ECOLOGY OF MIGRATORY LANDBIRDS DURING MIGRATION IN THE MIDWEST

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ABSTRACT.—Insectivorous landbirds migrating through the Midwest during spring and fall encounter a wide array of habitats. Habitat selection by migrants, which appears to be largely driven by food availability and shelter, varies seasonally and geographically. Spring migrants may be relatively food-limited compared to fall migrants, especially in northern portions of the Midwest; emerging aquatic insects provide an important food resource before foliage appears. Further, some migrants have narrow habitat requirements during migration, such as the northern waterthrush (*Seiurus noveboracensis*), or prefer to forage on particular tree species, which may further limit availability of high-quality stopover sites. Because the midwestern landscape has been drastically altered since European settlement, maintaining the quality of remaining stopover sites is critical if birds are to reach their breeding or wintering grounds in good physiological condition. Management and protection of stopover sites is needed for long-term conservation of migratory birds. We offer recommendations directed at protecting and managing sites for migrants. Much remains to be learned; further evaluation of factors governing migratory bird use of stopover habitats is needed.

Key words: food availability, habitat management, landscape, midwest, migratory birds, phenology, stopover sites.

A flood of landbirds moves through the Midwest during spring and autumn migrations when they temporarily inhabit stopover sites as diverse as grasslands, shrubby areas, old-growth forests, urban parks and even ships on the Great Lakes (Perkins 1964). Yet, the ecology of birds during migration is poorly understood. Just as adequate breeding grounds and overwintering areas are requisites for maintenance of migratory bird populations, so too are stopover sites, which provide critical resources necessary for successful seasonal passage. We review habitat requirements of migrant landbirds and provide recommendations for the protection and management of stopover sites in the Midwest to complement the design of hemisphere-wide conservation initiatives (see Moore and Simons 1992, Moore *et al.* 1993). We focus on stopover sites in eastern North America, especially the Midwest, that are used by insectivorous migrant landbirds in forested or coastal sites. Little is known, however, of stopover requirements for grassland (see Askins 1993), frugivorous, granivorous or omnivorous migrants.

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OVERVIEW OF IMPORTANCE OF STOPOVER SITES TO MIGRANTS

High energy requirements associated with migration, approximately 1 percent weight loss per hour of flight (Alerstam 1990), coupled with migrants' exposure to unfamiliar or changing environments en route, require migrants to assess food availability, predators, and shelter at each stopover site (Moore and Simons 1992). Individuals may use the same stopover sites each year although site fidelity appears to be low (Winker *et al.* 1991). Further, different routes may be taken in spring and fall by different species, populations, ages or sexes (Phillips 1951, Crawford and Stevenson 1984, Ramos 1988, Winker *et al.* 1992a). Because habitat selection by each species of migrant may depend upon or change with food availability (Laursen 1978, Bairlein 1983, Hutto 1985, Martin and Karr 1986, Blake and Hoppes 1986, Moore *et al.* 1990, Lindstrom 1989, Sealy 1988, Sealy 1989), intraspecific competition (Rappole and Warner 1976), interspecific competition (Laursen 1978), or habitat availability in different landscapes (see Morse 1980, Moore *et al.* 1990), assessment of the relative value of different habitats to migrants is challenging. However, the ability of a migrating bird to stop in high quality habitats (i.e., habitats with abundant food, low risk of predation and minimum environmental stress) determines whether it reaches the breeding and wintering grounds in good physiological condition. Recognizing these important components of fitness, we can apply our knowledge of habitat use at stopover sites to develop better conservation programs (Moore and Simons 1992). Moore and Simons (1992) succinctly expressed this concern: "Unless habitat requirements during migration are met, conservation measures which focus on temperate breeding grounds and/or Neotropical wintering areas will be compromised."

