Stopover Habitat: Management Implications and Guidelines

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Abstract — If persistence of migrant populations depends on the ability to find favorable conditions for survival throughout the annual cycle, factors associated with the en-route ecology of migrants must figure in any analysis of population change and in development of a comprehensive conservation "strategy." We view en-route habitat selection as a hierarchical process. Once migration routes are recognized and geographical variability in the route and timing are documented, important stopover habitat for Neotropical migrants can be delimited. The continent-wide pattern of migration concentrates migrants in relation to ecological barriers (e.g., the Atlantic Ocean, Gulf of Mexico). Protection and management of habitats used by migrants in relation to ecological barriers should be a prominent conservation priority. How effectively migrants satisfy energy demands and meet en-route contingencies depends not only on the habitat's intrinsic suitability, but also on time and energy available for selecting among alternative habitats, relative availability of more suitable habitats, the migrant's searching efficiency and probability of survival during migration.

STATEMENT OF PROBLEM

Conservation of Neotropical landbird migrants is complicated by the very life history characteristic that permits these birds to exploit seasonal environments, namely migration. Choice of habitat must be made in Neotropical wintering quarters, temperate breeding areas, and repeatedly during migration. Each habitat encountered during the annual cycle faces different threats of degradation and destruction (Gradwohl and Greenberg 1989).

Although debate over the causes of the decline in populations of landbird migrants will continue, attention has focused on events associated with the breeding and wintering phases of the migrant's annual cycle (Terborgh 1989; Askins et al. 1990). What has been largely overlooked in our developing conservation strategy is importance of habitat during migration. Habitat use during migration has profound consequences for a bird's (1) ability to satisfy energy requirements, (2) vulnerability to predators, and (3) exposure to environmental stress. How migrants respond to contingencies that arise during migration affects their survival and reproductive success. Unfortunately, we know little about what types of habitats are most important at this time, where they occur, and how their distribution and abundance are changing as a result of development and land conversion. Nor do we know much about migrant-habitat relations.

If persistence of migrant populations depends on the bird's ability to find favorable conditions for survival throughout the annual cycle, factors associated with en-route ecology of migrants must figure in any analysis of population change and in development of a comprehensive conservation "strategy" for Neotropical wintering landbird migrants (e.g., Moore and Simons 1992). Unless habitat requirements during migration are met, conservation measures that focus on temperate breeding grounds or Neotropical wintering areas will be compromised (Dunne et al. 1989).

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Our objectives are threefold: (1) Emphasize stopover habitat as a critical link in conservation of Neotropical landbird migrants, (2) appreciate importance of geographic scale in understanding en-route ecology of landbird migrants, and (3) identify management guidelines specific to the migratory phase of the annual cycle.

CONSEQUENCES OF EN-ROUTE HABITAT USE

The benefits of migration, regardless of whether they accrue through increased survivorship by overwintering in the tropics, increased productivity by breeding in temperate areas, or both, must be balanced against costs of migration. Besides energetic demands of transport, migrants must (a) adjust to unfamiliar habitats which vary in suitability, (b) resolve conflicting demands of predator avoidance and food acquisition, (c) compete with other migrants and resident birds for limited resources, (d) respond to unfavorable weather, and (e) correct for orientation errors. Moreover, migratory birds must balance conflicting demands between the need to stopover and satisfy energy requirements and selective pressures for timely arrival on breeding (Francis and Cooke 1986) and wintering areas. Whereas feeding meets energy demands and reduces risk of starvation, foraging migrants incur other costs, including a slower pace of migration and increased risk of predation. These problems are magnified when a migrant must cope with an ecological barrier (e.g., Rappole and Warner 1976, Moore and Kerlinger 1987, 1991), especially for a hatching-year bird on its first migration.

As stopover habitat is transformed, degraded or disappears, likelihood of solving those problems decreases, cost of migration increases, and a successful migration is jeopardized. Mortality during migration, though difficult to estimate, may be substantial, and probably falls disproportionately on the hatching-year age class (e.g., Ketterson and Nolan 1982, 1983). Whether an individual is recruited into the population will depend on events during the period between independence-from-parents to the bird's first breeding attempt. Hence, study of different age-classes during migration is essential to understanding causes of population change and the formulation of sound conservation policy.

Although it is difficult to measure the effect of en route habitats on survival or reproductive success, it is possible to evaluate the immediate consequences in relation to how effectively migrants satisfy energy demands during migration. Individuals in migratory disposition become hyperphagic and deposit substantial lipid stores which are mobilized to meet energetic requirements of migration. As lipid stores are depleted during migration, some free-ranging birds are capable of rapidly rebuilding reserves in a few days at rates approaching 10% of body mass/day (e.g., Moore and Kerlinger 1987).

Birds mobilize stored lipid for energy during migratory flight, so many individuals arrive in stopover habitat in a fat-depleted condition (e.g., Rappole and Warner 1976, Moore and Kerlinger 1987, Kuenzi et al. 1991). Several consequences follow if stores cannot be replenished soon after arrival: (1) lean migrants have a smaller "margin of safety" to buffer the effect of adverse weather on availability of food supplies during stopover (e.g., Moore and Kerlinger 1990), (2) efforts to satisfy energy demand may expose fat-depleted migrants to increased predation pressure (Lindström 1989), (3) if lean birds remain longer at stopover sites than birds in better energetic condition (e.g., Moore and Kerlinger 1987) and do not make up lost time, they will necessarily arrive later on the breeding grounds. Migrants that arrive late on the breeding grounds may jeopardize opportunities to secure a territory or a mate.

EXTRINSIC FACTORS AND THE EFFECT OF SCALE ON EN-ROUTE HABITAT USE

Habitat selection by nonbreeding land bird migrants is a hierarchical decision-making process (sensu Hutto 1985a; see Moore and Simons 1992). At the broad geographical level (i.e., highest level in hierarchy) most individuals are "programmed" to follow a migratory pathway between their breeding and nonbreeding areas, and the same intrinsic factors (e.g., amount of resource, protection from predation) that determine suitability of a nonbreeding habitat probably have influenced evolution of currently used migratory routes and wintering areas. Habitats not frequented may have high extrinsic costs associated with travelling to them rather than a high intrinsic cost associated with their use. By the same token use of some en route habitats may result from extrinsic benefits (short distance or favorable wind patterns) rather than the habitat's intrinsic qualities (see Gauthreaux 1980b).

