HABITAT USE BY LANDBIRDS ALONG NEARCTIC-NEOTROPICAL MIGRATION ROUTES: IMPLICATIONS FOR CONSERVATION OF STOPOVER HABITATS

DANIEL R. PETIT

Abstract. Most wildlife management and conservation plans are based upon patterns of habitat use by focal species. Lack of information on habitat use by birds during migration has prevented development of comprehensive strategies for their protection along migration routes, including identification of high priority habitat types and specific sites critical to long-term persistence of those species. In this review, published information about habitat associations of long-distance migrants along nearctic-neotropical migration routes was used to address several relevant questions about the patterns, proximate and ultimate causes, and management implications of habitat use during the migration period (primarily in North America). Most species used a restricted set of habitats from those available. In general, however, species were more variable in their use of habitats during migration than during the breeding season, and they exhibited substantial variation in use of habitats at different locations along migration routes and between spring and autumn migration periods. General patterns of habitat use by species during migration corresponded most closely to patterns of habitat use during the breeding season rather than to measures of the types or abundance of food found within habitat types, competition from other species, or presence of predators during migration. These preliminary results suggest that specific guidelines developed for conservation of migratory species during the breeding season will be useful for their management during migration periods as well. In addition, large tracts of structurally diverse forests, natural representation and distribution of habitats within landscapes, and sites adjacent to geographic barriers (large bodies of water, mountain ranges) should be of high priority for conservation of the stopover habitats of migratory birds.

Key Words: conservation priority, habitat use, migration, nearctic-neotropical migrants, North America, stopover habitat.

> "Where do the birds go each fall that have nested in our dooryards and frequented the neighboring woods, hills, and marshes? Will the same ones return again to their former haunts next spring? What dangers do they face on their round-trip flight and in their winter homes? These and other questions puzzle the minds of many who are interested in the feathered species. . . Lack of information on the subject may mean the loss of an important resource by unconsciously letting it slip from us. Ignorance of the facts may be responsible for inadequate legal protection for such species as may urgently need it. More general knowledge on the subject will aid in the perpetuation of the various migrants, the seasonal habitats of some of which are in grave danger from man's utilization, sometimes unwisely, of the marsh, water, and other areas they formerly frequented."—
> Frederick C. Lincoln, *The migration of North American birds (1935)*

The connection between environmental problems and health of some bird populations in North America was first widely recognized during the 1960s (Carson 1962), but nearly three decades passed before the extent of those problems was fully realized for migratory birds as a group (Robbins et al. 1986, 1989b). During that period, avian ecologists interested in conservation and management of long-distance migratory land birds worked along parallel tracks during the breeding season in temperate North America and during the overwintering period at tropical latitudes (see Keast and Morton 1980, Hagan and Johnston 1992). Habitat loss and fragmentation were identified as the most pressing avian conservation problems in both areas (e.g., Aldrich and Robbins 1970, Forman et al. 1976, Morse 1980b, Whitcomb et al. 1981, Lynch and Whigham 1984, Hutto 1988).

Long-distance nearctic-neotropical migrants are those species that breed in temperate North America and overwinter at tropical latitudes. The annual cycle of most species entails spending 3–4 months at breeding sites, 5–6 months at overwintering areas, and the remaining 2–4 months along migratory routes (Keast and Morton 1980). However, despite the relatively greater risks to birds travelling several thousand kilometers along migratory routes, inadequate attention has been devoted to understanding the habitat requirements, behavioral ecology, and energetic constraints of birds during migration. Hence, the level of scientific investigation during migratory periods has not been commensurate with the probable role these periods play in the population dynamics of nearctic-neotropical migrants (Sprunt 1975, Gauthreaux 1979).

Only in the past few years has attention been

given to conservation of landbirds along migratory pathways in the Western Hemisphere (Moore et al. 1993). However, basic knowledge of the types of habitats used by species at stopover sites has remained elusive. Documentation of the patterns of habitat use, as well as understanding the proximate and ultimate bases for that behavior, are fundamental to effective conservation plans since many conservation and management actions are directed at habitats and only indirectly at species.

