological forestry. Intensive forest management eliminates much of the structural complexity of old-growth longleaf pine woodlands that supports high avian community species richness. Two silvicultural systems that are candidates for a more ecological approach — irregular shelterwood and uneven-aged management — retain structural characteristics of old-growth forests, but more research is needed to contrast their relative effects on bird populations. Retention or development of old-growth characteristics — old trees, horizontal heterogeneity and openness, ground-cover integrity, sparse distribution of hardwoods, and coarse woody debris, including snags — would reintroduce valuable complexity within the longleaf pine ecosystem for supporting avian communities of higher species richness.

Key words Ecological forestry, Fire, Forest birds, Old-growth, Southeast United States

1 Introduction

Forestry in the United States has largely diverged into two approaches, one emphasizing increasing production of wood fiber and the other stressing maintenance of forest complexity, function, and biological diversity (Perry, 1998). Development of a more ecologically sensitive approach in the southeastern United States has been slow, in part because commercial models of timber production are deeply entrenched and old-growth forests that provide examples of high diversity and natural function are now very rare. Concerns over biological diversity, endangered species, particularly the red-cockaded woodpecker (*Picoides borealis*), and perpetuation of fire as a disturbance (Conner, 1988) have led to increasing interest in ecological forestry for longleaf pine forests (Means and Grow, 1985).

Ecological forestry, with emphasis on protecting natural function and native biological diversity, could have broad application on federal lands (National Forests, National Wildlife Refuges, military bases), state forests, and private forests where hunting, aesthetics, conservation, and production of high-quality wood are objectives. We assess how avian communities would be affected by application of ecological forestry, particularly retention of old-growth characteristics, in the longleaf pine ecosystem.

2 The longleaf pine ecosystem

Longleaf pine dominated forests occurred on 22.9 million ha pre-settlement in the southeastern United States, and extended over an additional 14.6 million ha in mixed forests (Frost, 1993). A combination of factors contributed to a 97% decline over a 150-year period (Frost, 1993), to approximately 1.3 million ha in 1993 (Outcalt and Sheffield, 1996). Contemporary longleaf pine forests are owned by the forest industry (18%), government (31%), and private landowners (51%), according to Outcalt and Sheffield (1996).

Longleaf pine woodlands contain some of the most species-rich ground-cover communities in North America (Peet and Allard, 1993). Relative dominance of grasses, shrubs, and mid-story trees within community types affects the resources and structure that determine patterns of avian abundance. An essential factor that affects the structure and composition of forest types throughout the entire ecosystem is fire (Harper, 1911), but very few of the remaining stands are still fire maintained (Frost, 1993). Development of shrub and mid-story levels and eventual truncation of pine regeneration are the consequences of extended intervals between fires or fire exclusion (Christensen, 1981). Vegetation changes in response to fire exclusion have dramatic effects on the avian community (Engstrom et al., 1984).

© 2006 动物学报 *Acta Zoologica Sinica*

Old-growth longleaf pine woodlands that have a structure and composition similar to those in the earliest descriptions are extremely rare. Means (1996) estimated that only 3902 ha of old-growth forest remains; and according to a 1993 inventory, most of the extant stands are only 21 to 60 years old (Outcalt and Sheffield, 1996). Overstory composition of many original forests were typically dominated by longleaf pine itself, which made up over 75% of individual trees (Wahlenberg, 1946).

A focus on attributes and dynamics of old-growth forests provides a guide for development of ecological forestry. Landers and Boyer (1999) estimate that old-growth characteristics begin to develop in longleaf pine after 112 years, but old-growth forests are not composed exclusively of older trees. More typically, all age classes are represented. Old-growth forest characteristics (large old pine trees, old persistent snags, coarse woody debris on the ground, tree age-class diversity, horizontal and vertical heterogeneity, diverse ground cover, a mixing of hardwoods, and tip-up mounds) should be considered when developing an architecture to manage for biological diversity (Landers and Boyer, 1999).