We begin with emphasis on large scale (inter-continental and continental) movements of birds between their breeding and wintering grounds and then move down the hierarchy of spatial scale to discuss particular geographical regions important to en route ecology of Neotropical migrants (e.g., northern coast of the Gulf of Mexico during spring and fall migration, Atlantic Coast in the fall, importance of riparian woodlands as stopover habitat in grassland and desert biomes).

Geographical Pattern of Seasonal Timing of Migration

Much of what we know about the seasonal timing of bird migration in North America comes from work of field observers and bird banders, and their findings have been regularly summarized in spring and fall migration issues of "American Birds" (formerly "Audubon Field Notes"). Virtually every state has a checklist or bird book containing information on seasonal

occurrences of migrant birds. Saunders (1959) examined variation in timing of spring arrivals among 50 different species in comparison with mean 40-year arrival dates and found that in late, cold springs migrants arrived later than in early, warm springs. Gauthreaux and LeGrand (1975) associated advancement or retardation of seasonal timing of migration with year-to-year changes in continental wind patterns. Robbins et al. (1983) summarized considerable data on seasonal timing of bird migration for most North American species. This information is presented on species maps as isochronal lines that show average first-arrival date where birds migrating to the north may be seen about the first of March, April, May, and June. Preston (1966) analyzed mathematically timing of spring and fall migration and found that in general those species that go early in fall return late in spring (e.g., waterfowl, sparrows). Preston discusses evidence that shows breeding birds occupy their summer habitat as soon as it is habitable and depart as soon as they have finished breeding. Variability in timing of a species' migration is less in spring than fall, hence birds are better synchronized in spring. During fall migration some species show an almost bimodal timing with young and adults traveling at somewhat different times (see Murray 1966). In the spring, males of most species arrive before females, and adults precede young (Francis and Cooke 1986, Moore et al. 1990).

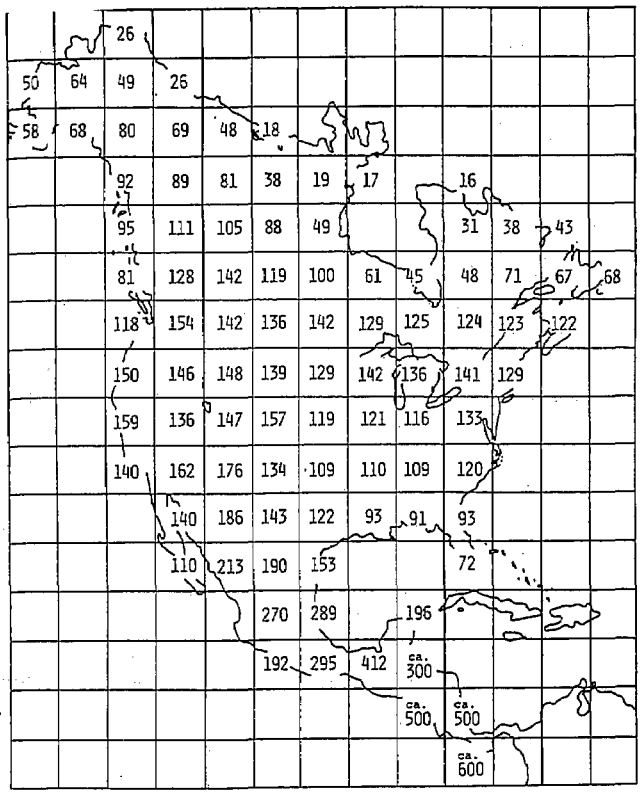
A number of factors must be considered in discussing seasonal timing of migration. The more important of these are vegetational development in spring, food availability, and climatic factors in spring and fall. Weydemeyer (1973), in a 48-year study of spring arrivals of migrants in Montana, found ranges in dates of arrival were greatest for species arriving late March and April and least for species arriving late May and June. Slagsvold (1976) working in Norway found for the country as a whole a 6-day delay in bird arrival for each 10-day delay in vegetation development. Thus, arrival of migrants at higher latitudes and altitudes was faster than development of vegetation. Slagsvold also found earlier arriving species varied considerably in arrival date at a particular locality from year to year, but late arriving species had much less variation in arrival time. Pinkowski and Bajorek (1976) examined spring arrival dates of 29 migrants and summer resident species in southern Michigan over a 7-year period. They concluded that granivorous, omnivorous, and aquatic species tend to arrive earlier than strictly insectivorous species, and earlier arriving species have a greater variance in arrival time than species arriving late in spring. Hagan et al. (1991) studied the long-term mean timing of spring migration, within-year, and among-year variance in timing of 27 free-living Nearctic migrant species. They found that tropical wintering species showed significantly less within-year and among-year variation in timing of migration, suggesting the mechanism regulating their migration is primarily endogenous while the mechanism that regulates migration of more temperate-wintering species is sensitive to environmental change.

Geographical Aspects of the Neotropical Migration System

A wealth of information on geographical patterns of bird migration in North America can be found in state bird books and check-lists; state, regional, and national bird periodicals (e.g., "American Birds"); and even range maps in some popular identification field guides (e.g., Robbins et al. 1983, National Geographic Society 1983).

A very coarse-grained picture of migration flux in North America can be found in analyses of gamma diversity (total number of land bird species breeding or wintering in quadrats of 500 km per side) in different parts of North and Central America (fig. 1a, b). For a particular geographical region it is possible to obtain a general impression of the amount of migration if one compares change in number of species between summer and winter for the same quadrat. Gamma diversity shows the greatest drop from summer to winter in Canada while little change can be found in the southern United States. In the latter region in fall departing migrants are replaced by arriving migrants from farther north. For quadrats south of the border gamma diversity is higher during winter than during summer as Neotropical migrants vacate their breeding grounds in late summer and fall and move into Central America and northern South America to overwinter. However, not all changes in gamma diversity over North America can be attributed to Neotropical migrants, because some migrants do not cross the southern border of the U.S. Also, some species are not recorded in summer or winter quadrats because they are strictly transient in that area.