I address several questions of habitat use that are significant to nearctic-neotropical migratory bird ecology and conservation: (1) Do migrating birds exhibit nonrandom use of habitat types? (2) Are certain habitat types or vegetative characteristics consistently related to use by migrating birds? (3) Do species show consistent use of habitat types at different locations along migratory routes? (4) Are patterns of habitat use consistent between spring and autumn migratory periods? (5) How does habitat use during migration compare with that during winter and breeding periods? (6) What are the ecological correlates of habitat use along migration routes? (7) Are guidelines for management of species during the breeding season in North America appropriate for migration periods as well? Evaluation of these questions, which complements the recent reviews by Moore and co-workers (Moore and Simons 1992a; Moore et al. 1993, 1995), is intended to provide direction for identifying and managing migratory stopover habitats and for guiding future research efforts.

DO MIGRATING BIRDS EXHIBIT NONRANDOM USE OF HABITAT TYPES?

Migratory birds are not distributed haphazardly among habitats during either the breeding (Hamel 1992) or wintering (Petit et al. 1993) periods, so nonrandom habitat use by migrating birds also would be expected. Results from the few systematic studies that have examined this question during migration indicate that populations of most species are not distributed equitably across major habitat types (Parnell 1969, Mason 1979, Hutto 1985a, Moore et al. 1990, Mabey et al. 1993). For example, the distribution of most species across habitats is highly skewed, such that habitat breadth (see Levins 1968) of individual species rarely reaches 50% of the maximum possible (Fig. 1, shaded bars; a mean of 40%, for example, indicates that the breadth of distribution of individuals across available habitats averaged only 40% of the value were individuals equally distributed across habitat types), and most species typically are not even detected in one-third of the available habitats (Fig. 1, diagonal bars; a mean of 65%, for
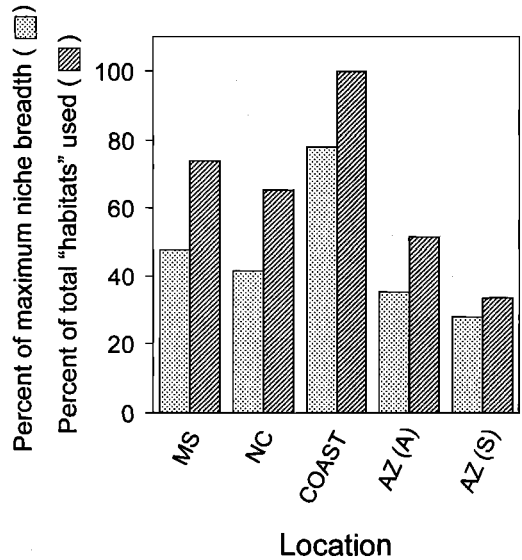

FIGURE 1. Examples of the overall distribution of migratory birds across available habitats in Mississippi (MS; Moore et al. 1990), North Carolina (NC; Parnell 1969), the mid-Atlantic coast (COAST; Mabey et al. 1993), and Arizona in autumn (AZ[A]) and spring (AZ[S]; Hutto 1985a). Percent of maximum niche breadth was derived by calculating the niche breadth (Levins 1968) of each species as a percentage of the maximum value possible, and then averaging over all species. Percent of maximum habitats used was calculated in a similar fashion, except that niche breadth was replaced by the percentage of all habitats occupied by each species, and then averaged over all species. (Measures are conservative estimates of the distribution of birds across habitats because most studies included only relatively abundant species and omitted uncommon and rare species that most likely had more restricted distributions.)

example, indicates that the "average" species was detected in 65% of all habitats surveyed). Thus, migrating birds exhibit selective use (defined as deviation of use from availability) of some habitats over others.