3 Birds of the longleaf pine ecosystem

Apart from migrants passing through, approximately 120 species of birds occur in the longleaf pine ecosystem (Engstrom, 1993; Hunter et al., 2001). This total comprises species that are resident (42%), breed and migrate (28%), or overwinter and migrate (30%). Standardized censuses (Breeding Bird Censuses) of 11 longleaf pine sites in four states showed a fivefold variation in bird density (8 to 41 territories per 8.1 ha), and species richness that ranged from 6 to 22 per 8.1 ha (R.T. Engstrom, unpublished data). Three of its species — the bald eagle (*Haliaeetus leucocephalus*), Mississippi sandhill crane (*Grus canadensis pulla*), and red-cockaded woodpecker — are federally listed as threatened. Moreover, twenty-six species that occur in fire-dependent habitats are in need of management attention (Hunter et al., 2001).

4 Silvicultural effects on birds in longleaf pine forests

4.1 General issues

From 1880 to 1930, when most of the original forest was harvested (Williams, 1989), little thought was given to its maintenance (Frost, 1993). Many forests were converted to other land uses then, but residual flowering in some was sufficient for regeneration. An intensive, commercially-oriented silvicultural approach that included clearcutting, debris raking, and soil disking developed in the latter part of the 20th century (Croker, 1987). It eliminated many native plants from the ground cover, including native grasses that provide the fuel for the frequent fires needed to maintain the ecosystem and are important for species such as Bachman's (*Aimophila aestivalis*) and Henslows' (*Ammodramus henslowii*) sparrows. Industrial pine forests typically are young, have a uniform structure of dense canopy, sparse ground cover, and few snags. Avian response to intensive silviculture is low species richness that increases as the forest matures (Repenning and Labisky, 1985; Dickson et al., 1995).

Fire, wind, lightning, and bark beetles are common disturbances that shape the structure and composition of longleaf forests. Wind and lightning are small-scale disturbances, killing trees, creating gaps in the canopy of variable size and providing coarse woody debris for birds. Two silvicultural approaches that imitate natural disturbances — irregular shelterwood and uneven-aged management — have been proposed to produce red-cockaded woodpecker habitat (Conner et al., 1991; Rudolph and Conner, 1996; Engstrom et al., 1996). In an irregular shelterwood, most overstory trees are harvested on long return intervals (120 years), but a low basal area of mature trees is permanently retained for structural reasons and as a source of seed and shelter for young pines (Smith, 1986). In uneven-aged management, all ages of trees can be thinned throughout a stand, but natural gaps may be enlarged and employed for regeneration. These techniques are at nearly opposite ends of the spectrum of overstory retention and have different implications for producing the structural elements needed to maintain biological diversity. We discuss below how characteristics of old-growth longleaf-pine forest within the context of uneven-aged management and irregular shelterwood influence populations of birds (Table 1).

4.2 Canopy tree age

Although longleaf pine trees can live to 500 years, noticeable old-growth features (large boles, contorted limbs, flat-topped crowns, and decay within living trees) start to appear at about age 112 (Landers and Boyer, 1999). These features are especially important for species like red-cockaded woodpeckers (amount of heartwood and fungal infection) and bald eagles (large limbs). Old trees probably tend to support primary (e.g., woodpeckers) and secondary (e.g., wood duck, *Aix sponsa*) cavity nesters in greater numbers because cavities may be more easily excavated in decayed crannies.

Harvest rotations in industrial forestry tend to be less than 50 years, but both irregular shelterwood and uneven-aged harvesting have the potential to produce old pines. In irregular shelterwood, mature pines are retained after harvest (basal area of approximately 9 m^2/ha). If some of the oldest pines remain through two or more harvest cycles (120 year rotation), pines may grow to 240 years old or more. When high basal areas of residual pines are left as shelterwood, and the forest is burned regularly, the resulting forest will develop through time the appearance of an uneven-aged forest as the second generation of trees matures. If the number of residual pines left is too low and wind-caused mortality is high, the resulting stand will resemble a clearcut more than a forest of mature pines, and suitable densities of old-growth pines will not result.