When information on breeding distribution is added to the picture, the geographical pattern of Neotropical migration is further clarified. Figure 2 shows a map of proportions of breeding songbird individuals in undisturbed vegetation communities that winter in the Neotropics (after MacArthur 1959). MacArthur found the eastern deciduous forest contained more Neotropical landbird migrants than northern coniferous forests and grasslands, and he correlated differences with the contrast between winter and summer food supplies in the given habitat. Willson (1976) in a partial reanalysis of MacArthur's (1959) findings showed: (1) North American Neotropical migrants are less prevalent in grasslands than forests, but there is no significant difference in proportion of Neotropical migrants in deciduous and coniferous forests, (2) most Neotropical migrant birds breed primarily in deciduous forests, and most of those that breed in coniferous forests are wood-warblers. In general considerably more Neotropical landbird migration occurs in the eastern two-thirds of the United States than in the West (Lowery 1951, Lowery and Newman 1955, 1966). One explanation for the greater amount of migration in the East comes from the fact the breeding ranges of several "eastern" species of Neotropical migrant extend considerably farther west and north of eastern forests of the U.S., but the birds migrate through the East. The breeding and migration range of the Philadelphia Vireo (*Vireo philadelphicus*) (fig. 3) illustrates this



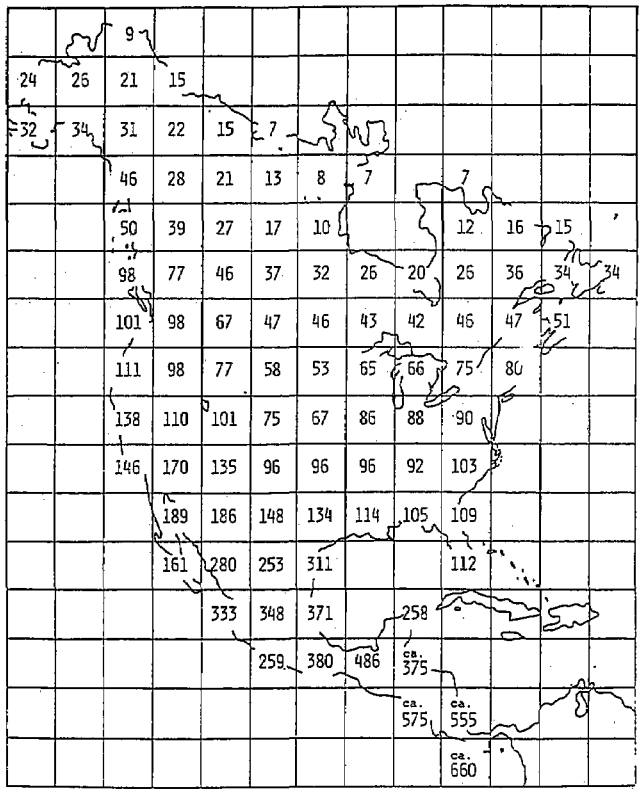


Figure 1a,b. — Gamma diversity (the total number of land bird species breeding (left) or wintering (right) in quadrats of 500 km per side) in different parts of North and Central America.

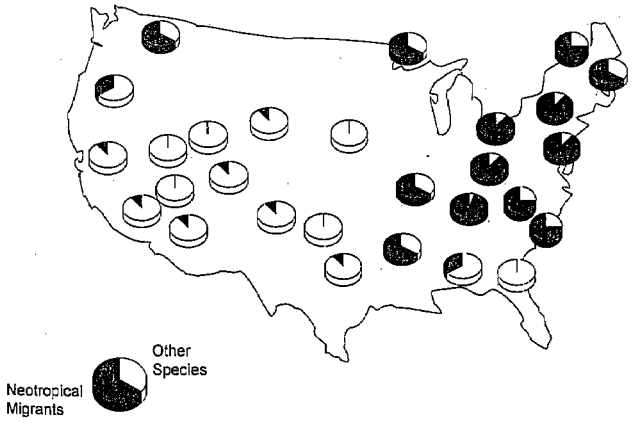


Figure 2. — Proportions of breeding bird individuals in undisturbed vegetation communities that winter in the Neotropics (see MacArthur 1959, Willson 1976).

point. Approximately 33 species of Neotropical migrants conform to this pattern. Another basis for the pattern of more migration in the East is that more Neotropical migrants (species and individuals) breed in the East (fig. 2). For example, among North American wood-warblers that migrate to the neotropics, 40 species occur east of the Rocky Mountains and 15 species of warblers are found west of the mountains. Western species winter almost entirely within a narrow strip of west Mexico from Sonora south to Guatemala while eastern warblers

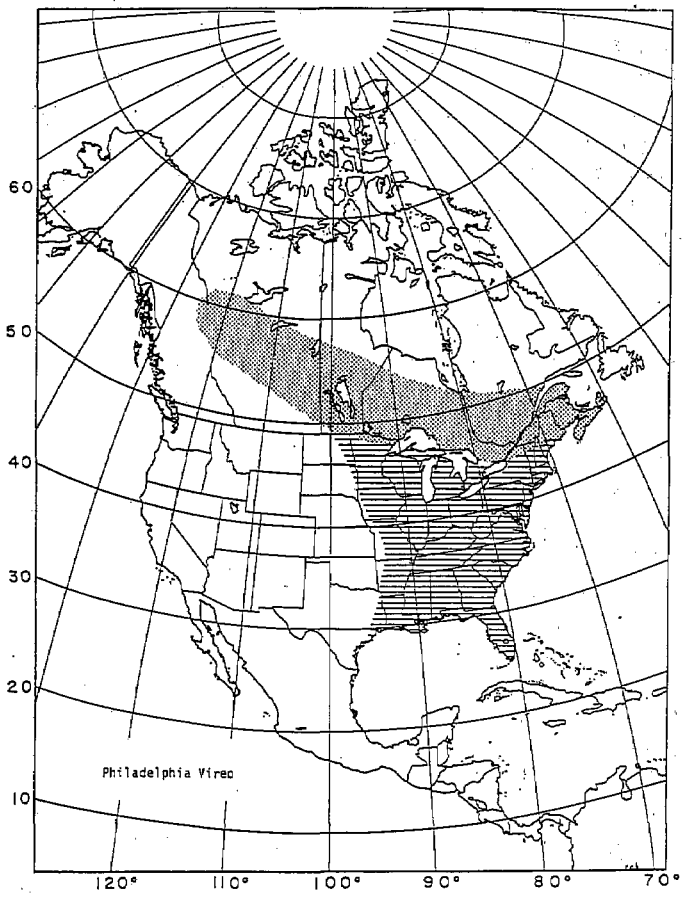


Figure 3. — The breeding (stippled) and migration (hatched) range of the Philadelphia Vireo (*Vireo philadelphicus*).

generally winter in geographically separate areas of the Bahamas, West Indies, eastern Mexico, Central America, and northern South America (Hutto 1985a).