Habitat selectivity varies widely among species, however. For example, in the lower Piedmont of North Carolina, Parnell (1969) found that Yellow-rumped (*Dendroica coronata*) and Black-and-white (*Mniotilta varia*) warblers were broadly distributed, while Yellow (*D. petechia*) and Prothonotary (*Protonotaria citrea*) warblers were detected in only two of seven habitat types. Likewise, Golden-crowned Kinglets (*Regulus satrapa*) migrating through southeastern Arizona were restricted to high elevation pine-fir forests, whereas Ruby-crowned Kinglets (*R. calendula*) moving through the same region were detected in a wide variety of habitat types (Hutto 1985a). Other studies have documented similar variation
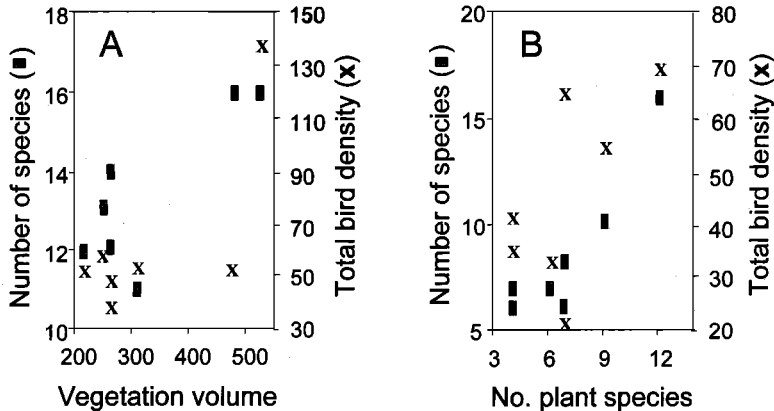
FIGURE 2. Relationship between measures of bird community composition (species richness represented by squares, total density of birds represented by crosses) and vegetative characteristics (volume of vegetation and woody plant species richness) during (a) autumn and (b) spring migrations in southeastern Arizona (Hutto 1985a).

in the breadth of species' habitat use during migration.

In summary, most migratory species exhibit selective use of locally-available habitats during migration, much as they do during other seasons. Many species concentrate locally in up to three habitat types (e.g., Hutto 1985a, Moore et al. 1990), with fewer individuals distributed among remaining habitats. However, as discussed above (and below), those apparent local preferences are both geographically and temporally flexible. This raises the question of whether certain major habitat types, or specific vegetative characteristics common to several habitats, are favored by migrating birds.

ARE CERTAIN HABITAT TYPES OR VEGETATIVE CHARACTERISTICS CONSISTENTLY RELATED TO USE BY MIGRANTS?

Because human societal values are not consistent with protecting all areas and habitat types necessary to sustain healthy populations of migratory birds, a serious dilemma is faced by those developing plans for the conservation of migration stopover sites: Which habitats are most critical to protect?

MacArthur and MacArthur (1961) and others (e.g., Willson 1974, Terborgh 1977, Beedy 1981) have empirically demonstrated the intuitive relationship between structural complexity of habitats and bird species diversity in both temperate and tropical areas. This relationship, however, breaks down when examining species diversity across habitats of relatively similar structure and plant species composition (e.g., Roth 1976, Szaro and Balda 1979, Erdelson 1984, Petit et al. 1985). Although the above par-

adigm has important ramifications for conservation of priority habitats or areas, it has not been addressed specifically for migratory birds occupying stopover habitats.

Several studies provide general support for the relationship between foliage complexity and bird species richness and abundance during migration. Moore et al. (1990) found that migrants arriving at the Gulf coast of Mississippi during spring were most diverse and abundant in pine forests and in 5-m-tall shrub habitats, and were least common in dunes and marshes. Sykes (1986) observed a similar pattern on North Carolina barrier islands during autumn migration. Blake (1984) showed that species richness and abundance of migrating birds were correlated with vegetation height and density across three plots in southern Nevada; that relationship, however, may have been confounded by elevational factors. Both Martin and Vohs (1978) and Yahner (1983) found that abundance and diversity of transient birds moving through the Great Plains were positively associated with measures of foliage diversity. Beaver (1988) suggested that the increased autumn bird use of irrigated old fields, compared to nonirrigated fields, may have been due to greater vegetative biomass (or arthropod abundance) on the former sites. Hutto (1985a) has gathered perhaps the most detailed data to address this hypothesized bird-habitat association. For birds migrating through Arizona, a general positive relationship was observed between vegetation characteristics (e.g., volume of vegetation, number of woody plant species) and bird species richness and density during both spring and autumn across seven sites (Fig. 2). In that study, all 10 of the correlation coefficients between bird community attributes and vegeta-

tion characteristics were positive during autumn, and 9 of 10 were positive during spring. In both autumn and spring, birds migrating through old-growth hammocks in Florida appeared to be attracted to areas with heterogeneous and complex vegetation—forest edges, natural gaps, and areas with dense understory (Noss 1991).

