National Park Service
U.S. Department of the Interior

Northeast Region
Philadelphia, Pennsylvania

Conceptual Ecological Model for Management of Breeding Shrubland Birds in the Mid-Atlantic Region

Technical Report NPS/NER/NRR--2006/043

ON THE COVER

These three species are all common breeders in shrubland habitat of the Mid-Atlantic Region: Gray Catbird (*Dumetella carolinensis*); Golden-winged Warbler (*Vermivora chrysoptera*); Chestnut-sided Warbler (*Dendroica pensylvanica*). Photographs courtesy of: Richard Yahner, School of Forest Resources, The Pennsylvania State University.

Conceptual Ecological Model for Management of Breeding Shrubland Birds in the Mid-Atlantic Region

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June 2006

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Introduction

While grassland birds have become the focus of increased conservation activities, the status of birds occupying shrubland habitats has received relatively little attention (Hunter et al. 2001). Yet, in eastern North America, shrubland birds exhibited consistent population declines during the past 40 years, based on data from the North American Breeding Bird Survey (Pardieck and Sauer 2001). These population declines primarily reflect large-scale changes in land use patterns during the previous century (Lorimer 2001). Large areas of marginal farmland were abandoned and underwent secondary succession during the first half of the twentieth century, producing abundant successional habitats favored by shrubland birds. As these habitats matured, combined with strict fire-suppression policies (Hunter et al. 2001), shrublands succeeded into mature forests, and shrubland bird communities were replaced by woodland birds (Irland 1982; Askins 1993). For example, while nearly 29% of New England forests were classified as sapling stage in 1950, only 8% remained at that stage in the 1980s (Askins 1993). The trend towards forest maturation and loss of shrubland habitats continues, yet concerted conservation activities have not been directed to benefit declining shrubland bird populations.

The National Park Service (NPS) could contribute to shrubland bird conservation in the Mid-Atlantic Region. The NPS maintains a number of historic sites and former battlefields managed for their cultural significance but also support wildlife populations. Many of these "cultural parks" maintain open landscapes, recreating land use patterns existing at the times of the historical events. While these open landscapes are frequently managed grasslands, some parks also support successional habitats that could be managed to benefit shrubland birds.

In 2005, the NPS initiated a project exploring the potential of "cultural parks" to support significant breeding grassland and shrubland bird communities. This project involved parks within three NPS Inventory and Monitoring Program (I&M) networks, Mid-Atlantic, National Capital, and Eastern Rivers and Mountains. Five parks were selected for the initial focus of this study, all of which maintain open landscapes for interpreting historic events. Most parks were selected because they contain the most extensive grassland habitats within their networks, although some also support shrubby successional habitats. The five parks included in this study are Antietam National Battlefield, Fort Necessity National Battlefield, Gettysburg National Battlefield, Manassas National Battlefield, and Monocacy National Battlefield.

This conceptual ecological model is one product of this project. The information presented below allows NPS network coordinators to understand which factors should be considered when making decisions concerning shrubland management within their networks. This model provides park resource managers with information on shrubland ecology in the Mid-Atlantic Region, the ecological requirements of shrubland birds likely to occur in their parks, and management issues influencing whether significant breeding populations can occupy shrublands created and maintained in the parks. Resource managers can then make informed decisions concerning their ability to create and maintain shrubland habitats. The emphasis of this conceptual model is restricted to management of breeding shrubland birds. Additional species occur during migration and winter, and habitat requirements of shrubland birds during nonbreeding seasons may differ from those described for the breeding season.

Terminology

Shrubland communities are dominated by shrubby or sapling vegetation generally <3 m (10 ft) tall (Hunter et al. 2001). Species considered to be "obligate shrubland birds" have never been defined. Birds regularly occurring in upland shrubby successional and edge habitats within the Mid-Atlantic Region are listed in Table 1. These species rely on shrubby habitats for part or all of their life cycles. Subcategorization of these shrubland birds is discussed below. This conceptual ecological model is restricted to upland successional habitats, but does not apply to scrub/shrub wetlands because processes driving wetland succession and subsequent changes in wetland bird communities are very different from those in uplands.

For this conceptual ecological model, "Mid-Atlantic Region" refers to Pennsylvania, Maryland, Virginia, and the District of Columbia. Habitat fragmentation is defined as "…the discontinuity, resulting from a given set of mechanisms, in the spatial distribution of resources and conditions present in an area at a given scale that affects occupancy, reproduction, or survival in a particular species" (Franklin et al. 2002). Fragmentation is species specific and operates at multiple spatial scales. Below, fragmentation is discussed from the local perspective of shrubland birds establishing breeding territories in a park, and the landscape perspective of birds finding suitable shrublands within a park among the mosaic of habitats present in the surrounding countryside. Secondary succession refers to sequential changes in the relative abundances of dominant species in a community, with sequential implying that a once-dominant species will not become dominant again unless a disturbance factor intervenes (Huston and Smith 1987). A seral stage refers to any community that temporarily exists as a result of secondary succession.

Table 1. List of shrubland birds regularly occurring in the Mid-Atlantic Region.

Common Name	Scientific Name	Field Specialist*	Ubiquitous*	Multiple Habitats*
Northern bobwhite	*Colinus virginianus*			X
Black-billed cuckoo	*Coccyzus erythropthalmus*			X
Yellow-billed cuckoo	*Coccyzus americanus*			X
Alder flycatcher	*Empidonax alnorum*	X		
Willow flycatcher	*Empidonax traillii*	X		
White-eyed vireo	*Vireo griseus*	X		
Carolina wren	*Thryothorus ludovicianus*		X	
Gray catbird	*Dumetella carolinensis*		X	
Northern mockingbird	*Mimus polyglottos*		X	
Brown thrasher	*Toxostoma rufum*		X	
Blue-winged warbler	*Vermivora pinus*	X		
Golden-winged warbler	*Vermivora chrysoptera*	X		
Nashville warbler	*Vermivora ruficapilla*	X		
Yellow warbler	*Dendroica petechia*	X		
Chestnut-sided warbler	*Dendroica pensylvanica*	X		
Prairie warbler	*Dendroica discolor*	X		
Common yellowthroat	*Geothlypis trichas*	X		
Yellow-breasted chat	*Icteria virens*	X		
Eastern towhee	*Pipilo erythrophthalmus*		X	
Field sparrow	*Spizella pusilla*	X		
Song sparrow	*Melospiza melodia*		X	
Northern cardinal	*Cardinalis cardinalis*		X	
Blue grosbeak	*Passerina caerulea*		X	
Indigo bunting	*Passerina cyanea*		X	

*See text for definitions of these categories.

Shrubland Bird Distribution Patterns

The status of breeding shrubland birds in the Mid-Atlantic Region is summarized in Table 2. Many species are widely distributed. Others occur widely in Pennsylvania, but more locally in Maryland and Virginia, where they are mostly found in the mountains; this distribution pattern is exhibited by black-billed cuckoo, alder flycatcher, willow flycatcher, blue-winged warbler, golden-winged warbler, and chestnut-sided warbler (scientific names provided in Table 1). Nashville warblers are rare in Pennsylvania and reach the southern limit of their breeding range in the mountains of Maryland. A few species reach the northern limits of their range in the region. Blue grosbeaks occur across Virginia and Maryland, but only locally in southern Pennsylvania, while northern mockingbirds and yellow-breasted chats are widespread, except in northern Pennsylvania (Brauning 1992; Robbins and Blom 1996; Trollinger et al. 2001).

Table 2. Status of shrubland birds in the Mid-Atlantic Region (Brauning [1992]; Robbins and Blom [1996]; Trollinger et al. [2001]).

Species	Pennsylvania	Maryland	Virginia
Northern bobwhite	U/R—widespread, but declined greatly in recent years	FC—eastern U/R and declining in central and western	FC—widespread, but declined recently
Black-billed cuckoo	FC—widespread	U—western R—very local central and eastern	U—local in mountains only
Yellow-billed cuckoo	FC—widespread	FC—widespread	FC—widespread
Alder flycatcher	U—northern PA and locally along mountains	U—Garrett County only	R—very local in mountains only
Willow flycatcher	FC—widespread	FC—northern R—very local in southern counties	U—northern counties and mountains only
White-eyed vireo	FC—southern and central R—northern and high elevations in mountains	FC—widespread, but U in mountains	FC—widespread, but U in mountains
Carolina wren	C—southern and central U/R—northern and high elevations in mountains	C—widespread	C—widespread
Gray catbird	C—widespread	FC/C—widespread	C—central and western FC—eastern
Northern mockingbird	C—southern and central U/R—northern and high elevations in mountains	C—widespread	C—widespread
Brown thrasher	U/FC—widespread	FC—widespread	FC—widespread
Blue-winged warbler	FC—widespread, becoming R at higher elevations in mountains	U/R—northern, mostly absent from southern MD	U—very local in western only
Golden-winged warbler	R/U— declining, local in mountains and western PA	R/U—Garrett and Allegany Counties only	R—very local in mountains only
Nashville warbler	R/U—local in mountains and northern counties	R—local in mountains	No documented breeding records
Yellow warbler	C—widespread	FC—widespread	U—widespread
Chestnut-sided warbler	FC—northern, central, and in mountains R—southern	FC—western MD only	U—in mountains only
Prairie warbler	FC—southern and central U/R—northern and high elevations in mountains	FC—widespread	FC—eastern and central U—western
Common yellowthroat	C—widespread	C—widespread	C—widespread
Yellow-breasted chat	FC—southern and central R—northern	FC—widespread	FC—widespread

Table 2. Status of shrubland birds in the Mid-Atlantic Region (Brauning [1992]; Robbins and Blom [1996]; Trollinger et al. [2001]) (cont.).

Species	Pennsylvania	Maryland	Virginia
Eastern towhee	FC—widespread	FC—widespread	FC—widespread
Field sparrow	FC—widespread	FC—widespread	FC—widespread
Song sparrow	C—widespread	C—widespread	C—central and western U—eastern
Northern cardinal	C—widespread	C—widespread	C—widespread
Blue grosbeak	U and local in southern counties only	FC/C—eastern and central R—western	FC/C—widespread, but local in mountains
Indigo bunting	C—widespread	C—widespread	C—widespread

C (Common): Regularly encountered and numerous in appropriate habitats.
FC (Fairly common): Regularly encountered, but normally in small numbers in appropriate habitats.
U (Uncommon): Observed only in small numbers and frequently absent from suitable habitats.
R (Rare): Known from only a few locations, frequently as isolated individuals and pairs. Most potential habitats are not occupied.

Shrubland Bird Ecological Requirements

Birds occupying shrubland habitats have generally received less attention than species occurring in grasslands and forests. Initial studies associated assemblages of birds with specific seral stages (e.g., Adams 1908). Once these associations were established, ecologists turned their attention towards understanding the factors directing changes in bird community composition as plant communities undergo secondary succession (Odum 1950; Johnston and Odum 1956; Kricher 1973; Shugart and James 1973). Despite regional differences, these studies demonstrate increased densities and species diversities in bird communities with increased ages of plant communities, reflecting the greater structural complexity and habitat diversity within older successional stages. More recently, some studies explore shrubland bird community dynamics at landscape scales (Cook et al. 2005), or in response to specific management activities (Schulte and Niemi 1998). Responses to area sensitivity and other habitat requirements are documented for a few species or locations (Annand and Thompson 1997; Burhans and Thompson 1999; Rodewald and Vitz 2005, but see Krementz and Christie 2000). Several studies document edge effects, such as higher densities of predators, increased nest predation near edges (Durner and Gates 1993; Woodward et al. 2001; King and Byers 2002), and avoidance of forest-shrub edges by some species (Rodewald and Vitz 2005). Other studies document the importance of successional habitats for forest birds, such as wood thrushes (*Hylocichla mustelina*) (Anders et al. 1998; Vega Rivera et al. 1998; Pagen et al. 2000). Most generalizations concerning breeding shrubland birds are based on small numbers of studies from few locations and should be extrapolated with caution across broader temporal and geographic scales.

While some shrubland birds exhibit specialized habitat requirements, such as golden-winged warblers (Confer 1992), many species occur in groups having similar requirements. In general, shrubland birds can be categorized into three groups: 1) species restricted to tracts of successional habitats (***field specialists*** in Table 1); 2) species occurring along linear edge habitats and fields (***ubiquitous species*** in Table 1); and, 3) species requiring habitats in addition to shrublands for breeding (***multiple habitat species*** in Table 1). Field specialists prefer patches 2–20 ha (5–50 ac), much smaller than the preferred field sizes of grassland birds. In the only study to examine habitat preferences in patches considerably >20 ha (50 ac), Rudnicky and Hunter (1993) found shrubland birds in Maine exhibit no area preferences once clear cuts exceed 20 ha (50 ac). These species also occupy shrubby corridors at least 60 m (200 ft) wide, such as along power line rights-of-way. Ubiquitous species occupy a wide range of shrubland communities including brushy woodland edges and roadsides, fencerows, hedgerows, and other narrow corridors <10 m (33 ft) wide. Some ubiquitous species occupy residential areas with dense ornamental shrubbery. Multiple habitat species require shrublands for portions of their life cycles but are also dependent upon other habitats. These species are absent unless all required habitats are available within a home range. Many species prefer specific seral stages as summarized in Figure 1 and described below.