Migrants in the Midwest

Presettlement landscapes in the Midwest were dominated by a mosaic of forests, wetlands, and grasslands. Habitat loss and fragmentation have drastically altered the landscape. Migrant passage through the region, already made hazardous by storms over the Great Lakes (see Peet 1908, Janssen 1976), must be more difficult than it was 200 years ago when large-scale alteration of the landscape began. Exceptions may occur in parts of Iowa and Minnesota, for example, where forest development in grassland landscapes may benefit some migrants (Faaborg, pers. comm.). Within these landscapes many factors determine which habitats are selected by migrants. Macroscale effects, such as weather, ecological barriers, and habitat availability, may determine when and where a migrant first settles; microscale effects, such as food availability, inter-and intraspecific competition, shelter, and predation, will determine how a migrant fares at a site or within a habitat.

LANDSCAPE ASPECTS OF HABITAT SELECTION

Migrants often accumulate near ecological barriers (Moore and Simons 1992). In the Midwest, particularly large concentrations of migrant landbirds occur along the Great Lakes' shorelines (Peet 1908, Beebe 1933, Tyrrell 1934, Bennett 1952, Weir 1972, Hussell *et al.* 1992, Brock 1992). Some areas have concentrations of many species of birds during both spring and fall migration while other sites are frequented by birds consistently during one season or only periodically. Nevertheless, probably every habitat-type bordering the Great Lakes is used by migrants to some extent during seasonal passage. Habitats adjacent to inland lakes, major rivers, urban areas and large expanses of agricultural land could also have relatively high concentrations of migrants, but these relationships are little known.

Phenological development of vegetation, which is weather mediated, may provide macroscale cues to migrants selecting habitat. In spring, migrants are likely to encounter increasingly unpredictable and sometimes harsh conditions (Blake and Hoppes 1986), as well as delayed phenological development in vegetation, as they proceed north (compare Graber and Graber 1983 with Keast 1980; see Slagsvold 1976). In contrast, fall migrants are likely to have completed their migration prior to first frosts (Bennett 1952) and before leaves have dropped from trees. This interaction between weather and development of vegetation, which is modified by large landscape features like the Great Lakes, results in inter-seasonal differences in habitat choice by migrants (Ewert and Hamas, unpubl. data).

Relationships between patches of habitat in a landscape mosaic and migrant distribution in the Midwest are best described from South Dakota. In this agricultural landscape, Martin (1980) found that the total number of species and abundance of spring migrants was highly correlated with area of small, isolated, homogeneous shelterbelts, but the density of birds feeding primarily in shelterbelts was independent of area. He also concluded that the degree of isolation of shelterbelts did not influence migrants' use of these areas. In unfragmented habitat on barrier islands along the Gulf Coast of Mississippi, Moore *et al.* (1990) noted that migrants moving among heterogeneous patches of habitat preferred shrub-scrub, suggesting that migrants assess and select different habitats where they are contiguous. It is not clear, however, if large patches are consistently more heterogeneous than small patches (Askins *et al.* 1990). Little is known about how or why migrants select a habitat patch or what dispersal occurs among habitat patches.

MICROSITE SELECTION

Food availability may be a primary factor in microhabitat selection within a habitat (Moore *et al.* 1993) and will be further constrained by flexibility in foraging behavior (Robinson and Holmes 1982, Greenberg 1983, Martin and Karr 1990, Parrish 1995), species-specific morphology (Moermond 1990), vegetation structure (Robinson and Holmes 1982), abundance of potential prey (Robinson and Holmes 1982), interspecific competition (Laursen 1978), and intraspecific competition (Rappole and Warner 1976). Because food availability varies among and within habitats, seasonally as well as annually (Laursen 1978, Busby and Sealy 1979, Bairlein 1983, Hutto 1985, Guinan and Sealy 1986, Moore and Yong 1991), migrants depend on a wide array of habitats over time. Yet, given this kaleidoscope of variability, there are some predictable foraging sites or microhabitat features selected by each migrant species for at least portions of migration (Parnell 1969, Power 1971, Rappole and Warner 1976, Bairlein 1983, Winker *et al.* 1992b). Some migrants appear to choose habitats, if available, with vegetation structure similar to that selected during the breeding season (e.g., MacArthur 1958, Parnell 1969). Examples include the northern waterthrush (*Seiurus noveboracensis*), which consistently selects wetlands at stopover sites (Parnell 1969, Rappole and Warner 1976, Winker *et al.* 1992b) and during the breeding season (Bent 1953), and the yellow-rumped warbler (*Dendroica coronata*), which uses a wide range of vegetation in many different habitats during migration (Parnell 1969) and the breeding season (Morse 1989).