Several studies, however, have found little evidence of a relationship between foliage complexity and measures of bird use. Spring migrants travelling through North Carolina (Parnell 1969) were slightly more abundant in low thickets ($\bar{x}$ = 14.1 ± 1.1 SD birds/hr) than in taller forests (11.7 ± 2.0; Mann-Whitney U-test, Z = 1.36, P = 0.17), although that nonsignificant trend was reversed when species richness was examined (thickets, $\bar{x}$ = 7.5 ± 4.9 SD species; forests, 14.4 ± 3.6; Z = −1.36, P = 0.17). Along the Delmarva and Cape May peninsulas of the Atlantic coast, no consistent relationships were obvious between bird species richness or abundance and the structural complexity of 17 plant community types (Mabey et al. 1993). Likewise, data in Weisbrod et al. (1993) suggest only a weak relationship between birds and habitat complexity. This latter data set, however, was based upon mist-netting and, therefore, probably was biased against taller vegetation types. In Arizona, numbers of both fall and spring migratory species passing through ponderosa pine (*Pinus ponderosa*) forests were lowest on sites with a high density of overstory trees and greatest on plots with many shrubs and saplings (Blake 1982). In contrast, total abundance of spring migrants in Blake's study was inversely related to understory density, while abundance of autumn migrants showed no relationship with either understory or overstory. In wooded riparian corridors of southeastern Arizona, Skagen et al. (1998) found no significant relationship between foliage density and either species richness or abundance of migrants.

In summary, at least as many (and often more) species and individuals are typically found in structurally diverse habitats compared to less diverse sites. However, the lack of a consistent relationship between bird community and vegetative characteristics probably results from the cumulative effects of species-specific responses to habitat structure. That is, each species responds to a unique set of environmental stimuli, such that divergent responses by the different species are likely to obscure a definitive pattern of habitat use by the bird community as a whole.

The meager information on avian use of vegetation types during migration, and the dynamic nature of plant communities across geographic regions, makes it difficult, and indeed probably

academic, to identify specific plant communities most important as stopover habitat (but see below). Rather, examination of the suite of habitats on a local or sub-regional level may be an appropriate scale at which to identify habitats most beneficial to migrants as a group.

In general, taller, more structurally diverse vegetation types within an area appear to support greater numbers of migrating birds than do habitats of lower stature and complexity. Clearly, those structurally complex habitats will not be adequate for all migratory species, but if a conservation goal is to protect those areas used most frequently by migrating birds, relatively tall, structurally diverse habitats may best serve that purpose. The plasticity in habitat use exhibited by most species during migration (see above) suggests that many species are able to effectively use the food resources and cover afforded by structurally complex habitats. Additional research is needed on this topic, however, as simple presence may not reflect the quality of a site, but rather "forced" selection driven by low energy stores after overnight flights (Hutto 1985b, Moore and Kerlinger 1987, Moore and Simons 1992a).

DO SPECIES SHOW CONSISTENT USE OF HABITAT TYPES AT DIFFERENT LOCATIONS ALONG MIGRATION ROUTES?

Many species show substantial geographic variation in habitat use, even among those studies where similar habitats were examined. For example, in a comparison of nine species of wood-warblers migrating through both the Piedmont of North Carolina (Parnell 1969) and along coastal areas several hundred kilometers to the north (Mabey et al. 1993), average within-species overlap (Colwell and Futuyma 1971) in habitat use between the two areas was only 63% (SE = 5.3, range = 38–84%). Yellow Warblers migrating through eastern coastal areas (Mabey et al. 1993), North Carolina (Parnell 1969), and Wisconsin (Weisbrod et al. 1993) nearly always (93–100% of individuals) were found in low scrub (including thickets and young second growth). In contrast, Yellow Warblers moving through Arizona (Hutto 1985a) and, especially, Kentucky (Mason 1979) were much less frequently found in that broad habitat type (80% and 39%, respectively). Hooded Warblers provide an even more striking example of geographic variation in use of stopover sites. In North Carolina and Kentucky, Hooded Warblers were never or rarely detected in old fields or thickets, being restricted primarily to tall forest habitats (Parnell 1969, Mason 1979). In contrast, along the Gulf coast of Mississippi and in Ve-

racruz, Mexico, 80% of migrating Hooded Warblers were found in scrub habitats and avoided taller habitats (Moore et al. 1990, Winker 1995).