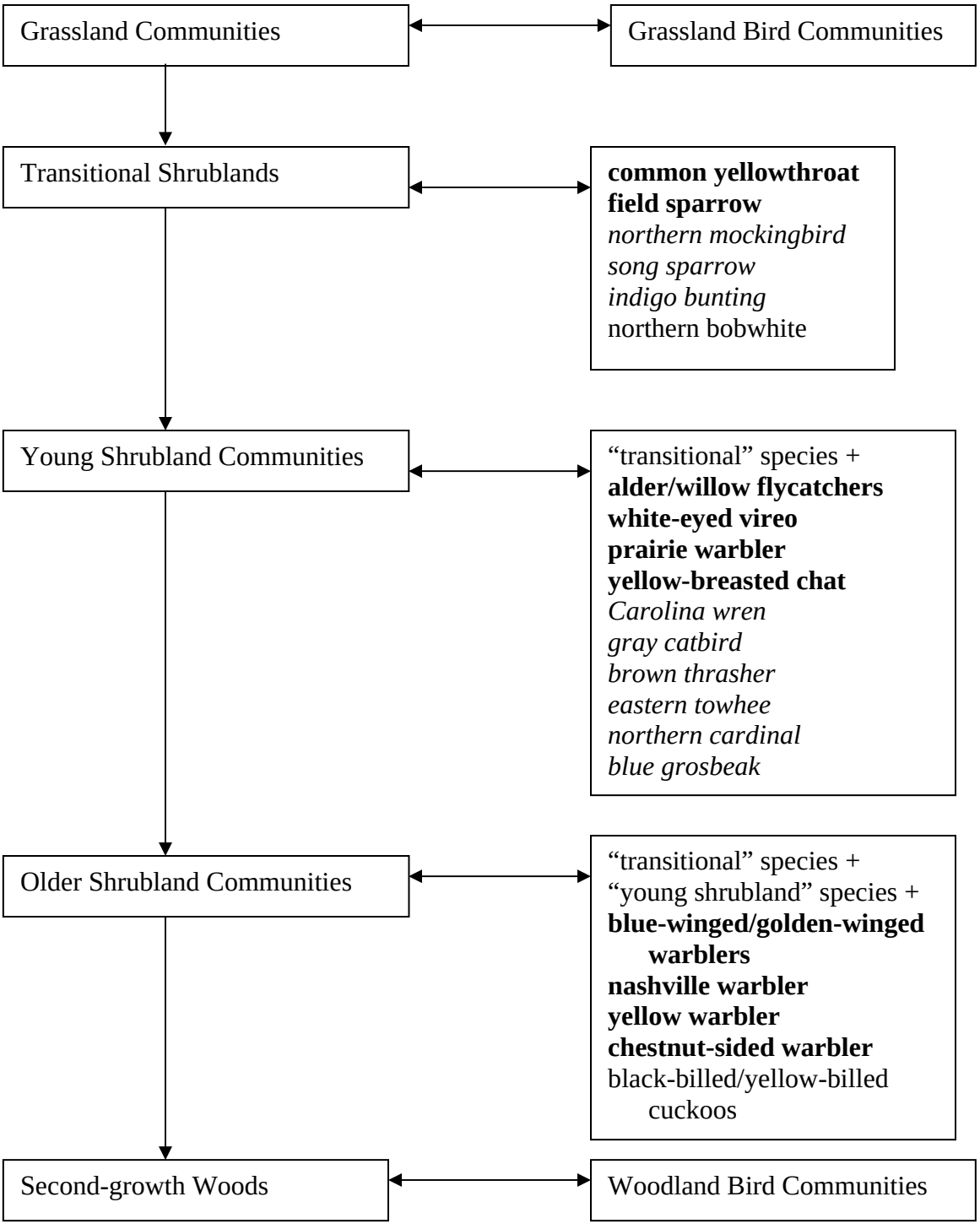

Figure 1. Shrubland bird communities in the Mid-Atlantic Region. Boldface species are field specialists, italics are ubiquitous species, and normal font represents multiple habitat species.

Transitional Shrublands

These fields represent the youngest communities in transition from bare soil to shrublands, beginning with dominance by annual herbs and grasses which are rapidly replaced by perennial herbs (Figure 2). Woody vegetation begins to emerge during the last seral stages of transitional shrublands with scattered shrubs and saplings generally <1 m (3 ft) in height and covering <50% of the area. The avian communities in these habitats are the least diverse of all shrubland bird communities.

Field Specialists

Common Yellowthroat: Yellowthroats prefer damp habitats but are also found in drier upland areas. They favor habitats where herbaceous vegetation is relatively dense with little or no bare ground (Guzy and Ritchison 1999).

Field Sparrow: These sparrows prefer upland habitats and avoid damp areas. They prefer herbaceous vegetation generally <20 cm (8 in) tall with patches of sparse cover for foraging (Carey et al. 1994). They also occur in taller and denser herbaceous vegetation if some open ground is available.

Ubiquitous Species

Northern Mockingbird: Mockingbirds prefer dry upland habitats and are most numerous in open areas with scattered dense bushes and small trees, such as residential lawns, overgrown pastures, roadsides, and fencerows (Derrickson and Breitwisch 1992). Their populations can be adversely affected by severe winter weather, although usually not to the same extent as Carolina wrens (Robbins et al. 1986; David et al. 1990).

Song Sparrow: These sparrows prefer habitats with low bushes scattered among dense herbaceous vegetation, but normally disappear when the brushy cover becomes too dense. Damp and dry habitats are equally suitable for this species (Arcese et al. 2002).

Indigo Bunting: Indigo buntings are numerous in most shrubby habitats but normally avoid residential areas. They are regularly found in open fields with scattered bushes, as well as along brushy woodland edges and clear cuts with partial canopies. They equally prefer damp and dry habitats (Payne 1992).

Multiple Habitat Species

Northern Bobwhite: Bobwhites mostly use shrublands between late autumn and spring, when this dense cover provides protection from predators. They are regularly found in brushy corridors as well as shrubby fields (Rosene 1969). Bobwhites prefer nesting in grasslands, although adjacent brushy areas provide cover for family groups during the breeding season.

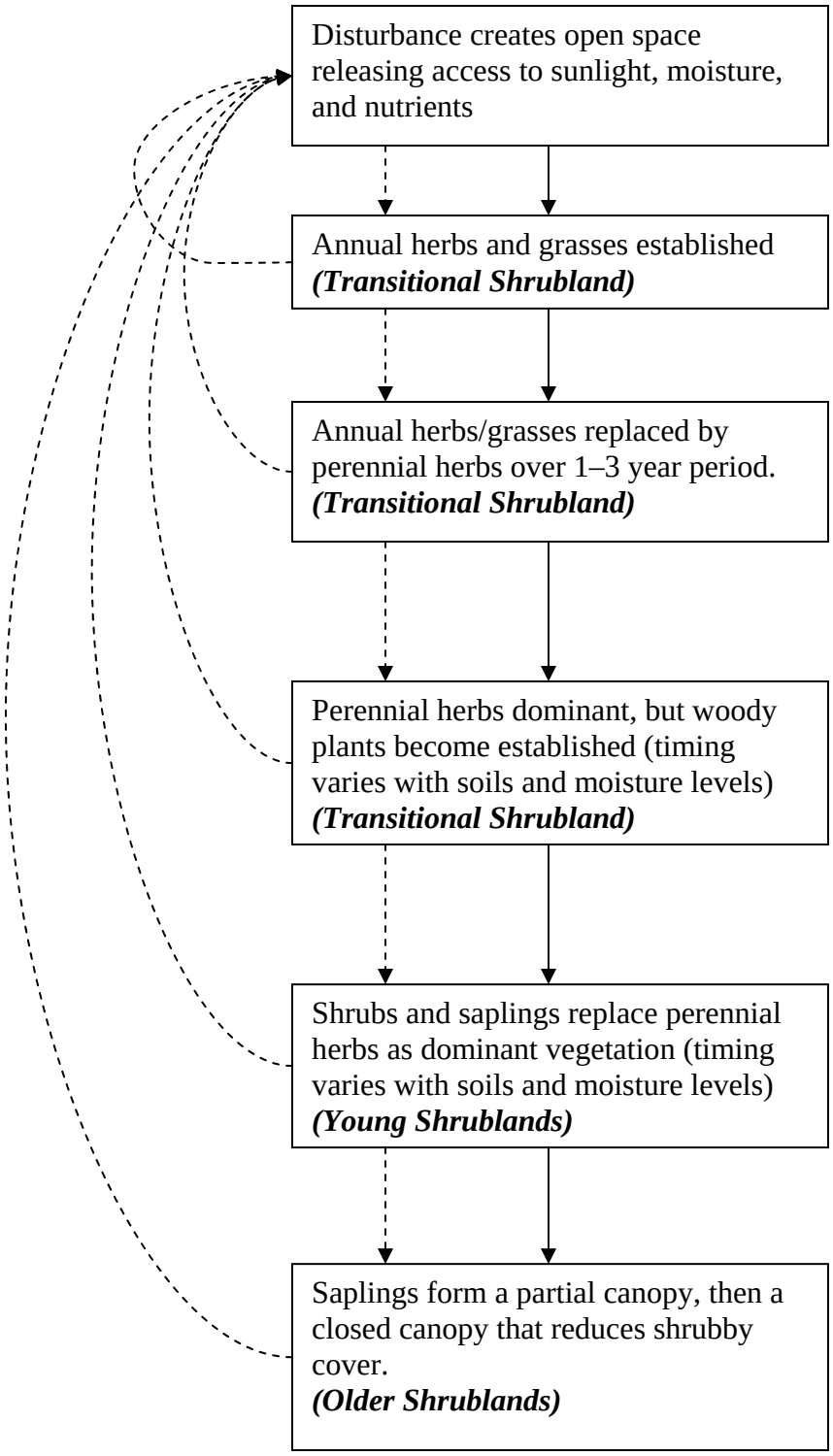

Figure 2. The "traditional" model of plant communities occurring during secondary succession (adapted from Connell and Slatyer 1977).

Young Shrublands

At this stage of succession woody vegetation becomes dominant, but patches of herbaceous vegetation remain. Woody plants continue to encroach on the herbaceous vegetation as these habitats advance in age. The woody vegetation is <3 m (10 ft) tall and normally dominated by shrubs and woody vines. The breeding bird community is more diverse than in the transitional shrublands. Transitional shrubland species occur where herbaceous vegetation is prevalent, but birds preferring dense brushy vegetation dominate these communities.

Field Specialists

Of the field specialists found in transitional shrublands, field sparrows tend to disappear once woody vegetation becomes dominant. Common yellowthroats are more tolerant of shrubby cover if patches of herbaceous vegetation persist.

Alder Flycatcher: These flycatchers prefer wetlands and the margins of damp habitats, especially communities dominated by alders (*Alnus* sp.) and willows (*Salix* sp.). They require small openings in the shrubby cover for foraging (Lowther 1999).

Willow Flycatcher: Their habitat requirements are similar to alder flycatcher, and both species are found together in some locations. While willows regularly occur along the margins of wetlands and streams, they also occupy somewhat drier upland habitats (Sedgwick 2000).

White-eyed Vireo: These vireos prefer fairly continuous shrubby cover. They are more numerous in moist habitats, but also occur in dry upland areas (Hopp et al. 1995).

Prairie Warbler: Prairie warblers thrive in young upland shrublands where patches of low, dense woody cover are interspersed with more open habitats. They are also numerous in habitats dominated by red cedars (*Juniperus virginianus*), even occurring along narrow edges if cedars predominate (Nolan et al. 1999).

Yellow-breasted Chat: Their habitat preferences are similar to white-eyed vireos, except chats are equally numerous in damp and dry fields (Eckerle and Thompson 2001).

Ubiquitous Shrubland Birds

Of the species found in transitional shrublands, northern mockingbirds and song sparrows disappear as open areas are replaced by dense shrubby cover.

Carolina Wren: These wrens prefer woodland edges and other habitats where there is a partial canopy over underbrush, vines, and tangles. They frequently occur in residential areas, along damp riparian corridors, and the margins of dry upland woodlots. Carolina wren populations fluctuate in response to severe winter weather, when extended periods of snow cover and cold temperatures can produce declines of $\geq$80% during a single season (Robbins et al. 1986; Haggerty and Morton 1995). Population recovery generally occurs within 3–5 years unless severe winter weather is repeated.

Gray Catbird: Gray catbirds prefer extensive dense shrubbery 2–3 m (6–10 ft) tall including woodland edges and openings, fencerows, abandoned and cut-over fields, utility line corridors, and residential areas. They are most numerous in damp habitats, but do occur in dry upland sites (Cimprich and Moore 1995)

Brown Thrasher: In contrast to gray catbirds, brown thrashers prefer dry upland areas. They occur in woodland edges and openings, fencerows, abandoned and cut-over fields, and utility corridors wherever sparse ground cover allows foraging along the ground. Thrashers regularly frequent narrow corridors bordering open fields (Cavitt and Haas 2000).

Eastern Towhee: Towhees are most numerous in shrubby fields and brushy woodland edges and openings. They prefer upland habitats with relatively sparse ground cover to allow foraging along the ground (Greenlaw 1996). They occur along narrow shrubby corridors, especially where red cedars are prevalent, but are less numerous in these habitats than other ubiquitous shrubland birds.

Northern Cardinal: Cardinals are regularly encountered in all shrubland habitats, as numerous in ornamental shrubs around residences as in large cut-over fields. Damp and dry habitats are equally preferred (Halkin and Linville 1999).

Blue Grosbeak: Blue grosbeaks prefer narrow brushy corridors along fencerows and roadsides. They occur in overgrown pastures and other shrubby fields, but generally along the edges, and in younger fields where bushes and saplings are interspersed with herbaceous cover. They are most numerous in dry upland locations (Ingold 1993).