When drawing inferences about continent-wide patterns, keep in mind that information on the spatial and temporal pattern of migration, not to mention migration volume ("traffic rate"), is not readily available for southwestern United States or the West in general. Radar and direct visual (ceilometer and moon watching) studies must be conducted to fill that gap. It is clear that riparian or riverine habitats in the southwestern U.S. are vital to landbird migrants, notably woodland species (Sprunt 1975), and concentrate a diversity of migrants in large numbers. Similarly, shelterbelts on the Great Plains represent islands of suitable habitat for woodland migrants (Martin 1980).

For the most part longitudinal separation of species and populations of migratory land birds that exists during breeding persists during migration and during winter (vireos [Barlow 1980], tyrant flycatchers [Fitzpatrick 1980], paruline warblers [Keast 1980; Hutto 1985a], and Neotropical migrants in general [Rappole et al. 1983]). At a continent-wide scale explanations for these patterns are varied and may relate to location of breeding and wintering areas, major topographical features, availability of suitable resources on the migration route, peculiarities of life history, and prevailing direction of winds during the migration seasons (Rappole et al. 1979, Gauthreaux 1980a, Hutto 1985a). Clearly the mild climate of the Pacific Coast, the north-south mountain ranges of western North America, and grasslands east of the mountains play an important role in maintaining the integrity of western land bird migration patterns. Likewise western mountains, extensive grasslands, and prevailing westerly winds help maintain the eastern bias to seasonal movements of "eastern" Neotropical migrants during migration.

Continent-wide, seasonal differences in migration pathways can be related to prevailing wind patterns at different latitudes such that in spring Neotropical migrants are biased westward by prevailing easterlies at low latitudes and eastward at higher latitudes by prevailing westerlies (Bellrose and Graber 1963, Gauthreaux 1980a). These prevailing wind patterns (fig. 4 top) produce a clockwise pattern of migratory pathways (fig. 4 bottom) that account for many Neotropical migrants being more abundant in fall on the East coast and the western Atlantic Ocean (Williams et al. 1977) as they move toward their tropical wintering grounds. In spring the clockwise flow (fig. 5 top) biases many migrants departing from the tropics toward the northern and northwestern coast of the Gulf of Mexico and the lower Mississippi Valley (fig. 5 bottom) with reduced numbers in most of Florida and extreme southeastern U.S. (e.g., Blackburnian Warbler [*Dendroica fusca*], see Crawford 1981; Crawford and Stevenson 1984).

Prevailing wind patterns, in concert with geographical differences in overwintering areas, also influence the relative magnitude of trans-Gulf and circum-Gulf spring migration such that several species that winter primarily in the Greater Antilles (e.g., Cape May Warbler (*Dendroica tigrina*) and Black-throated Blue Warbler (*D. caerulescens*) are abundant in Florida in spring and become quite rare westward along the northern Gulf Coast (Robertson and Woolfenden in press). Depending on the winds aloft during spring trans-Gulf flights, migrants may be "transported" anywhere from the coast of Mexico to the coast of Florida. Weather surveillance radar (WSR-57) has been used to delimit the geographical pattern of landing areas of trans-Gulf migrants as they arrive on the Louisiana coast in spring (Gauthreaux 1975). Virtually every day between the beginning of April and the middle of May, large scale trans-Gulf flights consisting of a variety of species of Neotropical migrants arrive on the northern Gulf coast when winds across the Gulf are favorable. With fair weather (about 80 per cent of the time) the majority of these birds overfly the 25 to 30 mile (40 to 48 kilometer) width of the coastal marshes and alight in inland forested areas.

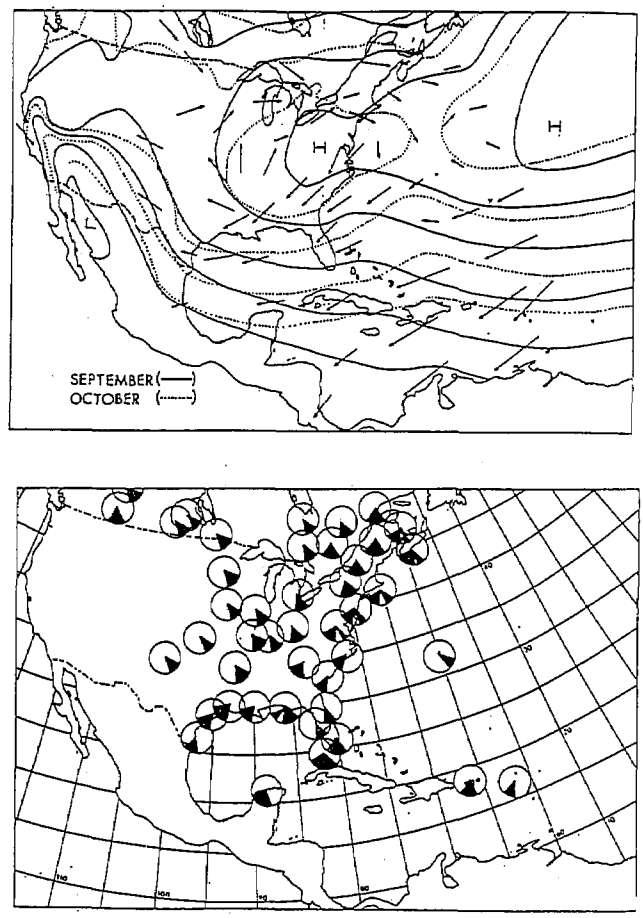


Figure 4. — (TOP) The distribution of sea-level barometric pressure patterns in fall. Continuous and dotted lines connect points of equal pressure for the months of September and October, respectively. The arrows indicate the resultant direction of surface winds. Prevailing wind patterns produce a clockwise pattern of migratory pathways. (BOTTOM) The directional tendencies of nocturnal passerine migration in fall. The circular plots show the predominant direction for a given area. The thickness of the wedge approximates the usual variability in direction. When two major directional tendencies exist for an area, they are both indicated.