On the other hand, several species, such as Blue-headed Vireo (*Vireo solitarius*), Ovenbird (*Seiurus aurocapillus*), and Pine Warbler (*Dendroica pinus*), have not been shown to exhibit extensive geographic variability in habitat use during migration (compare Parnell 1969, Hutto 1985a, Mabey et al. 1993).

The lack of geographic consistency in habitat use by many migratory species suggests that migrants are adapted to exploit the unpredictable environments encountered along migratory routes (Morse 1971), and that the distribution of individuals across habitats is the result of complex, hierarchical evaluations of habitat suitability (Hutto 1985b, Moore et al. 1993; also see below). The wide variability in use of specific habitat types also highlights the limitations of using broad habitat categorizations for identifying priority habitats for individual species (Petit et al. 1993). For example, more detailed, quantified characterizations of habitats would allow better evaluation of vegetative features associated with particular species, which in turn could foster more consistent identification and effective management of stopover areas. Furthermore, if species are (at least partially) constrained in their use of habitat types during migration, for example by their morphology (Leisler and Winkler 1985; also see below), detailed characterization of habitat features will be necessary to understand the ecological and evolutionary basis of habitat selection.

Geographic variation in habitat use also could result from different ecological and physiological requirements that must be fulfilled along the migration routes. Stopover sites near breeding grounds, for example, may serve as refugia that allow individuals to complete prebasic molts; fat deposition may not be as critical (Cherry 1985, Winker et al. 1992a). In contrast, energetic considerations probably are of overriding importance for migrants using habitats adjacent to ecological barriers (Loria and Moore 1990, Bairlein 1991, Moore 1991a). Thus, the varied requirements of migrating birds may result in use of dissimilar habitats at different locations along migration routes.

ARE PATTERNS OF HABITAT USE CONSISTENT BETWEEN SPRING AND AUTUMN MIGRATORY PERIODS?

Seasonal differences in ecology, behavior, and physiology of migrating birds can be pronounced. For example, rates of movement during spring migration may be twice as high as those during autumn (Pearson 1990); many typically insectivorous species consume fruit during autumn, but not spring (Martin et al. 1951); continental migratory pathways can vary substantially between the two seasonal legs (e.g., "loop migration;" Cooke 1915, Berthold 1993); reproductive behavior is more pronounced during spring migration than during autumn (Quay 1985, Moore and McDonald 1993); and characteristics of fat accumulation may differ between the two periods (Blem 1980, Moreau 1969).

Seasonally related constraints or opportunities may influence, or be dictated by, patterns of habitat use. Hutto (1985a) observed significant seasonal shifts in habitat use by more than half of the 26 species that migrated during spring and fall through southeastern Arizona. Those shifts were highly correlated with changes in overall insect abundance. Blake (1984) documented substantial seasonal shifts by the avian assemblage migrating through Nevada, and concluded that changes may have reflected responses to a changing food base, or physiological constraints imposed by elevational factors. Likewise, Farley et al. (1994) studied migratory bird use of a successional gradient of riparian cottonwood stands in New Mexico. They found that, whereas species richness increased linearly with stand age during the spring, migratory birds preferred younger woodlands during autumn. In Iowa, several species of *Vermivora* that forage in trees during spring migration often are found in agricultural fields and weed patches during the autumn period (Dinsmore et al. 1984). Swainson's Thrush (*Catharus ustulatus*) and Northern Waterthrush *(Seiurus noveboracensis)* exhibited seasonally different patterns of habitat use while migrating through Minnesota (Winker et al. 1992a).

In contrast, data in Weisbrod et al. (1993) show that, when taken as a group, the migratory bird assemblage passing through the Saint Croix River Valley of Wisconsin exhibited similar proportional use of six habitats during spring and autumn. However, a pronounced increase in autumn use of the pine forest site was detected in that study (Weisbrod et al. 1993).