Older Shrublands

These late shrubland successional stages are characterized by nearly complete (>90%) cover by woody vegetation. Initially, these habitats are dominated by shrubs with relatively few saplings. As they mature, saplings expand at the expense of the shrubby cover. When the saplings form a closed canopy, these communities represent the initial transition into second-growth woodlands. Composition of breeding bird communities tends to be the most diverse of all successional habitats. Transitional shrubland birds are scarce and restricted to the edges of these older communities. Species characteristics of young shrublands are numerous where brushy cover is well established, but decrease when saplings become dominant. Additional species may appear in habitats having closed canopies, such as ruffed grouse (*Bonasa umbellus*) (Askins 2001), while woodland birds such as Cerulean warbler (*Dendroica cerulea*) occur near openings provided by successional habitats adjacent to mature forests (Hunter et al. 2001).

Field Specialists

While all field specialists can occur in these habitats, the transitional shrubland species are scarce. Many of the young shrubland species will become scarce or disappear once saplings start to encroach into these habitats.

Blue-winged Warbler: This warbler favors dense shrubby habitats and encroachment by some saplings, but disappears once a complete canopy is formed. They occur in damp areas, but prefer somewhat drier upland habitats (Gill et al. 2001).

Golden-winged Warbler: Their habitat preferences are very similar to blue-winged warblers, except they tend to prefer damp areas. Where their ranges overlap, both species frequently breed in the same locations (Confer 1992). Golden-winged warbler is a species of conservation concern as a result of its relatively small population size, limited breeding distribution, and significantly declining population trends. While habitat loss contributes to golden-winged warbler population declines, other factors are also likely involved. Whenever blue-wingeds move into an area occupied by golden-wingeds, the latter species invariably disappears (Gill 1980). Whether this pattern is due to competition between the two species or other factors is uncertain. But as the breeding range of blue-winged warblers expands, the range of golden-wingeds retreats northward and to higher elevations where blue-wingeds are not present.

Nashville Warbler: Nashville warblers frequent sphagnum bogs and various upland habitats including pine barrens and regenerating forests dominated by birches (*Betula* spp.) and aspens (*Populus* spp.). Typical breeding habitats are fairly open areas with scattered small trees and relatively dense ground cover (Williams 1996).

Yellow Warbler: Yellow warblers prefer damp habitats bordering streams and wetlands and are seldom found in upland areas. Breeding pairs are most abundant in habitats dominated by small trees but retaining some shrubby cover (Lowther et al. 1999)

Chestnut-sided Warbler: Their habitat preferences are similar to yellow warblers, except chestnut-sideds prefer dry upland areas and avoid damp habitats. They are also more tolerant of habitats dominated by shrubs with few small trees (Richardson and Brauning 1995).

Ubiquitous Shrubland Birds

No ubiquitous species are restricted to these older successional habitats. All species occurring in the younger successional communities may be present depending upon the availability of suitable shrubby cover.

Multiple Habitat Species

These habitats are regularly visited by woodland birds, especially later in the breeding season when juveniles and molting adults find food and protective cover within successional communities. Additionally, older successional communities provide one component of the breeding habitats for:

Black-billed and Yellow-billed Cuckoos: Both cuckoos forage in woodlands but nest in dense upland thickets. These thickets are normally close to foraging habitats and may be in narrow corridors, woodland openings, and small fields. Both cuckoos occur in a variety of wooded habitats, but black-billeds prefer younger woodlands than yellow-billeds (Hughes 2001).

Shrubland Bird Ecological Requirements Summary

Shrubland bird management should recognize that the presence of most birds largely reflects moisture regimes and the physical structure of successional communities. For most birds, the dominant plant species are less important than the physical structure and hydrologic conditions. The important physical components include presence of bare ground, densities of shrubs and

herbaceous cover, height of woody vegetation, and presence of a partial or complete canopy of saplings. Some species prefer damp areas while others prefer dry upland habitats.

In transitional shrubland communities (Figure 1), breeding birds prefer open habitats where shrubs are scattered among dense cover dominated by herbs and grasses and small trees are scarce or absent. As shrubby vegetation becomes dominant, with a marked reduction in the extent of herbaceous cover, transitional shrubland birds will decrease in abundance and be replaced by breeding birds typical of young shrublands. When saplings become dominant and form a partial canopy over the shrub layer, species characteristic of older shrubland communities appear. Maintaining specific shrubland bird communities requires regular maintenance aimed at controlling the height and density of woody communities in order to maintain the appropriate physical structure preferred by the desired breeding avifauna.

Secondary Succession in the Mid-Atlantic Region

Few existing studies describe the composition of successional communities within this region (e.g., Keever 1979). Studies conducted elsewhere provide potentially relevant data, such as the dynamics of plant succession on the Piedmont of North Carolina and New Jersey described by Oosting (1942) and Bard (1952), and the relationships between avian and plant communities in Piedmont successional habitats of Georgia and New Jersey described by Johnston and Odum (1956) and Kricher (1973). Data from other physiographic strata are more limited. Odum (1950) describes relationships between avian and successional plant communities at high elevations in the Appalachian Mountains of North Carolina, while Kendeigh (1946) describes breeding birds associated with successional habitats within a beech (*Fagus grandifolia*)-maple (*Acer* spp.)-hemlock (*Tsuga canadensis*) community. Studies of succession patterns and avian communities in red cedar glades are relevant to similar communities on limestone areas of the Mid-Atlantic Region (Quarterman 1950; Shugart and James 1973). Avian and plant communities along the Coastal Plain have received little attention (Levin 1966).

Considerable caution is necessary whenever results of site-specific studies are applied to larger geographic areas. Recent studies indicate that numerous factors influence the composition of successional plant communities and their rates of change (e.g., Cook et al. 2005). Hence, inferences from published studies are not necessarily applicable to other sites within the same state or physiographic region if the factors influencing succession are dissimilar.

The diverse Mid-Atlantic Region supports numerous successional plant communities that vary considerably from sea level along the Coastal Plain to high elevations in the Appalachians. Even within a physiographic region, different successional communities develop, depending on factors including elevation, slope, aspect, soil type, bedrock type, moisture regime, previous land use, patch size and shape, and distance to other successional habitats. Describing every successional plant community in this region is beyond the scope of this study. Instead, this model emphasizes understanding the processes influencing succession and how to manage these processes to maintain desired successional plant communities.

Secondary Succession Models

The “classic” ecological model for secondary succession is outlined in Figure 2 (from Connell and Slatyer 1977). This model starts with bare ground resulting from disturbance. The initial species to appear are “colonizers” characterized by good dispersal capabilities, ability to survive in a dormant state until the right conditions occur, become established in unoccupied areas, and grow quickly to maturity. These “colonizers” do not compete well with established vegetation, so few young plants grow in the presence of mature plants. When the “colonizers” become established they create an environment facilitating establishment of the next stage of successional vegetation, which is dominated by perennial herbs. Throughout secondary succession, each seral stage produces an environment favorable for establishing the next seral stage, until a climax community is attained. If new disturbance occurs, then this process is repeated (the dashed lines in Figure 2).

When starting from bare soil, initial successional communities are dominated by annual herbs and grasses. These communities exist for 1–3 years until replaced by perennial herbs, such as asters (*Aster* spp.) and ragweeds (*Ambrosia* spp.) (Oosting 1942). Subsequent successional communities vary in their timing and composition, depending upon soils, moisture conditions, and many other factors. Some communities succeed directly from perennials to saplings, such as some riparian areas where birches and other saplings replace perennial herbs. In some dry upland situations perennial herbs are replaced by broom-sedge (*Andropogon virginicus*) and, eventually, by young pines (*Pinus* spp.) (Oosting 1942).

In clear cuts and other situations where woodlands have been removed succession patterns are different. Successional communities dominated by annual herbs do not form. Instead, initial communities are composed of perennial herbs, shrubs, vines, and saplings. The saplings grow quickly and can form closed-canopy communities in 8–12 years (Thompson and DeGraaf 2001).

A different successional model is illustrated in Figure 3 (from Connell and Slatyer 1977), where the initial colonists prevent new species from becoming established so that a dead mature plant is replaced by a young plant of the same species. The "colonizers" are eventually replaced by longer-lived species that survive in a suppressed state until an opportunity for unrestricted growth occurs. Hence, community composition changes more slowly as compared with the first model. A natural example is the pattern of succession forming red cedar glades. These glades are dominated by red cedars for several generations, but are eventually slowly replaced by oaks (*Quercus* spp.) (Quarterman 1950). A similar model is exhibited by communities dominated by invasives, such as multiflora rose (*Rosa multiflora*) and honeysuckles (*Lonicera* spp.), that form dense monocultures inhibiting establishment of native saplings for many years.

Temporal and Spatial Patterns of Secondary Succession

Spatial variation in secondary succession was documented by Gleason (1927) and remains a focus of ecological research. Temporal variation is less well documented (Cook et al. 2005), reflecting few long-term studies necessary to detect these changes. Most ecological studies are conducted in protected sites and reflect successional patterns largely unaffected by anthropogenic effects. However, recent research indicates silvicultural practices influence patterns of secondary succession (Thompson and DeGraaf 2001), demonstrating the influence of anthropogenic factors on successional community composition.

A detailed discussion of factors influencing spatial and temporal variation in secondary succession is beyond the scope of this paper. The more important factors are briefly discussed below within the context of managing successional communities in parks. Secondary succession should be viewed as numerous colonization and extinction events. When the dispersal and competitive abilities of species composing the desired communities are understood, then these communities can be created and managed.

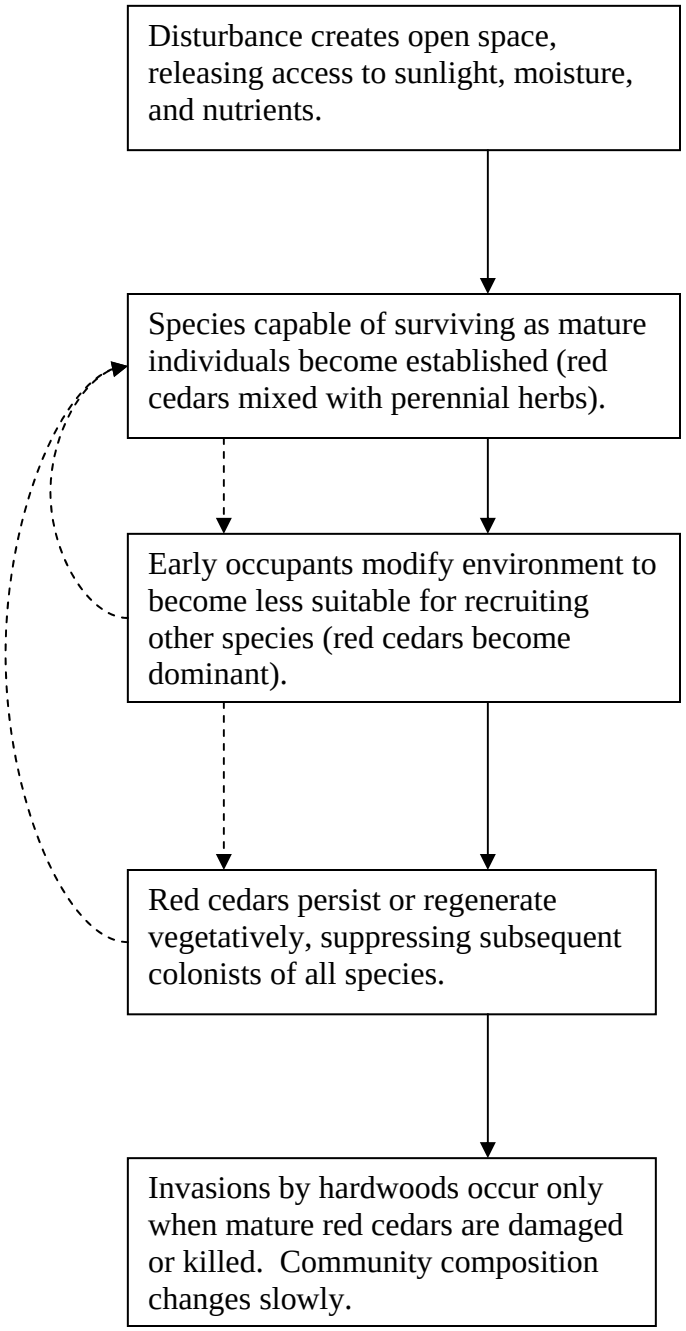

Figure 3. Secondary succession model where early colonists suppress growth of subsequent colonists (adapted from Connell and Slatyer 1977), using example of red cedar (*Juniperus virginiana*) glades.

Distance Effects

The surrounding landscape influences the composition and rates of change of successional communities. Distances isolating sources of potential colonists markedly affect the composition of successional communities (Grashof-Bodkam and Geertsema 1998). Plants with seeds persistent in seed banks or dispersed by wind or birds regularly occur in isolated patches (Bard 1952). Colonization by dispersive species requires little assistance from managers. These characteristics typify most early successional plants. In contrast, late successional species tend to be poor dispersers and their colonization is relatively slow (Clark et al. 1998). Assistance may be needed to establish these plants in isolated patches. Dispersal limitation can interact with other succession mechanisms to influence community composition. "Colonizers" facilitate establishment of later species through providing perches and food to promote visitation by avian dispersal agents (Werner and Harbeck 1982). This process improves spatial heterogeneity in successional communities, while succession is constrained if these facilitative species are absent (Cook et al. 2005). Where parks are isolated from other successional habitats, their successional communities are likely to be dominated by the most dispersive species. Intensive management may be necessary to assist establishment of poor dispersers into isolated parks.