Forests comprised of certain tree species and structure may be especially attractive to migrants. Gaps in a deciduous forest in central Illinois consistently attracted migrants during spring and autumn, including foliage-gleaning insectivores, presumably because many insects are available in areas with dense foliage (Martin and Karr 1986, Blake and Hoppes 1986). Moreover, some tree species support relatively large populations of foliage insects and are therefore attractive to migrants after these species have leafed out. Among these tree species are oaks (*Quercus* spp.) (Graber and Graber 1983), yellow birch (*Betula allegheniensis*) (Holmes and Robinson 1981), hackberry (*Celtus laevigata*) (Moore and Yong 1991) and perhaps blue beech (*Carpinus caroliniana*) (Parnell 1969). Other tree species may be avoided as foraging sites by some species and not others (see Robinson and Holmes 1984). These include sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) (Holmes and Robinson 1981) and sassafras (*Sassafras albidum*) (Graber and Graber 1983).

A stopover site may be more or less attractive to migrants within and between seasons. For insectivores, prey may be scarce when birds first arrive in spring (Nolan 1978, Busby and Sealy 1979, Martin 1980, Guinan and Sealy 1987, Gray 1993, Martin and Karr 1990), forcing migrants to search for sites wherever prey is available (see Keast 1980). Prey-rich sites at this time include areas with high concentrations of geometrid caterpillars on hackberry in Louisiana (Moore and Yong 1991) and oak in southern Illinois (Graber and Graber 1983). Farther north, in the Midwest and in Europe, where migrants encounter less phenologically advanced vegetation, midges (Diptera: Chironomidae) and other insects emerging from water may provide critical food resources, especially early in spring (Laursen 1978; Busby and Sealy 1979; Hamas 1982; Ewert and Hamas, pers. obs.). Thus many migrants and newly arriving summer residents

may concentrate near water (Petit 1991, see Weisbrod *et al.* 1993) while other habitats are avoided. The result is patchy use of the landscape by migrants.

Use of foliar insects increases (Petit *et al.* 1990) as leaves emerge. This may vary by 15 to 20 days from year-to-year at a single site (Nolan 1978), but is approximately early April in Tennessee (Petit *et al.* 1990), mid- to late-April in southern Indiana (Nolan 1978), and mid- to late-May in northern Michigan (Ewert and Hamas, unpubl. data) and northern Minnesota (Ahlgren 1957). At the latitude of northern Michigan, spruce budworm (*Choristoneura fumiferana*) larvae, and perhaps other caterpillars, become available as prey at the third instar in late May to early June (Baker 1972). Thus, aquatic habitats that produce large numbers of emerging insects may be particularly important early in spring migration, especially in northern areas where there may be less overlap between migration and emergence of leaves. These habitats may also be important to breeding birds as sources of emergent insects in some areas (Busby and Sealy 1979, Biermann and Sealy 1982, Guinan and Sealy 1987).