The above examples provide evidence of seasonal variation in habitat use by migrating birds, although only Hutto (1985a) and Yong et al. (1998) have systematically examined shifts at the species level. Indeed, seasonal changes in overall avian habitat use on a local scale may occur for several reasons unrelated to habitat shifts by species or individuals, such as high seasonal turnover of species (Lincoln 1935, Hutto 1985a), or seasonal changes in age structure of populations (Murray 1966, Ralph 1971). For example, Yong et al. (1998) found that patterns

of habitat use by Wilson's Warblers (*Wilsonia pusilla*) migrating through New Mexico varied between spring and autumn and that those differences could be attributed to seasonal differences in the age and sex structure of the populations. Seasonal variation in habitat use also may be dictated by the ecological and physiological constraints unique to each season (see above). The extent and ecological basis of seasonal variation in use of migratory stopover habitats needs further study. In the meantime, seasonal variation in habitat use needs to be incorporated into conservation strategies.

ARE HABITATS USED DURING MIGRATION SIMILAR TO THOSE OCCUPIED DURING OTHER SEASONS?

Seasonally related patterns of avian habitat use (e.g., Rice et al. 1980, Collins and Briffa 1982) have profound consequences for wildlife management and conservation. Indeed, otherwise solid conservation efforts can be hampered because temporal changes in habitat use are not considered (e.g., Bancroft et al. 1992). To maximize effectiveness, management strategies for migratory populations should integrate not only summer and winter habitat requirements, but also those of migration periods (Moore and Simons 1992a, Petit et al. 1993). Delaying development of those plans, however, is a lack of information on the similarity of habitats used throughout different periods of the year.

Habitat use by neotropical migrants during the breeding season, and to a lesser extent the overwintering period, has been examined in detail relative to that during migration. Many species occupy superficially similar habitats in temperate breeding and neotropical wintering areas (Hutto 1985b, Petit 1991), although numerous exceptions also can be found (Rappole et al. 1983, Robbins et al. 1989b, Petit 1991). The similarity between migratory bird habitat use during migration and either the breeding or wintering season has not been thoroughly addressed. Because most conservation plans focus only upon breeding and wintering areas (Finch and Stangel 1993), such comparisons could serve to identify gaps in protection of important stopover habitats that are not encompassed by existing components of conservation plans.

Parnell (1969; also see Power 1971) observed that habitat relationships among 12 species of wood-warblers were consistent between migration and breeding periods in North Carolina. In that study, between-season overlap (for formula see Colwell and Futuyma 1971) in habitat distribution averaged 82% (SE = 2.5, range = 65–98%) for each species. Likewise, McCann et al. (1993) found that forest- and scrub-breeding

species exhibited seasonal consistency in habitat use as they migrated through the coastal areas of the mid-Atlantic states.

In studies where the range of available habitats was more restricted, however, migrants used habitat types that were not characteristic of those used during breeding or wintering periods. For example, species migrating through coastal barrier islands of Mississippi occurred in habitats highly dissimilar to those used at other times of year, a phenomenon that Moore et al. (1990) attributed to lack of other, more preferred, habitats. Warblers that breed in deciduous forests exhibited strong habitat relationships while migrating through areas in Kentucky dominated by deciduous vegetation types (Mason 1979). In contrast, those species that nest in northern coniferous forests were more broadly distributed across vegetation types, suggesting less selectivity in those situations where preferred habitats are not present (Mason 1979). Most species passing through southeastern Arizona (Hutto 1985a) occupied an array of habitats at least superficially similar to those used during the breeding season.