Area Effects

Large isolated patches undergo succession more rapidly than small patches because they provide larger targets for long-distance dispersers (Holt et al. 1995). Larger sites also provide greater potential for developing nuclei of individuals that readily disperse within a patch, allowing later successional species to more rapidly replace early "colonists". Abiotic factors may operate differently in various sized patches. For example, edges tend to be hotter and drier than interiors. Because small patches have greater perimeter to area ratios, their microhabitats are different than larger patches, which may influence the composition and rates of change in successional communities. Patch size effects are more prevalent in later successional stages (Cook et al. 2005).

Dispersal Agents

Dispersal mode influences rates of plant succession and development of spatial structure in plant communities. Wind- and bird-dispersed plants exhibit different distribution patterns (Foster and Gross 1999). Wind-dispersed plants appear earlier and are more randomly distributed across the landscape. Bird-dispersed plants normally appear later and are clumped, reflecting their clonal stem production and the non-random use of habitats by birds.

Herbivory

Herbivores influence rates of plant community succession through their preferences for certain palatable species (Davidson 1993). In early seral stages, herbivory retards succession into intermediate stages because herbivores prefer to graze on vegetation found in these intermediate stages. Conversely, herbivory accelerates changes from later successional changes into persistent trees. Abundant herbivore populations may influence successional community composition at local and landscape scales.

Invasive Species

Disturbed systems are more prone to invasions by exotic plants than undisturbed systems (McIntyre and Lavorel 1994). Depending upon life history traits and edaphic limits, invading taxa may aggressively displace established communities. In the worst case, exotics develop uniform communities that effectively exclude native species and do not undergo normal successional changes (Young et al. 2001).

Prior Land Use Practices

The previous condition of a site can influence composition of successional communities. Myster and Pickett (1994) reported fields previously planted to orchard grass (*Dactylis glomerata*) underwent slower rates of change than cultivated fields. Thompson and DeGraaf (2001) indicate succession following land abandonment requires longer for colonization by trees than a regenerating forest. Silvicultural practices also influence successional patterns. Even-aged management produces discrete patches of early successional habitats that rapidly revert to shrub-sapling stage vegetation (Thompson and DeGraaf 2001). Uneven-aged management retains a partial canopy, thus creating unfavorable conditions for light-demanding plants and reducing herbaceous and shrub community richness. These studies and other research (Levin 1966; Keever 1983) demonstrate the importance of land use history in determining site-specific successional patterns. All of the above factors contribute to spatial and temporal variability in succession rates documented in ecological studies.

A Conceptual Ecological Model for Managing Shrubland Birds

This conceptual model provides background information for NPS networks and parks to support decisions concerning shrubland management to benefit breeding birds. Developing a coordinated approach to shrubland management across networks poses numerous challenges reflecting the complexity of spatial and temporal factors influencing the diversity of successional habitats within the Mid-Atlantic Region. Overall objectives should be developed by networks or across networks for a regional approach. These large-scale objectives provide a context for management decisions made within parks. This conceptual model and its recommendations are based on the professional judgment of the author as supported by the cited literature.

NPS Network Objectives

Developing network management objectives for shrubland habitats should recognize these habitats are disturbance dependent and no single prescription effectively manages every successional community (Askins 2001) (Figure 4). Physical structure, community composition, and succession patterns produced when cleared lands are abandoned differ from those occurring where forests are removed (Lorimer 2001). Managing specific successional communities requires detailed knowledge of the dominant species in each seral stage, their habitat requirements, life histories, and abilities to compete with other plants, as well as knowledge of the avian communities likely to develop within each park (Table 3). Managing for species of conservation concern, such as the golden-winged warbler, requires different strategies than managing for groups of shrubland birds. Given the ephemeral nature of natural successional communities, maintaining specific communities requires a commitment for intensive long-term management necessary to sustain them. At the scale of NPS networks, shrubland management objectives are best directed towards maintaining categories of successional habitats rather than specific plant communities. Once objectives for each category are identified, parks can determine which communities likely occur within their area.

Transitional Shrublands

These communities are relatively ephemeral with woody vegetation rapidly replacing herbaceous cover in unmanaged areas. Maintaining early seral stages requires periodic mowing and/or prescribed burns to prevent establishment of dense woody vegetation, combined with mechanical disturbance (disking or chopping) to expose bare soil and allow emergence of “colonist” plants (Figure 4) (Rosene 1969).

Young Shrublands

These habitats are more likely associated with secondary succession than cut-over forests and have larger proportions of woody vines and shrubs than typically found in regenerating forests (Askins 2001). They may be maintained by specific wet or dry hydrologic conditions that inhibit establishment of trees. Dense shrubby thickets may also prevent establishment of saplings until mature shrubs die and create opportunities for young trees to grow. In all likelihood, these habitats will require maintenance to prevent succession into young forests. These management activities are labor intensive, including selective removal of young trees combined with chemical

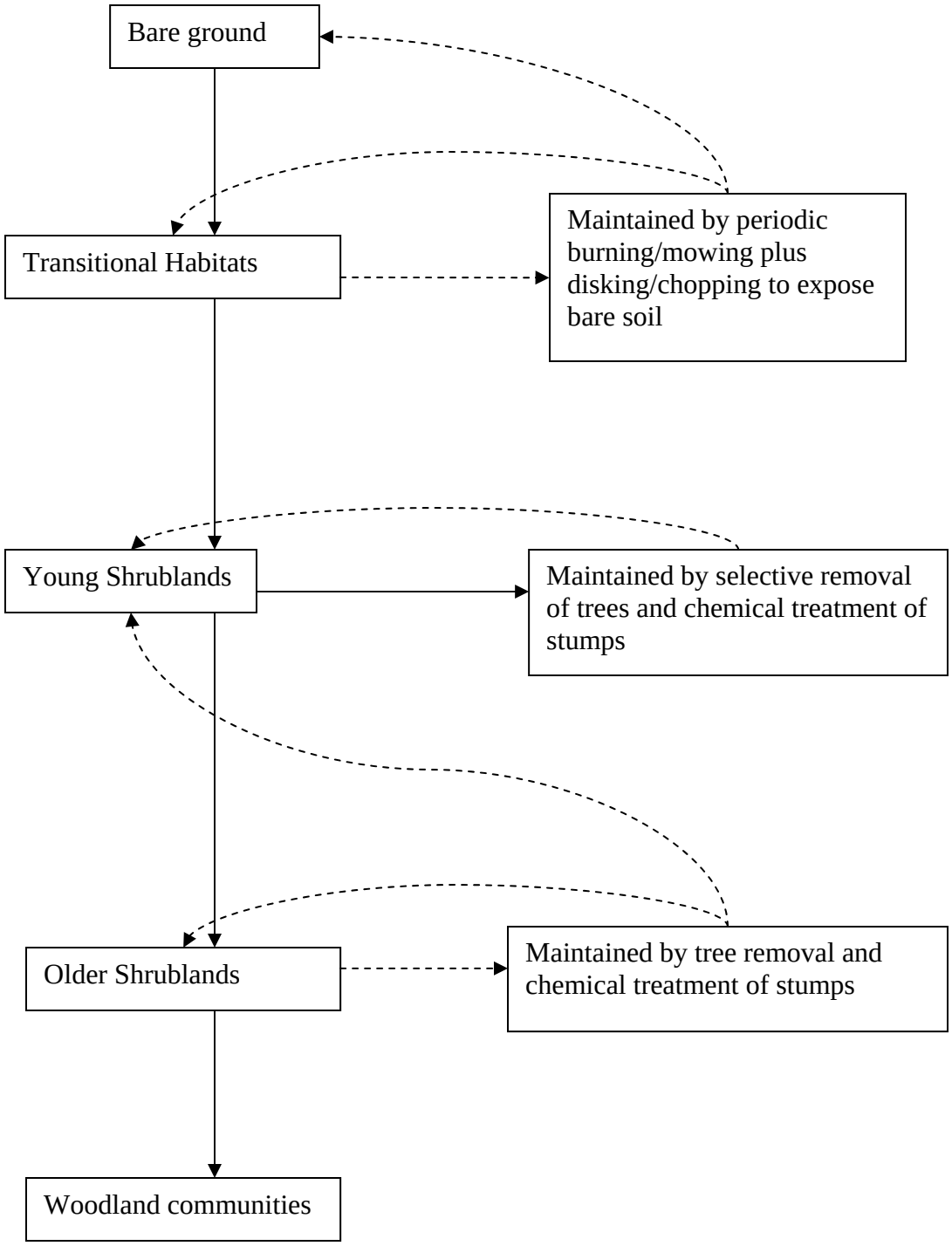

Figure 4. Management decisions concerning development of secondary successional habitats within Mid-Atlantic Region.

Table 3. Characteristics of early and late successional plants (from Huston and Smith [1987]).

Characteristic	Early Succession	Late Succession
Photosynthesis		
Light-saturation intensity	High	Low
Light compensation point	High	Low
Efficiency at low light	Low	High
Photosynthetic rate	High	Low
Respiration rate	High	Low
Water use efficiency		
Transpiration rate	High	Low
Mesophyll resistance	Low	High
Seeds		
Number	Many	Few
Size	Small	Large
Dispersal distance	Large	Small
Dispersal mechanism	Wind, birds, bats	Gravity, mammals
Viability	Long	Short
Induced dormancy	Common	Uncommon?
Resource acquisition rate	High	Low?
Recovery from nutrient stress	Fast	Slow
Root-to-shoot ratio	Low	High
Mature size	Small	Large
Structural strength	Low	High
Growth rate	Rapid	Slow
Maximum life span	Short	Long

treatment of stumps, practices that have created stable shrub communities along power line corridors (Askins 2001; Thompson and DeGraaf 2001).

Older Shrublands

As discussed by Lorimer (2001) and Askins (2001), these habitats are frequently associated with regenerating woodlands and openings in forested areas as well as later stages of secondary succession. They are characterized by a partial canopy of saplings over shrub and herbaceous layers. The saplings eventually form a closed canopy, shading out the undergrowth (Thompson and DeGraaf 2001), and rapidly succeeding into second-growth woods. Permanent patches of older shrublands could be maintained by continuously removing saplings to retain a partial canopy (Askins 2001). Another option is harvesting patches of forests on a rotating basis to create regenerating woods, although this option may conflict with the historic focus of some parks.

Park Objectives

At the park level, the primary emphasis should be directed towards managing succession to produce the desired density and height of shrubby/sapling vegetation to support specific shrubland bird communities. The primary concern is managing succession to produce the desired seral stages, recognizing the need to control invasive species that may interrupt normal successional patterns. A second concern is managing specific plant communities whose presence results from physical factors and natural processes that are difficult to control.

Managing Successional Stages: Two approaches are possible for managing successional habitats within parks. These approaches differ primarily in the amount of management effort required to maintain these habitats. In addition to biological considerations, the historical focus of each park may influence which management approach is most appropriate to produce the desired seral stages.

The “low management” approach involves setting aside areas where secondary succession occurs at natural rates (Figure 5). Initiation of secondary succession is staggered at 3–5 year intervals so that all seral stages are eventually represented in a park. Once succession advances into second-growth forests, then these woodlands are harvested to re-initiate secondary succession or additional fields are allowed to undergo succession. Eventually some woodlands have to be harvested or entire parks will become forested.

The primary advantage of this approach is that active management is not required as secondary succession advances across these areas. However, extensive management is required to change second-growth woodlands into the earliest seral stages. Simply harvesting trees produces successional communities dominated by saplings of forest species that relatively rapidly revert into closed-canopy woodlands. Reverting second-growth woods into early seral stages requires removal of all live and downed timber, repeated chemical treatment of stumps, and disking or chopping the soil to expose bare ground for invasion by colonizing herbs.

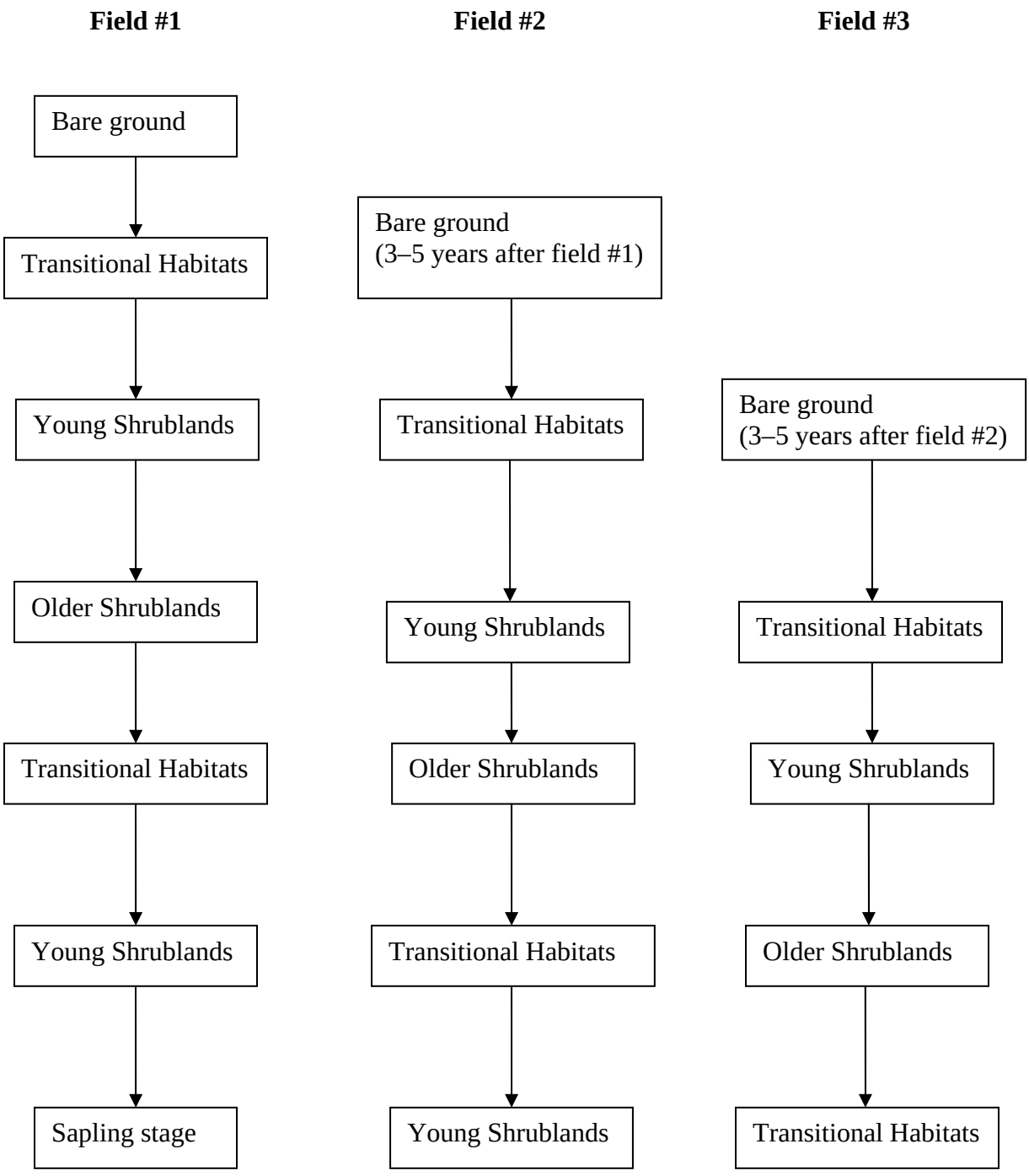

Figure 5. “Low Management” approach for establishing successional communities in parks.