High densities of old pines can be achieved by uneven-aged harvesting, but the occurrence and survival of pine reproduction is inversely related to the density of old-growth pines. Uneven-aged silvicultural systems are controlled by the number of pines harvested in each size (diameter) class. Typically, all pines are harvested beyond some maximum diameter (Farrar and Boyer, 1991), so it is critically important that the maximum diameter limit be set high enough to permit pines to grow to the desired maximum age. For uneven-aged silviculture to provide old-growth pines, the manager must know the ages of pines in all diameter classes, particularly the larger and presumably older diameter classes. If the maximum diameter of pines is set too low in such harvesting, old-growth pines will not result.

4.3 Horizontal heterogeneity

All forests develop heterogeneous spacing, no matter how uniform the initial regeneration; and different silvicultural techniques have large effects on tree spacing. Disturbances, such as lightning, wind, and fire, create small and large gaps in the canopy over time. The spacing of individual trees and clumps of trees is important for bird species that forage in open spaces within forests, such as flycatchers (e.g., eastern kingbird, *Tyrannus tyrannus*), common nighthawks (*Chordeiles minor*), and loggerhead shrikes (*Lanius ludovicianus*), as well as for the development of ground cover. In wetter areas, open woodlands interspersed with savannas are important habitat for sandhill cranes (*Grus canadensis*).

Irregular shelterwood harvesting and uneven-aged management will have different effects on horizontal heterogeneity. Irregular shelterwood will tend to produce stands that are horizontally homogeneous for 50 years or so after harvesting but will increase in heterogeneity as they approach harvest rotation age. In contrast, uneven-aged stands will be patchy as a result of the regular removal (every 7–10 years) of single and small groups of trees. In general, uneven-aged stands will have higher horizontal heterogeneity than stands produced by shelterwood harvesting.

4.4 Ground cover

Ground cover is strongly influenced by methods of tree harvest and regeneration within a silvicultural approach. To eliminate competition for young pine trees, industrial forestry frequently employs disking, chopping, and application of herbicides, which have detrimental effects on many of the native perennial ground plants that dominate undisturbed sites. Although intensive site-preparation techniques are not used in ecological forestry, harvesting procedures may still compact the soil and affect ground cover when

Table 1 Structural characteristics of old-growth longleaf pine forest of value to bird species

Structural components	Importance to birds	Bird species affected
Old trees	Large limbs, flat crowns; abundant heartwood; susceptibility to fungal infection that provides easy excavation of heartwood	*Aix sponsa* *Elanoides forficatus* *Haliaeetus leucocephalus* *Picoides borealis* *Sitta carolinensis*
Ground-cover integrity	Abundance of grasses (e.g., *Aristida beyrichiana*) for nesting material; functional role in providing fuel for fires	*Colinus virginianus* *Cistothorus platensis* *Aimophila aestivalis* *Passerculus sandwichensis* *Ammodramus savannarum* *A. henslowii, A. leconteii* *Sturnella magna*
Coarse woody debris	Large old snags that provide nesting and foraging substrate; tip-up mounds that provide escape cover	*Melanerpes erythrocephalus* *Colaptes auratus* *Dryocopus pileatus* *Sitta pusilla* *Sialia sialis*
Horizontal heterogeneity and habitat openness	Juxtaposition of foraging space and perches	*Grus canadensis* *Chordeiles minor* *Tyrannus tyrannus* *Lanius ludovicianus*
Hardwood distribution and abundance	Nesting and foraging substrate within an open-structured habitat	*Polioptila caerulea* *Piranga rubra* *Icterus spurius*