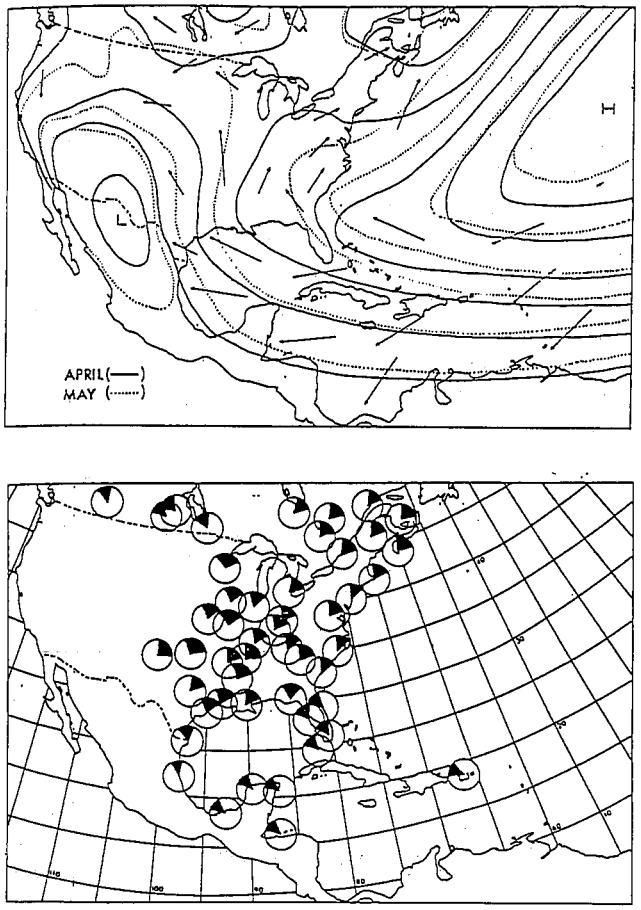


Figure 5. — (TOP) The distribution of sea-level barometric pressure patterns in spring. Continuous and dotted lines connect points of equal pressure for the months of April and May, respectively. The arrows indicate the resultant direction of surface winds. Prevailing wind patterns produce a clockwise pattern of migratory pathways. (BOTTOM) The directional tendencies of nocturnal passerine migration in spring. The circular plots show the predominant direction for a given area. The thickness of the wedge approximates the usual variability in direction. When two major directional tendencies exist for an area, they are both indicated.

INTRINSIC SUITABILITY AND SELECTION AMONG EN-ROUTE HABITATS

Now we turn to selection among habitat types within the landscape scale (e.g., pine versus deciduous woodland) and consider the en-route habitat requirements of Neotropical landbird migrants. Over the course of a season's migration a songbird like a Philadelphia Vireo encounters a variety of habitats, most with new food, competitors, and predators. After a night's migration a songbird often finds itself in a habitat very different from the one it occupied the previous day, let alone the previous year. Despite the diversity of habitat types encountered, largely correlative evidence indicates that migrants prefer certain habitat types and select among alternatives during stopover (e.g., Hutto 1985b, Moore et al. 1990, Winker et al. 1992).

Changes in distribution of migrants among habitat types from one migratory season to the next are consistent with en-route habitat selection. For example, foliage-gleaning, insectivorous migrants showed shifts in habitats used from one migratory season to the next during passage through southeastern Arizona (Hutto 1985b). Moreover, changes were tied to changes in availability of insect prey. Similarly, Winker and his colleagues (1992) reported seasonal shifts in distribution of Northern Waterthrush (*Seiurus noveboracensis*) among swamp, floodplain and willow habitats in the St. Crois River Valley, Minnesota, while Swainson's Thrush (*Catharus ustulatus*) shifted from drier habitats in spring toward wetter sites in autumn in the same study area.

When use of five habitat types was examined on Horn Island, a barrier island off the northern coast of the Gulf of Mexico (Moore et al. 1990), distribution of spring trans-Gulf migrants deviated from that expected based on availability of habitats (fig. 6). Whereas Scrub-Shrub comprised 14% of available habitat, it was characterized by the greatest number of species, highest species diversity, and the largest number of individuals.

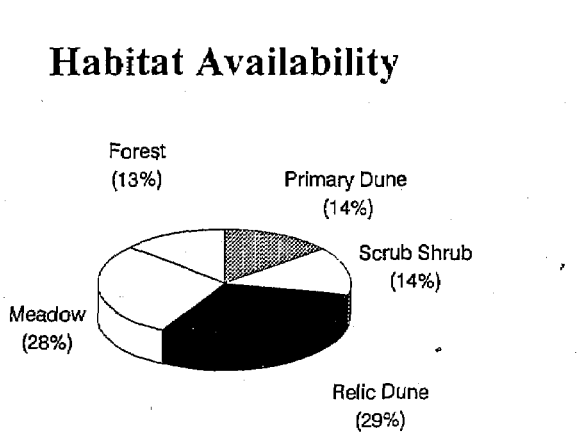
Habitat selection was apparent when fall migrants were mist-netted in five habitats in Cape May, New Jersey (Kerlinger pers. observations). For example, Connecticut Warbler (*Oporornis agilis*) were invariably found in hedge rows between old, grass fields. Moreover, most Connecticut Warblers were caught in mist-nets placed across rather than parallel to the hedge row. This species was never found in forest interior, nor were they seen frequently during transects done along hedge rows or other habitat types.