This approach may be inappropriate in areas prone to invasion by exotic shrubs. If unmanaged, areas could become dominated by invasives at the expense of natural communities. The invasives may form dense monocultures inhibiting establishment of later successional communities. Eliminating invasive shrubs and preventing their reoccurrence requires more intensive management than described above.

An alternative to this "low management" approach is the "repeated management" approach, allowing secondary succession to advance to the desired seral stage and then managing the area to retain that stage of vegetation. The required management activities vary with seral stage (Figure 6). Maintaining early successional habitats requires mowing and/or prescribed burns at 2–4 year intervals combined with disking or chopping the soil to expose bare ground to allow colonizing herbs to become established. Maintaining later successional communities aims to prevent closed canopies from developing through labor-intensive activities of removing selected saplings combined with chemical treatment of stumps and sprouts. These activities may be necessary at 3–5 year intervals to maintain desired shrubland communities.

Regular maintenance is necessary in areas prone to supporting invasive species. Eliminating invasives likely requires chemical treatment and/or hand removal, depending upon the characteristics of a particular species. These activities should occur as soon as invasives appear, rather than waiting for them to become dominant, and may be required for many years to prevent reoccurrence of species dispersed by the wind and/or birds.

Managing Specific Vegetative Communities: The presence of breeding shrubland birds is dictated more by the density and height of woody communities and hydrologic conditions than by plant community composition. However, specific plant communities may be desired in some parks to recreate environments existing at the times of historic events. Managing for specific successional plant communities poses a number of challenges as discussed below.

Succession reflects the association between unbuffered environmental factors with plant growth characteristics, size, life span, and dispersal mechanisms and survival of seeds (Huston and Smith 1987 [and references therein]). The physiological and life history traits of early and late successional plants are summarized in Table 3. While prevalence of certain successional communities is predictable, such as dominance of red cedars in dry habitats with limestone bedrock, the composition of most successional communities may be difficult to predict. Even in areas where secondary succession is well described, factors such as elevation, slope, aspect, soil type, bedrock, and hydrologic conditions, combined with the biological traits of each plant species, influence where species become established (Huston and Smith 1987; Foster and Gross 1999).

When starting from bare soil, the earliest successional species are wind dispersed and exhibit a fairly random pattern of distribution. Bird-dispersed species follow and have a more clumped distribution reflecting the clonal reproduction and activity patterns of birds (Foster and Gross 1999). Seed consumption by mice, especially under the cover of herbs, is an important factor regulating the spatial distribution of woody vegetation following dispersal (Gill and Marks 1991). The uncertainty surrounding seed dispersal by wind and birds, seed predation by mammals, and interspecific competition among plants, combined with landscape-scale patterns

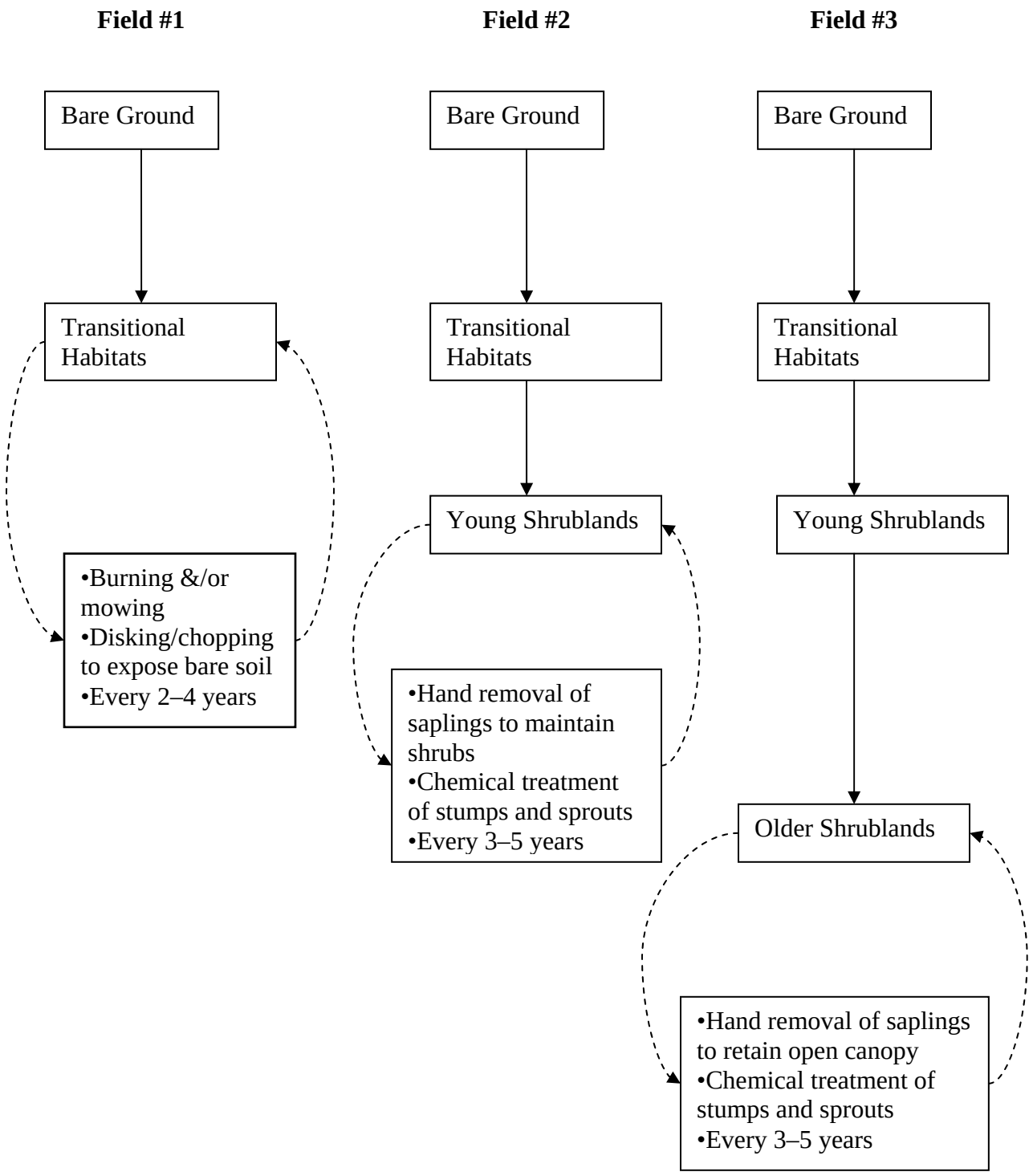

Figure 6. "Repeated Management" approach for establishing successional communities in parks.

of distribution and abundance all influence the composition of plant communities at a site (Keever 1983; Gill and Marks 1991). These factors may be responsible for producing markedly different successional communities in nearby locations.

If specific successional plant communities are desired, management may be necessary to develop these communities. Removing unwanted species is labor intensive and requires chemical treatment and/or hand removal. Planting desired species is most likely to succeed only when occurring at the appropriate successional stage. A good understanding of the physiological requirements of each species is required in relation to the physical conditions at each site. Knowledge of the competitive abilities of desired species is important to determine if they can become established within existing plant communities.

Other Considerations for Creating Shrubland Habitats. Unlike grassland birds that prefer landscapes with open views towards the horizon, shrubland birds are not deterred by patches of habitats within largely wooded landscapes. Creating shrubland habitats in largely wooded or open landscapes has little influence on shrubland bird community composition. Surrounding landscapes influence the composition of shrubland vegetative communities, however, which may be an issue if managing for a specific plant community.

An important factor to consider is the width of the newly-created habitats. Corridors less than 30 m (100 ft) wide will be occupied only by ubiquitous shrubland birds regardless of the length of the corridor. If managing for field specialists is important, then the minimum corridor width should be 50–70 m (165–230 ft).

Effects of patch size on occupancy vary among shrubland birds. Ubiquitous species require only enough suitable habitats to support their breeding territories; 1–2 ha (2.5–5 ac) patches are sufficient to support most breeding pairs. However, fields <2 ha (5 ac) support few field specialists. While available data on patch size preferences of shrubland birds is still sparse, the few studies conducted to date indicate minimum sizes of 4–5 ha (10–12 ac) are required to attract most field specialists, assuming these habitats are at least 50–70 m (165–230 ft) wide. Patch sizes up to 20 ha (50 ac) are more attractive to shrubland birds, but creating patches >20 ha (50 ac) appear to have few benefits for these species.

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Appendix. Life history information for shrubland birds within the Mid-Atlantic Region.

Alder Flycatcher (*Empidonax alnorum*)

Status: In the Mid-Atlantic Region, this flycatcher is a widely distributed summer resident only across the northern tier of counties in Pennsylvania. Alder flycatchers are locally distributed at higher elevations (>610 m [2,000 ft]) along the Appalachians of Pennsylvania and Maryland, but are known from only a few isolated locations in Virginia.

Arrival Dates: A very late spring migrant, alder flycatchers normally return during the last half of May and their northward migration continues through mid-June.

Departure Dates: Few records, but most probably depart during August and early September.

Breeding Habitats: Alder flycatchers are most numerous in brushy wetlands and damp thickets at the border of streams and wet areas. They also occur in damp abandoned fields and cut-over areas dominated by shrubby vegetation. While there is some overlap, alder flycatchers tend to occupy wetter habitats than willow flycatchers.

Nest Site: Alder flycatcher nests are normally placed low in dense bushes, normally at heights of 0.6–0.9 m (2–3 ft). A few nests may be as high as 1.8 m (6 ft).

Territory Size: Based on data from two studies, breeding territory size varies between 0.2–3.0 ha (0.5–7.4 ac).

Mating System: Believed to be monogamous, but no detailed studies have been conducted.

Breeding Phenology: Its breeding biology is relatively poorly documented in the literature.

Pair Formation: No available information.

Nest Building: Few data from this region. Most likely occurs during the last week of May and first half of June, but renesting attempts may continue through late July.

Egg Dates: Few nesting records from this region. Peak nesting activity during June while renesting attempts produce clutches into early August.

Number of Broods: Believed to be single-brooded, but alder flycatchers may renest if their initial attempt is unsuccessful.

Nests with Young: Few data, but nests with young probably peak during the last half of June and first half of July. A late nest is reported on 24 August in Maryland.

Fledgling Dates: Most young probably fledge during July and early August.

References: Brauning (1992); Robbins and Blom (1996); Lowther (1999); Trollinger et al. (2001).

Willow Flycatcher (*Empidonax traillii*)

Status: Willow flycatchers are widely distributed and fairly common summer residents across Pennsylvania. They have a similar status in northern Maryland west of the Chesapeake Bay and south to the Washington, D.C. area, but are mostly absent from the eastern shore and southern counties. In Virginia, these flycatchers are uncommon and rather locally distributed in the northern and western counties, but absent from the Piedmont and Coastal Plain.

Arrival Dates: Very late spring migrants, willow flycatchers normally return during the last half of May and their northward migration continues into the first half of June.

Departure Dates: Most willows probably depart during August and early September.

Breeding Habitats: Their preferred habitats consist of moist shrubby areas near streams, marshes, ponds, or other water. However, these flycatchers also regularly occupy drier brushy fields, utility corridors, and edge habitats that are not particularly wet.

Nest Site: Low in shrubs or dense saplings, but tends to be located towards the edges of thickets. Mean nest height is normally between 1.0–1.5 m (3–5 ft), but may be as low as 0.5 m (1.6 ft) and as high as 20 m (65 ft).

Territory Size: In eastern North America, mean territory sizes vary between 0.7–1.8 ha (1.7–4.4 ac).

Mating System: Normally monogamous, but polygyny is fairly regular ($\leq$15%) in some populations.

Breeding Phenology: Probably typical for a single-brooded neotropical migrant in eastern North America, but few nests are reported from the Mid-Atlantic Region.