Based on Breeding Bird Censuses (Engstrom, 1993; Hunter et al., 2001). The structural components are not necessarily independent, and bird species may respond to more than one aspect of habitat structure.

tree trunks are removed. The grasses that provide nest material and cover, and shrubs that act as nesting substrate, are likely to be different in old-field and undisturbed sites. 30% to 40% of the species and 35% to 60% of the territorial individuals in the breeding bird community in one old-growth forest are ground nesters and forage primarily on the ground (Engstrom, unpublished data). Northern bob-white (*Colinus virginianus*), the resident Bachman's sparrow, a wide array of wintering sparrows, the sedge wren (*Cistothorus plantensis*), and the eastern meadowlark (*Sturnella magna*) are sensitive to composition and structure of the ground cover.

The ground cover in pine stands depends more on the fire regime than on the silvicultural system used to regenerate the pine canopy. Therefore, both irregular-shelterwood harvesting and uneven-aged management are compatible with maintaining a diverse flora in the herbaceous layer as long as frequent prescribed fire and natural pine regeneration are part of the overall management program. If managers use mechanical site preparation in conjunction with irregular-shelterwood harvesting, the floral diversity of the ground cover will decline.

4.5 Coarse woody debris

Snags are highly important to the diverse community of cavity nesters in longleaf pine forests, and woody debris on the ground, especially tip-up mounds, provides refugia for wrens and species such as Bachman's sparrow. Tree age and cause of death have an important effect on the persistence and rate of decay of standing snags because of the amount and density of heartwood needed to support dead trees. If high basal areas of residual pines are left during irregular shelterwood harvesting, natural mortality of residual pines and competitive mortality among growing younger pines will probably produce a continuous supply of snags. Snag production is not as certain in uneven-aged systems because regular tree removal during frequent harvests decreases competition among growing pines and can remove many of the older pines because of the maximum diameter limit. However, the length of time between harvest cycles and the maximum diameter limit can be increased to increase snag production. The density of snags and logs is also affected by the frequency and intensity of fire: hot, frequent fires will burn up most logs and snags yet may also kill some live pines to create new snags (Conner, 1981).

4.6 Hardwoods

The distribution and species of hardwoods within longleaf pine forests has a major effect on the bird communities. In old-growth forests that are burned frequently, scattered oaks (*Quercus* spp.) and hickory (*Carya* sp.) were probably normal. This small hardwood component in well-maintained forests is important for bird species such as the blue-gray gnatcatcher (*Polioptila caerulea*), summer tanager (*Piranga rubra*), and orchard oriole (*Icterus spurius*). As hardwoods increase in abundance, additional bird species may appear (e.g., red-eyed vireo, *Vireo olivaceous*); but others, such as the red-cockaded woodpecker, may disappear (Hunter et al., 1994). Increasing abundance of hardwoods also strongly affects the flammability of sites, as grasses and forbs are reduced or die from shading. Maintaining hardwoods within a longleaf pine forest is a balancing act: too much fire can eliminate hardwoods, and too little can provide the hardwoods with a competitive edge and cause a shift in species dominance and composition. If hardwoods are not intentionally removed during harvesting operations, the occurrence of hardwoods in longleaf pine forests will become more a function of the fire regime than of the silvicultural system used to regenerate pines.

References

Christensen NL, 1981. Fire regimes in southeastern ecosystems. In: Mooney HA, Bonnicksen TM, Christensen NL, Loton JE, ReinsersWA ed. Fire Regimes and Ecosystems Properties. General Technical Report WO-26. U.S. Department of Agriculture, Forest Service, 112–136.

Conner RN, 1981. Fire and cavity nesters. In: Wood GW ed. Prescribed Fire and Wildlife in Southern Forests. Georgetown, South Carolina: Belle W. Baruch Forest Science Institute of Clemson University, 61–65.

Conner RN, 1988. Wildlife populations: minimally viable or ecologically functional? Wildl. Soc. Bull. 16: 80–84.