The analysis conducted below (see WHAT ARE THE ECOLOGICAL CORRELATES OF HABITAT USE ALONG MIGRATION ROUTES?) demonstrates that species that occupy similar breeding habitats often are found together in the same habitats during migration. Furthermore, habitats used during those two periods are comparable in structural characteristics. In particular, species that breed in young successional growth tend to be found in scrubby areas and thickets during migration (Fig. 3). In Belize, Petit (1991) found that scrub-breeding migratory birds tended to overwinter in early successional habitats, whereas species that nested in taller forests were more generalized in their habitat distributions. In migration, forest-breeding species also tended to occur in the tallest habitats available, although as Petit (1991) suggested for overwintering birds, those species typically occur in a more diverse set of habitats than scrub-breeding species. Survey information from Parnell (1969), Moore et al. (1990), and Mabey et al. (1993) suggest that scrub-breeding species may be more restricted in habitat distributions during migration than are forest-breeding species (Fig. 4). In fact, species that nest in tall, forested habitats had an average niche breadth during migration that was 20% broader than those species that nest in younger successional habitats. That scrub-dwelling species make relatively limited use of the array of available habitats during migration indicates that some conservation efforts should focus on habitats of short stature because species that con-
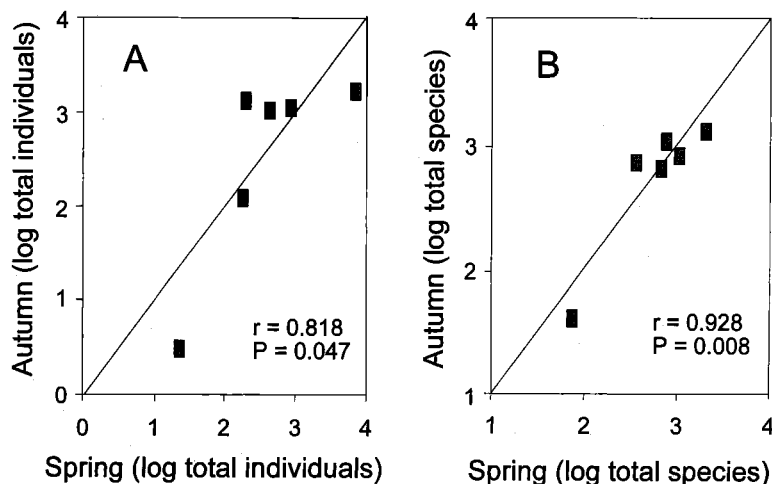
FIGURE 3. Comparison of seasonal use of six habitat types by birds migrating through Wisconsin summarized by relative numbers of (a) individuals and (b) species. Pearson correlation coefficients (r) were calculated from log-transformed raw values presented in Weisbrod et al. (1993; Figs. 2 and 3). Diagonal line represents identical habitat use between seasons.

centrate in them are less likely to use other habitat types. The apparent discrepancy between the preceding statement, promoting preservation of scrubby habitats for specialized species, and that made earlier advocating structurally diverse habitats to optimize species diversity, highlights the need for biologists to identify regional or other large scale conservation priorities before imple-
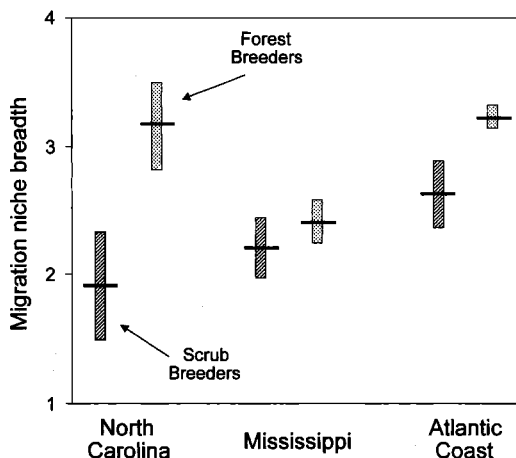

FIGURE 4. Comparison of habitat breadth (Levins 1968) during migration for species that nest in mature forest habitats (forest breeders) and species that nest in early successional habitats (scrub breeders). Horizontal line represents group average and vertical bar indicates one standard error. Data taken from Parnell (1969; North Carolina), Moore et al. (1990; Mississippi), and Mabey et al. (1993; Atlantic coast).

menting local management plans for migrating birds (see L. J. Petit et al. 1995).