Pair Formation: No available information.

Nest Building: Primarily occurs during June, but renesting attempts continue through mid-July.

Egg Dates: Most initial clutches are laid during June. Renesting attempts produce a nest with eggs as late as 28 July in Maryland.

Number of Broods: Single-brooded, but renests if initial attempt is unsuccessful.

Nests with Young: Most are reported between mid-June and mid-July. The latest attempts produce nestlings during early August.

Fledgling Dates: Most young probably fledge during July and early August.

References: Brauning (1992); Robbins and Blom (1996); Sedgwick (2000); Trollinger et al. (2001).

White-eyed Vireo (*Vireo griseus*)

Status: A fairly common and widespread summer resident across most of Virginia and Maryland, becoming locally rare at higher elevations in the mountains. In Pennsylvania, white-eyed vireos are fairly common summer residents at lower elevations in the southern half of the state, but are generally uncommon to rare elsewhere.

Arrival Dates: First migrants normally appear between mid-April in Virginia and early May in northern Pennsylvania; most return by mid-May.

Departure Dates: Most vireos depart during September with small numbers remaining through mid-October.

Breeding Habitats: White-eyed vireos are occupants of overgrown fields, cut-over areas, brushy hillsides, and swampy thickets. They equally prefer damp and dry upland habitats, but tend to avoid narrow shrubby corridors and woodland edges.

Nest Site: Nests are usually placed in dense shrubby vegetation at an average height of 0.8–1.0 m (2.6–3.3 ft) and a range of 0.3–2.1 m (1.0–6.9 ft).

Territory Size: Variable, depending upon habitat quality and the bird's age. Average territory size is 1.0–1.3 ha (2.5–3.2 ac), in two studies, with a range of 0.6–1.8 ha (1.5–4.4 ac).

Mating System: These vireos are apparently strictly monogamous.

Breeding Phenology: Typical for multi-brooded neotropical migrants in eastern North America.

Pair Formation: Males return first to the breeding range. Courtship lasts several days once the females return, since they wander from territory to territory until they settle on a mate.

Nest Building: Nest construction occurs during late April in the southern portion of the region, but is most prevalent during May. These activities continue into the second half of July for later nesting attempts.

Egg Dates: A nest in Maryland is reported from 22 April, but first nests are usually discovered during May. Later attempts are responsible for clutches through 24–26 July.

Number of Broods: Normally double-brooded across its range.

Nests with Young: Initial clutches normally hatch between mid-May and early June. Later attempts produce nests with young as late as the first half of August.

Fledgling Dates: First broods normally fledge during June while later attempts produce recently fledged young into the second half of August.

References: Brauning (1992); Hopp et al. (1995); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

Carolina Wren (*Thryothorus ludovicianus*)

Status: A common permanent resident east of the mountains in all three states and also in southwestern Pennsylvania, although numbers are temporarily reduced following winters with extended severe weather. Carolina wrens become uncommon to rare and locally distributed in the mountains and the northern third of Pennsylvania.

Breeding Habitats: Carolina wrens occupy various habitats supporting dense brushy undergrowth, including woodland edges, fencerows, utility line rights-of-way, abandoned fields, and ornamental shrubbery around residences. They regularly occur in lowland and upland habitats, but are somewhat less numerous in damp areas.

Nest Site: A wide variety of natural and artificial sites are used for nesting. Natural sites include vine tangles, tree cavities, overturned roots, and tree stumps, while nests are reported from bird houses and various other artificial sites, such as mailboxes, hanging flower baskets, clothes left hanging outside, inside abandoned cars, and inside garages. Nests are normally located 1–2 m (3–6 ft) above ground, but some are placed on the ground, while others are as high as 9 m (30 ft).

Territory Size: Territories are maintained throughout the year. Territory size is inversely related to population density, which may explain variability in published studies where mean territory size varies between 1–4 ha (2–10 ac) with a maximum of 8 ha (20 ac).

Mating System: Normally monogamous, although polygyny is very rare (only one report).

Breeding Phenology: Typical for a multi-brooded permanent resident in eastern North America.

Pair Formation: May occur any time of the year, but most frequently during the first autumn of their life. Pairs are believed to mate for life.

Nest Building: Nest building is possible during late February in southern Virginia. During warm springs the earliest nests are built in late March and early April, but these activities normally peak during April and early May. Nest building continues into the first half of August.

Egg Dates: The earliest published egg dates are 2–11 March in Virginia. Most first clutches are laid during April. The peak period for second clutches is during July, while the latest clutches are noted through 13 September in Maryland.

Number of Broods: Normally double-brooded, but some pairs raise three broods in southern portions of the region.

Nests with Young: Earliest broods are possible between late March and mid-April, but most initial broods hatch during May. Later attempts regularly produce broods into August and occasionally into the last half of September.

Fledgling Dates: Peak periods for fledglings are mid-May through early June and during July. The earliest young could leave the nest by late April, while the last broods fledge in late September.

References: Brauning (1992); Haggerty and Morton (1995); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

Gray Catbird (*Dumetella carolinensis*)

Status: Generally a common and widespread summer resident, although breeding pairs are locally scarce along portions of the Delmarva Peninsula. Small numbers winter along the Coastal Plain and Piedmont of Maryland and Virginia, but wintering catbirds are rare to absent elsewhere.

Arrival Dates: Northward migrants normally appear during the last half of April and become numerous by early May.

Departure Dates: Southward movements are most evident during the last half of September and October with stragglers into November.

Breeding Habitats: Gray catbirds breed in a wide variety of shrubby habitats, including overgrown fields, cut-over areas, brushy fencerows, shrubby woodland edges, swampy thickets, and bushes near residences.

Nest Site: Nests are located at an average height of 1.5 m (5 ft), primarily in dense shrubs, but also in saplings and vines. Most nests are <2 m (6.5 ft) in height, but a few are >15 m (50 ft). Two ground nests are exceptional.

Territory Size: Breeding territories are small, only 0.2–0.4 ha (0.5–1.0 ac) in several studies. Nests of neighboring pairs may be <20 m (65 ft) apart.

Mating System: Normally monogamous, but there is one record of a male mated with two females in separate territories.

Breeding Phenology: Fairly typical for a multi-brooded neotropical migrant in eastern North America, with many detailed studies of its breeding biology.

Pair Formation: Occurs shortly after arrival on the breeding territories. Pairs are noted the same day that females return.

Nest Building: Nest building occurs during late April in southern portions of the region, but most initial nests are built during May. These activities continue into early August for later attempts.

Egg Dates: Initial clutches are laid during May, while the peak of later attempts occurs during July. The latest reported clutch is 19 August in Maryland.

Number of Broods: Double-brooded in most areas, but may raise three broods in the southeastern states, and only one brood at the northern edge of its range.

Nests with Young: Primarily between mid-May and mid-June for first broods, with a peak during July and early August for later broods. A nest with young is reported through 27 August in Maryland.

Fledgling Dates: Initial clutches normally fledge during June, while later attempts produce recently fledged young through late August, with a peak in late July-early August.

References: Zimmerman (1963); Nickell (1965); Brauning (1992); Cimprich and Moore (1995); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

Northern Mockingbird (*Mimus polyglottos*)

Status: A conspicuous, common to abundant permanent resident east of the mountains in all three states and also in southwestern Pennsylvania. Mockingbirds become uncommon to rare and locally distributed in the mountains and the northern third of Pennsylvania.

Breeding Habitats: Northern mockingbirds prefer open habitats, such as roadsides, agricultural fields, and residential areas where dense shrubs are present along fencerows or as ornamental plantings around buildings.

Nest Site: Nests are generally located at heights of 1–3 m (3–10 ft) in dense shrubs and trees, with some nests as low as 0.5 m (1.6 ft) and others as high as 19 m (62 ft). On rare occasions, other nests sites are selected, such as eaves of buildings or a cavity in a tree.

Territory Size: Territories are normally defended throughout the year, but are usually smaller in winter than during the breeding season. Breeding territories generally vary between 0.4–2.5 ha (1–6 ac) with a mean of 1.0–1.2 ha (2.5–3.0 ac). Winter territories are normally <1 ha (2.5 ac) with a mean value of 0.3 ha (0.7 ac).

Mating System: Normally monogamous, but polygyny is rare (<5% of territorial males).

Breeding Phenology: Typical for a multi-brooded permanent resident in eastern North America.

Pair Formation: Some birds remain paired throughout the year and mate for life. However, most pairs exist for only one breeding season, or the female deserts the territory after nest failure. Timing of pair formation is unavailable.

Nest Building: Occurs as early as the last half of March in Virginia and Maryland and mid-April in Pennsylvania. These activities normally peak during May and continue into the first half of August.

Egg Dates: The earliest egg dates vary between 30 March in Maryland and 12 April in Pennsylvania, but most first clutches are probably laid during May. Later clutches are produced into the first half of August.

Number of Broods: In this region, most pairs raise two to three broods per year.

Nests with Young: Nests with young are reported between 19 April and 1 September. Peak periods are between late May and mid-June for initial broods and July for later attempts.

Fledgling Dates: Recently fledged young appear as early as the last half of May, but most first broods fledge during June. Fledglings are regularly encountered into the last half of August, with the latest dependent young reported from early September.

References: Means and Goertz (1983); Brauning (1992); Derrickson and Breitwisch (1992); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

Brown Thrasher (*Toxostoma rufum*)

Status: A fairly common and widespread summer resident of shrubby fields and edge habitats across the region. Small numbers regularly winter along the Coastal Plain and Piedmont of Maryland and Virginia, but wintering thrashers are rare to absent elsewhere.

Arrival Dates: Spring migration normally begins by the last week of March and continues into early May in Pennsylvania.

Departure Dates: Southward movements are most evident during the last half of September and October, with stragglers into November.

Breeding Habitats: Occurs in a variety of habitats dominated by shrubby thickets and underbrush, including fencerows bordering open fields, shelterbelts, overgrown pastures, abandoned fields, cut-over areas, wooded draws, pine barrens, savannahs, and the brushy margins of woodlands. Thrashers prefer dry upland sites with a canopy cover <30% and the ground covered by litter.

Nest Site: Nests are normally located 1–2 m (3–6.5 ft) above ground, but ground nesting is frequent. Thrashers prefer dense thorny shrubs and bushes entangled with vines for nest sites.

Territory Size: Normally 0.5–1.25 ha (1.2–3.0 ac), but pairs occasionally nest in close proximity (15 m [50 ft]) to each other.

Mating System: Thrashers are considered to be strictly monogamous.

Breeding Phenology: Breeding activities may be advanced during warm springs and delayed by cold weather conditions.

Pair Formation: Occurs as soon as the females return to the breeding range, as early as mid-March in southern Virginia and as late as mid-May in northern Pennsylvania.

Nest Building: Begins by late March in southern Virginia, but generally occurs between mid-April and mid-May. Later nests are constructed through mid-July.

Egg Dates: As early as 8–18 April, with most first clutches by early May in Virginia and Maryland. Earliest clutch is 24 April in Pennsylvania, where most initial clutches are produced during May. Late clutches are reported through 20–30 July.

Number of Broods: Varies among populations, but some individuals are double-brooded, especially in southern portion of range.

Nests with Young: The earliest clutches hatch by late April, but most first broods appear during May and early June. The last clutches hatch by early August.

Fledgling Dates: Success rate increases as season progresses. First fledglings appear by mid-May in southern areas, but most are noted during June. Last broods fledge by mid-August.

References: Van Velzen (1968); Brauning (1992); Robbins and Blom (1996); Clapp (1997); Cavitt and Haas (2000); McWilliams and Brauning (2000); Trollinger et al. (2001).

Blue-winged Warbler (*Vermivora pinus*)

Status: Blue-winged warblers are fairly common and widespread at lower elevations across Pennsylvania, but rare to absent in the mountains. In Maryland, they are widely distributed in the northern counties west of the Chesapeake Bay, but mostly absent from the mountains, the Delmarva Peninsula, and counties south from the D.C. area. These warblers are mostly absent from the eastern two-thirds of Virginia, but small numbers are locally distributed in the western counties.

Arrival Dates: The first migrants appear during the last half of April in Virginia and Maryland and by early May in Pennsylvania; most return by mid-May.

Departure Dates: Most depart during August, with small numbers lingering into the first half of September.

Breeding Habitats: Blue-winged warbler territories normally include shrubby thickets, some woodland, and patches of dense herbaceous growth. Cut-over areas, abandoned fields, and broad utility corridors are preferred. While pairs occur in both damp and dry upland areas, blue-wingeds prefer slightly drier habitats than golden-wingeds.

Nest Site: Nests are frequently located within 30 m (98 ft) of forest-field edges in dense patches of small trees and shrubs. Nests are placed on or within 30 cm (12 in) of the ground, usually at the base of bushes or clumps of herbaceous vegetation. Nests are well concealed by leafy vegetation.

Territory Size: One study documents a mean territory size of 1.1 ha (2.7 ac) within a range of 0.3–5.0 ha (0.7–12.3 ac).

Mating System: Normally monogamous, but polygyny occasionally occurs. Helpers are also reported at nests of a few pairs.

Breeding Phenology: Apparently typical for a single-brooded neotropical migrant in eastern North America, but relatively little data are available.

Pair Formation: Males normally arrive on their territories two to nine days before the females. Pairs form within a few days of the female's arrival.

Nest Building: Most initial nests are constructed during May, with renesting attempts through mid-June.

Egg Dates: The few reports are between mid-May and mid-June.

Number of Broods: Believed to be single-brooded, but pairs renest if the first attempt is unsuccessful.

Nests with Young: Most nests with young are reported during June, with late attempts through mid-July.