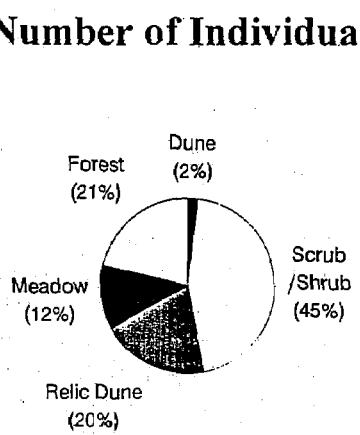
Determinants of Habitat Suitability

En-route habitat selection occurs because the probability a migrant will meet its energetic requirements and achieve safe passage is correlated with the intrinsic suitability of stopover habitat. Three factors constrain migrants to certain types of habitats: foraging opportunities, competition with other migrants and with resident birds, and shelter against predators and adverse weather (see Hutto 1985a, Moore and Simons 1992). Possibly the single most important constraint during migration is to acquire enough food to meet energetic requirements, especially for long-distance migrants which must overcome geographic barriers (e.g., Wood 1982, Bairlein 1987, Biebach 1990, Moore 1991). It is no wonder that differential use of en-route habitat is tied to food availability (e.g., Bibby et al. 1976, Bibby and Green 1983, Martin 1980, 1985, Graber and Graber 1983, Hutto 1985b, Moore and Yong 1991).

The physical structure of habitat, including plant species composition and foliage structure, influences habitat suitability by affecting how birds move through habitat and how they see and capture prey (Holmes and Robinson 1981, Robinson and Holmes 1982, 1984). Such constraints could affect rate at which migrants replenish energy reserves.

Habitat Use by Migrants





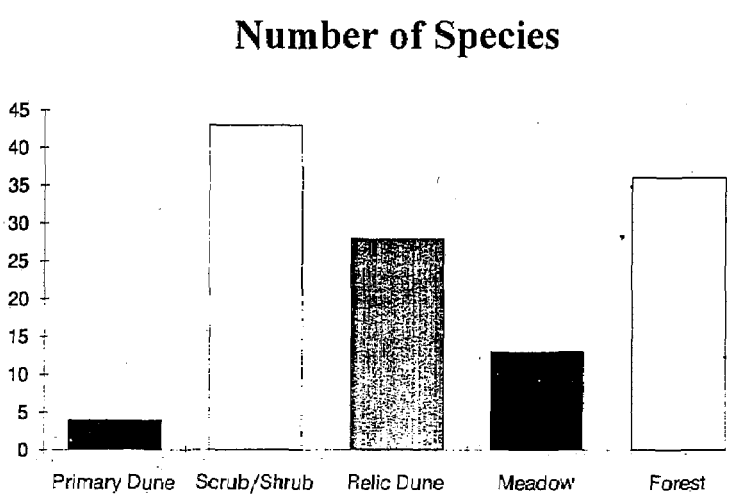


Figure 6. — Differential use of five habitat types by Neotropical landbird migrants on Horn Island, a barrier island off the northern coast of the Gulf of Mexico (after Moore et al. 1990).

Habitat extent or "patchiness" also contributes to habitat suitability. Bird species require different threshold levels of habitat area below which they find habitat unsuitable (Robbins et al. 1989). Sensitivity to area might affect habitat use during migration and the rate at which migrants replenish energy reserves. Suitable habitat associated with ecological barriers are often fragmented and many woodlands average only a few hectares in area. Whereas dehydration does not appear to be a serious en-route problem for small landbird migrants (Haas and Beck 1979, Biebach 1990), water economy might constrain migratory range and could explain why some individuals stop despite sufficient reserves for continued migration.

A safe place to rest may be as an important determinant of suitability as food availability. In Cape May, New Jersey, where as many as 80,000 migrating hawks and falcons have been counted in a single autumn migration season, predation on songbirds is intense (Wiedner et al. 1992). Kerlinger (1989) speculated that some hawks migrate along coasts because of the seasonal concentration of potential prey, notably energetically stressed birds which might be easy prey. If habitat offers refuge from predators and provides appropriate foods in sufficient quantities, there is little question about its suitability for stopover. When the best areas for depositing fat are also the most dangerous, the migrant must trade off energy gain against mortality risks. In general, we expect fat-depleted migrants to be more willing to "trade off" risk of predation to meet energetic requirements than are birds that arrive with unmobilized fat stores.

Migrants might suffer muscular fatigue during sustained flight over ecological barriers and might stopover to metabolize lactate and "repay" oxygen debt, regardless of their fat status. Stopover would also be required for tissue repair if migrants are forced to catabolized muscle tissue to offset unexpected energy demands or if muscle fibers are damaged during sustained, long-distance flight.

Mechanism(s) of Habitat Selection

Many researchers believe selection of a location to make a migratory stopover occurs during daylight hours. Although most birds end their migratory flight before dawn, many make short

flights after sunrise (Wiedner et al. 1992) -- a phenomenon often called "morning flight". Morning flight differ from normal nocturnal migration in that it usually occurs within two hours after dawn, at low altitudes (sometimes from treetop to treetop), flights are of short duration, and migrants are often in flocks. In addition, the direction of morning flight is rarely the same as the previous night's migration. On the Cape May peninsula, New Jersey, thousands of migrants can be observed in morning flight north, away from the end of the peninsula, toward forested areas up the Delaware Bayshore (Wiedner et al. 1992). At other sites in the New Jersey coastal plain, morning flight is west or northwest, again toward forested areas (Gauthreaux, pers. comm.). Once birds reach forested areas they diffuse, presumably their preferred habitats. Similarly, we would not be surprised if riparian areas "attracted" landbirds following a night's migration (see Terrill and Ohmart 1984).

Although it may not be obvious why certain habitats are more attractive to migrants, observations of migrants arriving along the northern coast of the Gulf of Mexico following a trans-Gulf crossing suggest that migrants "rank" alternative habitats during an initial exploratory phase shortly after arrival. An initial "exploratory phase" to habitat selection might be adaptive if availability of highly suitable habitat is unpredictable, as it probably is for a passage migrant.

What cues migrants use to select among alternative habitats is poorly understood. Habitat assessment involves acquiring information about alternatives. One source of information comes from sampling a habitat, which might include number of food items harvested, time spent in a habitat, and time since the last food item was consumed. Migrants may also pay attention to the number of other migrants present. Presumably a more suitable habitat would attract more individuals, although more migrants would intensify competition for resources.