Evidence from recent studies suggests that emerging aquatic insects are important to spring migrants. Preliminary results indicate that forested sites within 0.8 km of the Lake Ontario coastline in New York (Agard and Spellman 1994) and along coastlines of Lake Huron and Lake Superior in Michigan (Ewert and Hamas, unpubl. data; Johansen 1993) have the highest concentrations and species richness of migrants during spring migration. Attack rates by black-throated green warblers (*Dendroica virens*) and American redstarts (*Setophaga ruticilla*) on prey, mostly midges in spring, were higher along the shoreline compared to inland sites in spring and in fall (Seefelt, unpubl. data). Additional work is needed to determine if differences in attack rate correlate with changes in weight during migration. Nonetheless, these data suggest that migrants may select or remain near the shoreline as a result of a relatively abundant and perhaps predictable supply of midges emerging from the water.

When cold spring weather delayed phenological development and reduced insect activity, Sealy (1988, 1989) found that Cape May warblers (*Dendroica tigrina*) moved from trees, where they foraged on insects, to the edge of water where they fed on flying insects or defended willow catkins from conspecifics and other species. Territorial behavior has also been noted in migrant northern waterthrushes in coastal Texas wetlands (Rappole and Warner 1976) and in response to locally rich food supplies by Cape May warblers (Kale 1967) and palm warblers (*Dendroica palmarum*) (Wunderle 1978) in Florida. In extremely cold weather, even habitats near water will not sustain migrants and starvation occurs (Ligon 1968, Whitmore *et al.* 1977).

During fall migration, most insectivorous migrants in the Midwest move south in late August and early September (Bennett 1952, Brock 1992) when insect densities may be near their maximum (see Kendeigh 1979) while frugivorous and granivorous birds migrate somewhat later (Bennett 1952). Food for birds feeding off foliage may be more widely distributed in fall compared to spring, particularly in the northern Midwest. Further, at least some of these species feed on fruit in fall, a resource typically not available during spring migration (Parrish, in press). Thus, in fall, migrants may occupy a wide range of habitats (see Weisbrod *et al.* 1993), or at least select different habitats compared to spring (Winker *et al.* 1992b). This assessment, based on field observations by ourselves and others, has yet to be adequately tested in the Great Lakes region and is only partially supported by studies in other landscapes. In Arizona, for example, different species groups of migrants occupied either wider or narrower ranges of habitats in fall compared to spring, but the habitats they selected generally had relatively high insect abundance (Hutto 1985). Much additional work is needed to evaluate the relationship between food availability and the breadth and regional variation of habitat selection by migrants in the fall.

Predation pressure during migration may also affect microsite selection. Along the shores of the Great Lakes, predation on landbird migrants may be relatively high because shorelines are also migratory corridors for raptors (Peet 1908, Tyrrell 1934, Berger 1954, Weir *et al.* 1980). Predation pressure should vary seasonally along Great Lakes shorelines because raptors tend to be most abundant along eastern and southern shores of the lakes in spring and along western and northern shores in fall. Herring gulls (*Larus argentatus*)

and ring-billed gulls (*Larus delawarensis*) also prey on migrants along the shoreline (Ziarno 1994, French 1994, Kielb 1994). By selecting areas with complex vegetation structure, migrants may decrease the probability of predation by raptors and other birds (see Davidson 1994). Birds may also aggregate in flocks to avoid predation during migration (e.g., Lindstrom 1989), although it is unclear how habitat selection or social organization during migration is modified by the presence of predators.

RECOMMENDATIONS

Managing and protecting stopover sites for migratory birds should be components of conservation programs to protect and manage landscapes. For that reason, we believe protection of natural processes and native species, including the full range of non-avian species and natural communities, should ultimately guide management programs at stopover sites for neotropical migrants wherever possible. Where lands are managed, we suggest a range of successional habitats be maintained with a distribution that does not fragment habitat for area-sensitive species. We recognize that management, such as creation of early successional or perhaps aquatic habitat, may occasionally be needed for species with exacting requirements, and this could be decided on a case-by-case basis. It is not clear if this is needed for any landbird migrants in the Midwest although certainly some species, such as northern waterthrush, have relatively narrow habitat requirements during migration.