Fledgling Dates: Adults accompanied by recently fledged young are mostly reported between mid-June and mid-July.

References: Brauning (1992); Robbins and Blom (1996); Gill et al. (2001); Trollinger et al. (2001).

Golden-winged Warbler (*Vermivora chrysoptera*)

Status: A rare to uncommon, but declining summer resident of damp shrubby fields at elevations >305 m (1,000 ft) in the mountains of Pennsylvania, Maryland, and Virginia. They become locally distributed towards the southern edge of their range and also north and west of the mountains in Pennsylvania.

Arrival Dates: Early migrants return during the last week of April, but most appear during the first half of May.

Departure Dates: Most depart during August, with small numbers lingering into the first half of September.

Breeding Habitats: Breeding habitats are patches of herbs and shrubs, scattered small trees, and forested edges that contain trees 10–15 m (32–50 ft) tall, mostly in fields undergoing secondary succession.

Nest Site: Most nests are located <10 m (32 ft) from forest-field edges and edges created by small openings and trails. Nests are normally located on the ground at the base of herbaceous or shrubby vegetation.

Territory Size: Varies between 0.4–6.0 ha (1–15 ac).

Mating System: Mating system may be similar to blue-winged warbler, but only monogamous pairs are reported.

Breeding Phenology: Typical for single-brooded neotropical migrants in eastern North America.

Pair Formation: Males arrive on breeding territories two to seven days before the females. Pairing occurs shortly after the females return.

Nest Building: Limited data are available. Most initial nests are probably constructed during May, with renesting attempts through mid-June.

Egg Dates: The few reports are between mid-May and mid-June.

Number of Broods: Single-brooded, but pairs renest if the first attempt is unsuccessful.

Nests with Young: Limited data indicate most nests with young occur during June with late attempts through mid-July.

Fledgling Dates: Adults accompanied by recently fledged young are mostly reported between mid-June and mid-July.

References: Frech and Confer (1987); Brauning (1992); Confer (1992); Robbins and Blom (1996); Trollinger et al. (2001).

Nashville Warbler (V*ermivora ruficapilla*)

Status: A rare to locally uncommon summer resident in the mountains and northern counties of Pennsylvania, becoming rare and very locally distributed in the mountains of western Maryland where the few confirmed breeding records are confined to Garrett County. There are no confirmed breeding records from the mountains of Virginia, where nonbreeding Nashville warblers are accidental during summer.

Arrival Dates: Spring migration mostly occurs during the first three weeks of May.

Departure Dates: Most fall migrants depart during September, with small numbers lingering through mid-October.

Breeding Habitats: These warblers occupy sphagnum bogs and various dry upland habitats, including pine barrens and young regenerating forested areas where birch (*Betula* spp.) and aspen (*Populus* spp.) are prevalent.

Nest Site: Nests are located on the ground and are well concealed by dense herbaceous cover, usually under bushes or small trees near the edge of a clearing or bog.

Territory Size: Few data are available, but a study in New Hampshire indicated an average territory of 1.1 ha (2.7 ac) (no range was provided).

Mating System: Nashville warblers are believed to be monogamous.

Breeding Phenology: A poorly studied species in eastern North America, but probably similar to other neotropical migrant warblers.

Pair Formation: No information is available.

Nest Building: Most nests are probably constructed during May and early June, with renesting attempts throughout June.

Egg Dates: The few published regional egg dates are between 30 May–15 June. First clutches are probably produced during the last half of May and early June, with renesting attempts possible into July.

Number of Broods: Believed to be single-brooded.

Nests with Young: The only published regional date is 16 June. Nests with young are most likely to be discovered during June, while renesting efforts could produce broods into July.

Fledgling Dates: Primarily during the last half of June and first half of July.

References: Brauning (1992); Robbins and Blom (1996); Williams (1996).

Yellow Warbler (*Dendroica petechia*)

Status: Yellow warblers are widely distributed summer residents, generally common across Pennsylvania and Maryland, except along the Delmarva Peninsula, where they become uncommon and locally distributed. In Virginia, they are uncommon to fairly common summer residents, but locally distributed in the eastern half of the state.

Arrival Dates: The first spring migrants appear during the last half of April, but most return during the first half of May.

Departure Dates: An early fall migrant, southward movements begin during late July and early August. Most depart by late August, but small numbers linger into mid-September.

Breeding Habitats: Yellow warblers are normally found in deciduous thickets bordering streams and wetlands, as well as in shrubby swamps. They occasionally occupy damp abandoned fields and wet meadows supporting willow thickets and other shrubs.

Nest Site: Most nests are placed at heights of 1–2 m (3–6.5ft) in an upright fork of a shrub or sapling. Some nests are as low as 0.3–0.5 m (1–1.6 ft), and others as high as 14–18 m (46–60 ft).

Territory Size: Territory boundaries are dynamic and shift during the breeding season. Territory size varies with population density and mating system. In dense populations, territories may average 0.04 ha (0.1 ac), although the adults forage outside of these boundaries. Territory sizes vary between 0.2–0.8 ha (0.5–2.0 ac) in areas where these warblers are less numerous.

Mating System: Primarily monogamous, but occasional polygynous matings are expected (Della Sala 1986).

Breeding Phenology: A well-studied species that is typical for a neotropical migrant warbler in eastern North America.

Pair Formation: Most females pair within one day of arrival.

Nest Building: Normally occurs during May, but continues into June for renesting efforts.

Egg Dates: Most initial clutches are laid during May, while renesting attempts produce clutches through 23 June in Maryland.

Number of Broods: Normally single-brooded, but second broods are rarely attempted.

Nests with Young: Peak dates are between 25 May and mid-June, while late attempts are reported through 10 July.

Fledgling Dates: The earliest fledglings appear by mid-June, but most are noted during late June and early July.

References: Brauning (1992); Robbins and Blom (1996); Clapp (1997); Lowther et al. (1999); Trollinger et al. (2001).

Chestnut-sided Warbler (*Dendroica pensylvanica*)

Status: Summer residents are common and widely distributed across the northern half of Pennsylvania, and along the Appalachian Mountains at elevations >305 m (1,000 ft) south through western Virginia.

Arrival Dates: The first migrants normally return during the first week of May, and spring migration continues into early June.

Departure Dates: Most depart during late August and September, with stragglers into early October.

Breeding Habitats: Chestnut-sided warblers are typically found in regenerating forests, cut-over areas, abandoned fields, and similar shrubby fields. These habitats are characterized by high densities of shrubs and saplings within 1 m (3 ft) of the ground.

Nest Site: Nests are normally placed at heights of 0.3–1.3 m (1–4.3 ft), occasionally as high as 2 m (6.6 ft), anchored to a small crotch or vertical stems within small shrubs or dense saplings, and well concealed by briars, vines, or dense foliage.

Territory Size: Varies between 0.4–1.1 ha (1.0–2.7 ac), but may be larger during incubation.

Mating System: Chestnut-sideds are believed to be strictly monogamous.

Breeding Phenology: Probably typical for neotropical migrant warblers in eastern North America, but nests are difficult to find, and relatively little data are available.

Pair Formation: Males return to the breeding range five to seven days before females. Pair formation occurs within a few days after the females return.

Nest Building: Begins during mid-May, with later attempts through 24 June.

Egg Dates: Most initial clutches are laid during the last half of May and early June. Later clutches are noted through the first week of July.

Number of Broods: Normally one per season, although double-brooding is possible.

Nests with Young: Most first broods are noted during June, with later broods into late July and early August.

Fledgling Dates: Generally between 20 June and 25 July, with a few later attempts through mid-August.

References: Tate (1970); Brauning (1992); Richardson and Brauning (1995); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

Prairie Warbler (*Dendroica discolor*)

Status: Prairie Warblers are widely distributed and fairly common summer residents across most of Virginia and Maryland, becoming locally uncommon to rare at higher elevations in the mountains. In Pennsylvania, they are widely distributed in the southern two-thirds of the state, but rare in the mountains and northern counties.

Arrival Dates: The first spring migrants return during the last half of April in Virginia and Maryland ,and early May in Pennsylvania; most return by mid-May.

Departure Dates: Hard to detect once the males cease singing, most probably depart during August and early September, with small numbers remaining into late September.

Breeding Habitats: Prairie warblers breed in a variety of shrubby habitats lacking closed canopies, including pine barrens, cedar glades, cut-over areas, abandoned fields, and utility corridors. They prefer dry upland habitats in the Mid-Atlantic Region.

Nest Site: Nests are frequently placed within or at the edge of small thickets of bushes and/or small trees. Prefers woody vegetation with numerous branches and thick cover. Mean nest height is 2.3 m (7.5 ft) within a range of 0.24–13.7 m (0.8–45 ft). First nests are somewhat lower than later attempts.

Territory Size: Varies slightly with vegetation age, with a mean of 1.62 ha (4 ac) in young successional stages, and 1.47 ha (3.6 ac) in older stages. Some territories as small as 0.4–0.5 ha (1–1.2 ac), while the largest are 2.4–3.5 ha (6–9 ac). Males rarely defend two disjunct territories.

Mating System: Variable and sometimes complex, pairs are often socially monogamous, but some males are polygynous. Females frequently change mates, especially following nest failures.

Breeding Phenology: Typical for double-brooded neotropical migrants in eastern North America.

Pair Formation: Females normally arrive two to six days later than males. Most pairs form within a few days of the females return.

Nest Building: Begins during the last half of April in Virginia, but most first nests are built during May. Later attempts result in nest building through late June.

Egg Dates: As early as 26 April in Virginia, but most first clutches are produced during May. Later nests with eggs are reported through 11 July in Maryland.

Number of Broods: Frequently double-brooded, especially more experienced pairs.

Nests with Young: Most initial clutches hatch during late May or early June. Later attempts produce nestlings through 17–25 July.

Fledgling Dates: Most young fledge during June, with a smaller peak around mid-July.

References: Nolan (1978); Brauning (1992); Robbins and Blom (1996); Clapp (1997); Nolan et al. (1999); Trollinger et al. (2001).

Common Yellowthroat (*Geothlypis trichas*)

Status: A common to abundant and widespread summer resident of shrubby fields. Very small numbers are found during winter in coastal areas and southern Virginia.

Arrival Dates: The first migrants arrive during mid-April in Virginia and Maryland, and the first week of May in Pennsylvania; they become common by mid-May.

Departure Dates: Most summer residents depart during September, with small numbers remaining into early October in Pennsylvania, and late October farther south.

Breeding Habitats: Common yellowthroats are equally numerous in upland and wetland habitats. They occupy a variety of wetlands, including freshwater and brackish marshes, wet meadows, and shrubby swamps. In upland areas, they are found in overgrown fields, recently cut-over areas, and other weedy areas with scattered shrubs. They normally avoid linear edges and woodland borders.

Nest Site: Yellowthroat nests are normally located on the ground or within 10 cm (4 in) of the ground and are well concealed by dense herbaceous vegetation. A few nests are located at heights up to 1.2 m (4 ft) in dense tangles or shrubs.

Territory Size: Variable, but generally <1 ha (2.5 ac), although may be as large as 2.2–2.9 ha (5.5–7 ac).

Mating System: Normally monogamous, although males are rarely polygynous. Behavioral observations suggest extra-pair copulations may be frequent.

Breeding Phenology: Considering the difficulty in locating yellowthroat nests, their breeding biology is relatively well-known. The breeding phenology is fairly typical for a multi-brooded neotropical migrant bird in eastern North America.

Pair Formation: Males return to breeding territories approximately one week before the females. Pairs form within one to two days of the arrival of females.

Nest Building: Nest building begins by late April in Virginia and Maryland, but most initial nests are constructed during May. These activities continue until late July for later broods.

Egg Dates: Initial clutches are laid during May, as early as the first week in Maryland and Virginia. Later clutches peak between late June and mid-July, with a few as late as the first week of August.

Number of Broods: Probably double-brooded across the Mid-Atlantic Region.

Nests with Young: Reports between mid-May and mid-August, with first broods primarily between late May and mid-June and later broods mostly in July.

Fledgling Dates: Recently fledged young appear in late May, but most first broods fledge during June. Later broods mostly fledge between mid-July and early August, with a few broods during the last half of August.

References: Stewart (1953); Brauning (1992); Robbins and Blom (1996); Clapp (1997); Guzy and Ritchison (1999); Trollinger et al. (2001).

Yellow-breasted Chat (*Icteria virens*)

Status: A widespread and uncommon to fairly common summer resident across Virginia, Maryland, and the southern two-thirds of Pennsylvania, becoming rare in the higher elevations and northern counties of Pennsylvania.

Arrival Dates: Normally returns by the last week of April in Virginia and Maryland and the first week of May in Pennsylvania. Migration continues throughout May.

Departure Dates: Chats become very secretive post-breeding; most probably depart during September with a few into early October.

Breeding Habitats: Chats occupy various habitats dominated by dense shrubs <4.5 m (15 ft) tall, including cut-over areas approximately four to five years post harvest, abandoned fields, and woodland clearings. They can be numerous along power line corridors, but avoid very narrow corridors such as fencerows. They equally prefer damp and dry upland habitats.

Nest Site: Chat nests are normally placed close to the ground in dense bushes, preferring larger patches of dense interlocking shrubby vegetation. Average nest height is 0.8–1.2 m (2.6–4.0 ft), and all nests are located <2.5 m (8 ft) above ground.

Territory Size: Territory size is normally 0.8–1.2 ha (2.6–4.0 ft) with a reported range of 0.4–2.4 ha (1–6 ac). Mean territory size is smaller in dense populations, usually <1.0ha.

Mating System: Normally monogamous, but polygyny is rarely (<5%) reported.