A second source of information involves knowledge of distribution of resources in the environment (i.e., prior information). Prior information might increase foraging efficiency. During migration, however, birds experience a variety of unfamiliar habitats and often do not spend much time in one location -- circumstances likely to preclude use of prior information.

Constraints on Habitat Selection

How effectively migrants satisfy energy demands and meet en-route contingencies depends not only on the habitat's intrinsic suitability, but also on (1) time and energy available for selecting among alternative habitats, (2) relative availability of more suitable habitats, (3) migrant's searching efficiency and (4) probability of survival during migration. For example, when adverse weather conditions are encountered while aloft, a migrant might be forced to land in habitat it would otherwise bypass. If energy reserves are depleted, stopover "options" are more narrowly circumscribed (i.e., suitable en-route habitat may be effectively limited if migrants do not have the luxury of searching for the "best" stopover site). For a fat-depleted migrant unfamiliar with availability of favorable stopover habitat, benefits of rejecting suboptimal habitat may be outweighed by cost of finding a better site (see Moore and Simons 1992).

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Ecological diversity of migratory species, coupled with the often variable weather patterns that steer migratory movements, make assessment of habitat requirements and development of management strategies for migrants particularly difficult. The complexity of this issue, and the fact that the abundance of migrants found at individual stopover sites can vary dramatically from year to year, makes it tempting to devalue the migratory period when developing conservation programs. Because Neotropical migrants spend more of their lives in breeding and wintering habitats, these would seem a natural target for conservation efforts. Certainly, the characteristics and distribution of breeding and wintering habitats are somewhat easier to define.

It is generally assumed that higher energetic costs and mortality rates experienced by birds during migration are offset by higher productivity and/or survival on the breeding and wintering grounds (e.g., Lack 1946, Greenberg 1980). If mortality is concentrated in the migratory period, then we must assume factors that increase cost of migration could have a disproportionate influence on overall population levels. Thus, while individual fragmented woodlots may represent local population sinks on breeding grounds, birds in these habitats can often select alternative or more productive habitats. In contrast, the rigors of migration often place birds close to their physiological limits in unfamiliar landscapes, where they simply do not have the luxury of selecting alternative habitats. Therefore, a lack of suitable stopover habitat will result in death or reproductive failure for Neotropical migrants and contribute substantially to future population declines. Some management guidelines and recommendations are organized according to geographic scale (see below) and listed in Table 1.

Within-Habitat Scale

In light of these threats, there is a pressing need for information on stopover ecology and habitat requirements of Neotropical migrants. Unfortunately, we still know very little about the fine scale habitat characteristics that influence prey availability or other aspects of habitat quality. For example, satisfying the energy demand of migration is not simply a matter of hyperphagia. Availability of nutrients that specifically enhance migratory fattening has as strong an effect on the course of migration as the gross abundance of food at a particular stopover site (Bairlein 1991). It must also be recognized that migrating birds use en-route habitat in different ways -- for different

Table 1. — Suggested guidelines and recommendations specific to the migratory period and organized according to geographic scale.

A. WITHIN-HABITAT SCALE
1. Migrants use en-route habitat for different reasons: Rest, fat deposition, molt, hydration, safety from predators.
2. A variety of foods, including insects and fruit, is important both spring and fall migration. Fruit facilitates fat deposition and provides a rapid (short-term) solution to nutrient deficiencies which result from prolonged activity (i.e., migratory flight).
3. Management practices that reduce food (insect, fruit) abundance should be scrutinized (e.g., pesticide application).
B. LANDSCAPE SCALE
1. Given diversity of migratory species, a diverse array (mosaic) of habitats is preferred.
2. Floristic and structural diversity is desired (e.g., mixed forest and scrub/shrub habitats "attract" more individuals and are characterized by greater species richness).
3. Maintain mixed communities in urban and agricultural landscapes as well as managed forests. For example, city parks can host dozens of species and many individuals during migration.
C. GEOGRAPHIC SCALE
1. Because migratory pathways are only loosely defined and influenced by seasonal weather patterns, suitable stopover habitat should be managed across a breadth of possible migratory pathways. A matrix of widely distributed habitats may be more effective than a small number of large habitat areas.
2. The continental-wide pattern of migration concentrates migrants in relation to ecological barriers. Crossing barriers can place extreme energetic demands on migrants.
3. Protection and management of habitats used by migrants in relation to ecological barriers should be a priority, especially along the northern coast of the Gulf of Mexico (spring and fall), the Atlantic Coast (fall), and riparian habitats in the Southwestern U.S. (spring and fall). Conservation is exacerbated by population growth and land conversion taking place in both coastal and riparian areas.
4. Migrants and their habitats should be included as significant coastal resources in state Coastal Zone Management plans.

reasons; some birds try to deposit lipid stores, others use the site as a molting ground (e.g., Winker et al. 1992), and still others simply rest until nightfall (Biebach 1991). As we refine our understanding of determinants of habitat suitability, we must combine this knowledge with an analysis of habitat status and trends to develop future conservation priorities.

Among-Habitat Landscape Scale

Recent studies along the northern coast of the Gulf of Mexico (e.g., Moore et al. 1990; Kuenzi et al. 1991), in the Upper Mississippi Valley (Winker et al. 1992), and the Delmarva Peninsula (Mabey et al. 1992) have begun to identify some of the local and landscape scale features important to migrants. For example, spring migrants clearly preferred habitats with greater structural diversity when they arrived on the northern Gulf coast following a trans-Gulf flight (Moore et al. 1990). Structurally complex habitats, comprised of forest with a mixed shrub layer contained the greatest diversity and abundance of migrants. Similarly, species richness is greatest in mixed forest, deciduous forest, and scrub/shrub habitats associated with the Delmarva Peninsula (Mabey et al. 1992).