The following recommendations directed at protecting and managing sites for migrants are very tentative and broad, a reflection of our poor knowledge of stopover sites. Still, we hope the recommendations prompt interest in protection of stopover sites by landowners and encourage researchers to evaluate factors which govern habitat use by migrants. We propose the following measures for better protection of stopover sites:

1. A network of habitat patches (ideally to include riparian or other lowland habitats and upland habitats) be established throughout the Midwest. This may be especially critical in highly altered landscapes, such as urban areas, and in large expanses of agricultural land, as in portions of Iowa, Illinois, Indiana and Ohio, where relatively few patches of forest, grassland or wetlands remain. The network should include existing protected federal, state, county, non-profit, and corporat lands as well as lands owned by individuals. More research, similar to the design of Martin (1980), is needed to determine if these lands should be connected and, if not connected, how far apart the patches of habitat should be located. Habitat restoration may be needed to complete a network of stopover sites.

Larger, more ecologically diverse tracts of land with natural mosaics of forests, wetlands, grasslands and openings, are likely to be consistently attractive to many migrant species and individuals given the complex interaction that occurs between species-specific requirements, food availability and shelter. This may be most important for spring migrants when food may be relatively scarce and locally distributed. However, habitats should be managed based on principles of natural process as much as possible and should not result in adverse effects on area-sensitive or habitat-interior species.

Small patches of habitat that are unsuitable for breeding birds (Robinson 1996) may be acceptable to migrants, although this relationship has not been adequately tested. Consequently, small, isolated patches could be considered when implementing comprehensive conservation plans for stopover sites. However, for both large and small patches of habitat that can be protected or managed we recommend that stopover sites have as many of the following features as possible:

a. Ecologically diverse plant communities with water that produces good numbers of emergent, aquatic insects, particularly in northern areas where phenological development of vegetation is delayed.

b. Forest gaps, or at least areas with a well-developed shrub layer and high foliage density; these gaps may result from windthrow, fluctuating water levels, other disturbances, or carefully designed management which does not result in increased nest predation or cowbird parasitism.

c. Structurally complex and diverse vegetation layers.

2. Insect populations at the site and in immediately surrounding areas should be maintained. Use of biological control or spraying of insecticides should be avoided at critical stopover sites and in the immediate vicinity of these stopover sites whenever possible.

3. Introduction of alien or exotic plants and animals should be evaluated critically because this often results in disruption of ecological communities and perhaps loss of food supplies for migrants. Purple loosestrife (*Lythrum salicaria*), for example, supports few native animal species and displaces native plant species (see Thompson *et al.* 1987) that may be critical sources of food for birds at stopover sites.

4. Identification and protection of spring stopover sites may be especially important because migrants may be more susceptible to food limitations and climatic variability compared to fall. However, fall migrants may be subject to periodic food shortages because of drought, or other conditions, and this may be disproportionately stressful on young birds, especially at sites where competition for food and shelter is severe. Research directed at evaluating these relationships and identifying these stopover sites should be a high priority because the nature of resource limitations varies geographically and temporally.

5. Coastal areas along the Great Lakes and other large bodies of water should receive special attention because of their importance as landfall areas. Protection of water quality and subsurface bottom features should also be sought where nearshore larval insects occur. More research is needed to define which areas of shoreline, both terrestrial and aquatic, are most important to migrants during both the spring and fall migrations and should focus on the interaction between food supplies and distribution of migrants especially.

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Reviews status of Neotropical migratory landbirds and effects of land-use practices in the Midwestern United States, from a landscape perspective, through a series of papers authored by regional experts. Includes recommendations for the conservation of Midwestern Neotropical migratory landbirds.

KEY WORDS: Neotropical migratory landbirds, Midwestern United States, landscape ecology, land-management practices, grassland habitat, agricultural habitat, forest habitat, bottomland forest.

Our job at the North Central Forest Experiment Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.

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