Breeding Phenology: Fairly typical for a single-brooded neotropical migrant in eastern North America. Its breeding biology is well studied.

Pair Formation: Females arrive shortly after males and pair formation occurs as soon as the females return.

Nest Building: First nests are constructed during May and continue through late June for later attempts.

Egg Dates: As early as 8–15 May for initial broods in Virginia, but normally during the last half of May and first half of June. Late nests with eggs are reported through 16–18 July.

Number of Broods: Normally single-brooded, but a very small proportion of pairs are double-brooded.

Nests with Young: First clutches hatch during late May in Virginia, but generally during June elsewhere. Late nests with young are reported into the last half of July.

Fledgling Dates: Peak fledging for initial clutches is during the last half of June and early July, while later nests produce fledglings into early August.

References: Thompson and Nolan (1973); Brauning (1992); Robbins and Blom (1996); Clapp (1997); Burhans and Thompson (1999); Eckerle and Thompson (2001); Trollinger et al. (2001).

Eastern Towhee (*Pipilo erythrophthalmus*)

Status: A fairly common and widespread summer resident across the region. Wintering towhees are generally rare or absent at higher elevations of all states and in northern Pennsylvania, but become uncommon to fairly common elsewhere.

Arrival Dates: Migration periods are poorly defined due to substantial wintering populations. Most spring migration occurs between mid-March and late April.

Departure Dates: Fall migration occurs between late September and mid-November.

Breeding Habitats: Nesting habitats are normally dominated by dense shrub and sapling cover near the ground and a well-developed litter layer. Mesic and dry habitats are equally preferred. Breeding pairs prefer cut-over areas, abandoned fields, pine barrens, utility line corridors, and woodland edges and openings.

Nest Site: Initial nests are normally laid on the ground, while later nests are higher, normally up to 1.5 m (5 ft), and occasionally as high as 5.5 m (18 ft). Ground nests are normally located at the bases of shrubs or saplings and concealed under herbaceous cover. Above-ground nests are frequently located in vines or other dense tangles in shrubby cover.

Territory Size: Territory size varies with habitat conditions and inversely with population density. Mean size is 1.2–1.6 ha (3–4 ac), but can be as small as 0.3 ha (0.75 ac) in dense populations. Maximum reported territory is 2.4 ha (6 ac).

Mating System: Normally monogamous pairing, but polygyny is rarely reported.

Breeding Phenology: Fairly typical for a short-distance migrant in eastern North America.

Pair Formation: Little information, but pair bonds apparently form quickly upon females returning to the breeding range.

Nest Building: Most initial nests are built between mid-April and mid-May. Later attempts result in nest construction through late July and early August.

Egg Dates: The earliest published egg date is 22 April in Maryland, but most first clutches are produced during May and early June. A second peak occurs during the first half of July, while the latest reported egg data is 28 August in Maryland.

Number of Broods: The number of multiple broods by successful pairs has been questioned (Greenlaw 1996), although double broods are documented in some populations. Evidence for latitude effects on number of broods is not available.

Nests with Young: The earliest reported nest with young is 30 April in Maryland, but most first clutches hatch between mid-May and mid-June. Later attempts are responsible for broods into the second half of August.

Fledgling Dates: Some young fledge as early as mid-May, but most initial nesting attempts produce young during the last half of June. Adults accompanied by recently fledged young are regularly noted into August.

References: Brauning (1992); Greenlaw (1996); Robbins and Blom (1996); Clapp (1997); McWilliams and Brauning (2000); Trollinger et al. (2001).

Field Sparrow (*Spizella pusilla*)

Status: A fairly common and widespread summer resident in early successional fields across the region. Wintering field sparrows are generally rare or absent at higher elevations of all states and in northern Pennsylvania, but become uncommon to locally common elsewhere.

Arrival Dates: Migration periods are poorly defined due to substantial wintering populations. Most spring migration occurs between mid-March and late April.

Departure Dates: Fall migration occurs between mid-September and early November.

Breeding Habitats: Field sparrows prefer younger seral stages dominated by dense herbaceous cover and scattered small shrubs and saplings. They normally avoid narrow edge habitats and woodland borders, instead, occupying weedy fields, abandoned pastures, Christmas tree plantations, and recently cut-over areas.

Nest Site: Early nests are located on or very close to the ground in clumps of grass at the base of shrubs or saplings. Later nests are normally 0.3–0.6 m (1–2 ft) high in dense shrubs or thorny saplings. A few nests are up to 3 m (10 ft) above ground.

Territory Size: In one Illinois study, mean territory size is 0.76 ha (1.8 ac) with a range of 0.3–1.6 ha (0.75–4 ac).

Mating System: Almost exclusively monogamous, but rarely (<2%) males are polygynous.

Breeding Phenology: Fairly typical for a multi-brooded short-distance migrant passerine in eastern North America.

Pair Formation: Few data are available, but females arrive 10–20 days later than males and pairs form within one to two days of the arrival of females.

Nest Building: Normally begins during the last half of April in Virginia and Maryland and during May in Pennsylvania. Later nests are constructed through early August.

Egg Dates: First clutches are laid as early as 21–27 April in Virginia and Maryland, but most are produced during May. Second clutches peak during late June and July. The latest clutches are reported through 25 August.

Number of Broods: Multi-brooded, raising two to three broods per season.

Nests with Young: Initial clutches hatch during May and early June. Hatching of later clutches peaks during July, with the last nests hatching during August.

Fledgling Dates: The earliest fledglings appear in late May, but most first broods fledge during June. Later broods normally fledge during late July and August.

References: Best (1978); Brauning (1992); Carey et al. (1994); Robbins and Blom (1996); Clapp (1997); McWilliams and Brauning (2000); Trollinger et al. (2001).

Song Sparrow (*Melospiza melodia*)

Status: A common and widespread summer resident, except in Virginia where song sparrows become uncommon and locally distributed in the Piedmont and Coastal Plain of the central and southern counties. Winter residents are uncommon to rare in the northern counties and higher elevations of Pennsylvania, but common elsewhere.

Arrival Dates: Spring migration begins by early March and continues through mid-April in northern Pennsylvania.

Departure Dates: Fall migration occurs between mid-September and mid-November.

Breeding Habitats: Song sparrows occur in all types of shrubby habitats, including overgrown fields, brushy fencerows, shrubby woodland edges, swampy thickets, power line corridors, and ornamental bushes near residences.

Nest Site: Initial nests are placed on the ground concealed under dense herbaceous vegetation. Later nests are built higher as the vegetative cover develops, normally <2 m (6.5 ft), but some nests are located up to heights of 4 m (13 ft).

Territory Size: Normally between 0.2–0.6 ha (0.5–1.5 ac), but varies with habitat and the smallest territories are found adjacent to wetlands.

Mating System: Primarily monogamous, but up to 20% of females and 13% of males breed in polygamous groups at least once during their lifetime.

Breeding Phenology: Fairly typical for a multi-brooded, short-distance migrant passerine in eastern North America.

Pair Formation: In migrant populations, occurs primarily during March and early April when the females return to the breeding territories. Resident females may remain paired throughout the year.

Nest Building: Initial nests are normally built during April, and later attempts continue into the first half of August.

Egg Dates: The earliest reported clutches are April 5–12, and most first clutches are produced during April. Late clutches are reported through August 21.

Number of Broods: Multi-brooded, normally raising two to three and rarely four broods per season.

Nests with Young: Earliest nests with young occur during the last half of April, but most first broods are noted during May. Later broods generally peak in late June and early July. The latest nests with young are reported through September 23.

Fledgling Dates: Most first broods fledge during May and early June, while the peak for later nesting attempts is during late June and July. Last attempts produce adults accompanied by dependent young into September.

References: Nice (1937); Brauning (1992); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001); Arcese et al. (2002).

Northern Cardinal (*Cardinalis cardinalis*)

Status: A common and widely distributed permanent resident, somewhat less numerous at high elevations in the mountains.

Breeding Habitats: Northern cardinals occur wherever shrubby habitats are found, including overgrown fields, brushy fencerows, shrubby woodland edges, swampy thickets, and ornamental bushes near residences.

Nest Site: Cardinal nests are normally located at heights of 1–2 m (3–6.5 ft) in dense bushes and tangles over small trees. The range of reported nest heights varies between 0.25–12.0 m (1–39 ft).

Territory Size: Territories are generally between 1.0–1.5 ha (2.5–3.7 ac) in size within a range of 0.2–2.6 ha (0.5–6.4 ac).

Mating System: Normally monogamous, but some polygyny is reported. Extra-pair copulation rates appear to be relatively low.

Breeding Phenology: Typical for a multi-brooded permanent resident in eastern North America.

Pair Formation: Some cardinals remain paired throughout the year. For others, pair formation occurs between mid-January and early April.

Nest Building: Nest construction begins "as soon as the thickets turn green." In the Mid-Atlantic Region, nests are built between late March and late August. The first nests take two to three weeks to build, but later nests are built more rapidly.

Egg Dates: The earliest clutches are reported during the last week of March, but most first clutches are produced during April. Nests with eggs are found into the last half of August.

Number of Broods: Cardinals are multi-brooded and regularly raise three broods per year. Some pairs probably raise four broods in the Mid-Atlantic Region.

Nests with Young: Reported between 3 April and 5 September; the peak for initial nesting attempts is mid-May.

Fledgling Dates: The earliest fledglings appear during May, and they are regularly encountered into the second half of September.

References: Brauning (1992); Robbins and Blom (1996); Clapp (1997); Halkin and Linville (1999); Trollinger et al. (2001).

Blue Grosbeak (*Passerina cerulea*)

Status: In Virginia and Maryland, blue grosbeaks are widely distributed summer residents east of the mountains, becoming common on the Coastal Plain, and uncommon to fairly common in the Piedmont and Ridge and Valley regions. They are largely absent from the mountains of both states. In Pennsylvania, they mostly occur in the southeastern counties bordering Maryland and New Jersey, but their breeding range is expanding northward.

Arrival Dates: Small numbers return during the last week of April, but most spring migrants appear during May.

Departure Dates: Most blue grosbeaks depart during September, with small numbers remaining through mid-October.

Breeding Habitats: Blue grosbeaks prefer shrubby edge habitats. They are regularly encountered along roadsides, shrubby fencerows and hedgerows, woodland edges, and the margins of overgrown fields.

Nest Site: Nests are normally placed in small trees, shrubs, or tangles at heights of 0.3–3.0 m (1–10 ft). A few nests are reported as high as 7.8–9 m (25–30 ft).

Territory Size: No published studies, but one pair with a territory of 5–6 ha (12–15 ac) reported from South Carolina.

Mating System: No published studies. Believed to be monogamous, but this assumption is uncertain, given the breeding behavior of the closely related indigo bunting.

Breeding Phenology: Given its wide distribution in the southern U.S., its breeding biology is surprisingly poorly documented.

Pair Formation: No published studies; males apparently arrive before females on the breeding territories.

Nest Building: Normally begins during May. Blue grosbeaks have a prolonged nesting season in the Mid-Atlantic Region, and late nests are constructed well into August.

Egg Dates: Nests with eggs are reported as early as 5 May in Maryland, but most initial clutches are found during late May and June. Later attempts produce clutches throughout August, with the latest report on 3 September in Maryland.

Number of Broods: Generally double-brooded in most of its range.

Nests with Young: Initial clutches hatch during June, while later attempts produce nests with young through August. The latest report is 11 September in Maryland.

Fledgling Dates: Some fledglings are noted during June, but most are discovered in July and August. Late attempts produce adults accompanied by dependent young into the last half of September.

References: Brauning (1992); Ingold (1993); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

Indigo Bunting (*Passerina cyanea*)

Status: An abundant and widespread summer resident of shrubby fields and edge habitats.

Arrival Dates: The first migrants arrive during the last week of April and first week of May, and become common by mid-May.

Departure Dates: Most summer residents depart during September, with small numbers remaining into early October in Pennsylvania and mid-October farther south.

Breeding Habitats: Indigo buntings occur in various habitats dominated by shrubby thickets and dense herbaceous cover, including fencerows bordering open fields, overgrown pastures, abandoned fields, cut-over areas, forest openings, roadsides, and woodland edges.

Nest Site: Nests are open cups, normally located 0.3–1 m (1–3.3 ft) above ground, but some are as high as 10 m (33 ft). Indigo bunting nests are placed in dense shrubs, small saplings, or herbaceous vegetation such as goldenrods (*Solidago* sp.).

Territory Size: Average territory size is 1.4 ha (3.5 ac), but varies between 0.4–8 ha (1–20 ac).

Mating System: Most pairs are monogamous, although extra-pair copulations are frequent. Up to 15% of males are polygynous, supporting as many as four females in their territory. Some females nest in territories having no resident males.

Breeding Phenology: Fairly typical for a multi-brooded neotropical migrant in eastern North America.

Pair Formation: Females arrive one to two days later than males and pairs form immediately.

Nest Building: Initial nests are constructed between early May and early June, with subsequent attempts continuing into early August.

Egg Dates: As early as 8 May in Virginia, but most first clutches are produced between mid-May and early June. Another peak occurs during July. Late nests with eggs are reported through 18–23 August.

Number of Broods: Multi-brooded, with some females producing three broods in a season.

Nests with Young: Most initial clutches hatch during June, with a second peak of hatching during July and early August. The last attempts hatch during late August.

Fledgling Dates: First clutches fledge during June, with a second peak evident during August. Adults accompanying dependent young are observed as late as mid-September.

References: Carey (1982); Brauning (1992); Payne (1992); Robbins and Blom (1996); Clapp (1997); Trollinger et al. (2001).

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