Conner RN, Snow AE, O'Halloran KA, 1991. Red-cockaded woodpecker use of seed-tree/shelterwood cuts in eastern Texas. Wildl. Soc. Bull. 19: 67–73.

Croker TC Jr, 1987. Longleaf Pine: A History of Man and a Forest. U.S. Department of Agriculture, Forest Service, Southern Region, R8-FR-7.

Dickson JG, Thompson FRIII, Conner RN, Franzreb KE, 1995. Silviculture in central and southeastern oak-pine forests. In: Martin TE, Finch DM ed. Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues. New York: Oxford University Press, 245–266.

Engstrom RT, 1993. Characteristic birds and mammals of longleaf pine forest. Tall Timbers Fire Ecology Conference 18: 127–138.

Engstrom RT, Crawford RL, Baker WW, 1984. Breeding bird populations in relation to forest structure following fire exclusion: a 15-year study. Wilson Bull. 96: 437–450.

Engstrom RT, Brennan LA, Neel WL, Farrar RM, Lindeman ST, Moser WK, Hermann SM, 1996. Silvicultural practices and red-cockaded woodpecker management: a reply to Rudolph and Conner. Wildl. Soc. Bull. 24: 334–338.

Farrar RM Jr, Boyer WD, 1991. Managing longleaf pine under the selection system — promises and problems. In: Proceedings of the Sixth Biennial Southern Silviculture Research Conference, Vol. 1. USDA Forest Service, General Technical Report SE-70, 357–368.

Frost CC, 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Tall Timbers Fire Ecology Conference 18: 17–43.

Harper RM, 1911. The relation of climax vegetation to islands and peninsulas. Bull Torrey Bot. Club 38: 515–525.

Hunter WC, Mueller AJ, Hardy CL, 1994. Managing for red-cockaded woodpeckers and neotropical migrants — is there a conflict? Proceedings of the Annual Conference Southeastern Association Fish and Wildlife Agencies 48: 383–394.

Hunter WC, Buehler DA, Canterbury RA, Confer JL, Hamel PB, 2001. Conservation of disturbance-dependent birds in eastern North America. Wildl. Soc. Bull. 29: 440–455.

Landers JL, Boyer WD, 1999. An old-growth definition for upland longleaf and south Florida slash pine forests, woodlands, and savannas. U.S. Department of Agriculture, Forest Service, Southern Research Station, General Technical Report, SRS-29.

Means DB, 1996. Longleaf pine forest, going, going, … In: Davis MB ed. Eastern Old-growth Forests. Washington, D.C.: Island Press, 210–229.

Means DB, Grow G, 1985. The endangered longleaf pine community. ENFO, 1–12.

Outcalt KW, Sheffield RM, 1996. The longleaf pine forest: trends and current conditions. U.S. Department of Agriculture, Forest Service, Southern Research Station, Resource Bulletin SRS-9.

Peet RK, Allard DJ, 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf coast regions: a preliminary classification. Tall Timbers Fire Ecology Conference 18: 45–91.

Perry DA, 1998. The scientific basis of forestry. Annu. Rev. Ecol. Syst. 29: 435–466.

Repenning R, Labisky RF, 1985. Effects of even-age timber management on bird communities of the longleaf pine forest in northern Florida. J. Wildl. Manage. 49: 1 088–1 098.

Rudolph DC, Conner RN, 1996. Red-cockaded woodpeckers and silvicultural practices: is uneven-aged silviculture preferable to even-aged? Wildl. Soc. Bull. 24: 330–333.

Smith MS, 1986. The Practice of Silviculture, 8th edn. New York: Wiley.

Wahlenberg WG, 1946. Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth, and Management. Washington, D.C.: Charles Lathrop Pack Forestry Foundation, in cooperation with the U.S. Department of Agriculture, Forest Service.

Williams M, 1989. Americans and Their Forests. Cambridge: Cambridge University Press.