Maintenance of mixed communities in urban and agricultural landscapes as well as managed forests should improve habitat quality for migrants. For example, city parks can host dozens of species and many individuals during migration. Without these habitat "islands" many birds would not have any place in which to stopover. Although these "migrant traps" are important habitat, they should not be construed as alternatives to larger, undeveloped areas. In general, given the ecological diversity of this group of birds, avoid monoculture forests while maintaining floristic and structural diversity at stopover sites should be a habitat management goal. Efforts at habitat restoration should emphasize scrub/shrub and mixed forests communities.

Geographic Scale

First, it is clear that migratory pathways are only loosely defined and are shaped by seasonal weather patterns. Second, radar and field studies confirm that importance of an individual patch of habitat varies from year to year; a function of the number of migrants stopping-over and their energetic condition. The conservation implications of these observations argue for protection of suitable stopover sites across the breadth of known migratory routes. When managing for migratory species, a matrix of smaller and more widely-distributed habitats may be more effective than a small number of large habitat patches.

Once migration routes are recognized and geographical variances in the route and timing documented, one can delimit important stopover habitat for Neotropical migrants. A number of important stopover locations have been identified where concentrations of Neotropical migrants occur (e.g., Block Island, Rhode Island; Delmarva Peninsula; Cape May, New Jersey; High Island, Texas; Dry Tortugas, Florida; Long Point Bird Observatory, Ontario), but in nearly all cases habitat is limited, or areas are small and isolated, or both. Neotropical migrants require more extensive stopover habitat, particularly along the

Atlantic Coast in fall and along the Gulf Coast in spring and fall. Stopover habitat in the interior is also critically important in North America wherever extensive deforestation and fragmentation have occurred (intensive and extensive agricultural areas) and, of course, in expansive areas of grassland and desert where stopover habitat for migrants that prefer woodlands is almost nonexistent except for narrow riparian woodlands. Such areas must be maintained and even increased (e.g., Platte River in Nebraska).

The continent-wide pattern of migration concentrates migrants in relation to ecological barriers. Crossing ecological barriers such as water bodies, mountain ranges, deserts, and more recently, agricultural and urban landscapes, can place extreme energetic demands on migrants. Furthermore, problems associated with ecological barriers are magnified for hatching-year birds on their first migration. When food is plentiful even an inefficient forager may have few problems finding enough food to deposit sufficient lipid stores. However, inefficiency and lack of experience in young migrants could become important if food becomes scarce or when migrants experience increased energy demand (e.g., trans-barrier flights).

Therefore, protection and management of habitats used by migrants before and after they cross ecological barriers should be a prominent conservation priority. Examples include; cheniers and coastal woodlands along the northern coast of the Gulf of Mexico, riparian habitats in the Southwestern U.S. and maritime forests and shrub communities along the eastern seaboard. Consider the consequences of en-route habitat loss on landbird migrant populations: Densities will increase in remaining areas, which will intensify competition. Increased competition may reduce food availability and increase interference, thereby slowing migration, delaying arrival on breeding and wintering areas, and increasing predation pressure. Increased competition may also re-distribute birds among habitats, with younger, less experienced migrants forced into poorer sites where mortality rates are expected to be higher. The challenge of identifying and protecting coastal habitats will be heightened by explosive population growth taking place in these areas. Concentration of the U.S. population along coasts is projected to continue well into the next century (Figure 7; Cullitan 1990). About half of our total population now live in coastal areas. By 2010, coastal populations will have grown from 80 million to more than 127 million people, an 60% increase. The Northern Gulf Coast, collectively the most important migratory stopover area in North America, is expected to see significant population increases (Figure 7; Cullitan 1990). The southern migration of industry coupled with changing demographics will increase development pressure of stopover habitats in the decades ahead. Some coastal habitats spared from development are threatened by accelerating rates of coastal erosion (Dolan et al. 1989). The combined effects of coastal subsidence, disruption of sediment supplies, and sea level rise will add further to loss of important stopover habitats. Creation of new habitats to replace those lost to coastal erosion will be a major conservation challenge in the next century.

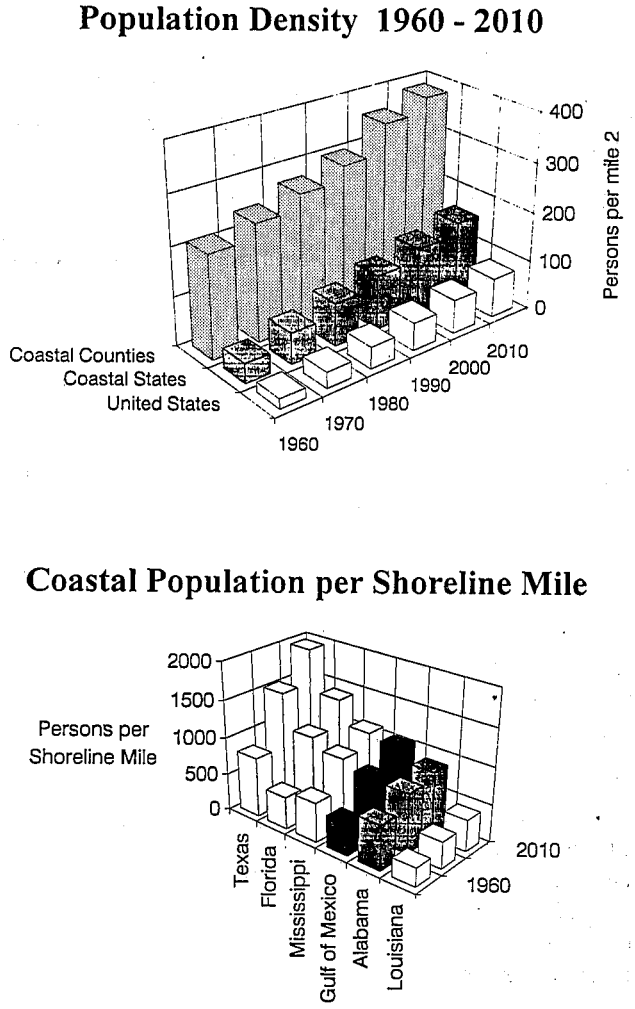


Figure 7. — (TOP) Projected changes in population density for coastal counties, coastal states, and the United States from 1960 to 2010. (BOTTOM) Coastal population per shoreline mile for the northern coast of the Gulf of Mexico.

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