Several studies in Europe have demonstrated that, in general, species show greater variability in habitat use during migration than during either breeding or overwintering periods (Alatalo 1981, Bilcke 1984; but see Hansson 1983). In North America, Rice et al. (1980) also presented data in support of that pattern. Distributional data from regional works also show similar patterns. For example, approximately one-third of common nearctic-neotropical migrants that both migrate through and breed in California were identified by Zeiner et al. (1990) as occupying more habitat types during migration (Chi-square goodness-of-fit test; $\chi^2 = 28.7$, df = 2, P < 0.001); no species were more diverse during the breeding season. Likewise, of those nearctic-neotropical migrants noted to exhibit more diverse habitat use in one season or the other, 62% (8 of 13) in Missouri (Clawson 1982) and 64% (7 of 11) in North Carolina (Parnell 1969, Power 1971) were more diverse during migration than in the summer. Data from Stiles and Skutch (1989) indicate that, whereas 57% of the nearctic-neotropical migratory species that both migrate through and overwinter in Costa Rica did not exhibit noticeably different seasonal patterns of habitat use, 43% were more varied in habitat distribution during migration ($\chi^2 = 23.2$, df = 2, P < 0.001). Finally, observations by many amateur birdwatchers and bird banders during migration (e.g., Rudy 1971, DiGioia 1974) provide a wealth of anecdotal support for the above
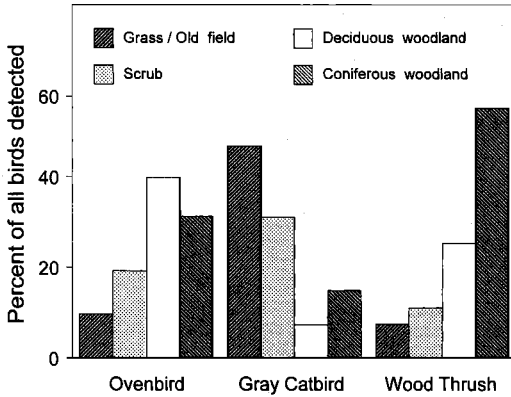
FIGURE 5. Year-round distribution of several species in different habitats in Pennsylvania (Davis and Savidge 1971). The data demonstrate the broad use of habitats by species that characteristically breed in mature forest (Ovenbird, Wood Thrush) and young successional growth (Gray Catbird).

generalization. For example, data from a year-round mist-netting effort in Pennsylvania (Davis and Savidge 1971) revealed that two forest-breeding species, Wood Thrush (*Hylocichla mustelina*) and Ovenbird, regularly occurred in brushy oldfields and other early successional growth, and approximately one-fifth of the scrub- and edge-nesting Gray Catbirds (*Dumetella carolinensis*) were captured in mature woodlands (Fig. 5).

Several patterns arise from the above observations. First, while seasonal variability in habitat use does occur, many species do have generally consistent, year-round affinities with broad habitat types. In particular, species that nest in relatively low vegetation types tend to use those habitats disproportionately during migration. Most exceptions to the generalization are detected in studies where species' preferred habitats are not available or are not incorporated into distributional surveys. The advantage of maintaining some consistency in habitat use throughout the year presumably relates to more efficient exploitation of those habitats for which the species is best adapted (Morse 1971, Greenberg 1984c).

Second, many long-distance, migratory species are capable of using a wide variety of habitat types during migration, some of which resemble neither their summer nor wintering habitats (Simons et al. *this volume*). Much of this apparent "indiscriminate" habitat use may be the outcome of a tradeoff between the cost of searching for higher quality habitats and the benefits of remaining in the already occupied habitat. From a theoretical standpoint, habitat as-

sessment (and, hence, selection) should occur during migratory stopovers as individuals should be genetically predisposed or have the behavioral flexibility to locate those habitats that offer the greatest chances of survival (Hutto 1985b). Habitat switching by migrants has been observed at stopover sites (e.g., Moore et al. 1990) and early morning flights of nocturnal migrants heading inland along coastlines have been documented both in Europe and North America (Alerstam 1978, Wiedner et al. 1992). Other studies, however, have not detected significant reverse flights or movements between habitats (Bairlein 1983, Winker 1995). Regardless of whether local movements regularly occur or not, many individuals that settle into habitats in the early morning after nocturnal flights may have little option but to forage and rest in the locally available sites. For example, along coastlines where much of the native vegetation has been destroyed and where over-water flights were just completed, migratory birds may be "forced" into occupying the first habitats encountered because of depleted energy stores (Moore and Simons 1992a).

WHAT ARE THE ECOLOGICAL CORRELATES OF HABITAT USE ALONG MIGRATION ROUTES?

Data summarized in the preceding sections provide clear evidence of nonrandom use of habitat types by many species during migration. Although most species appear to be more generalized in habitat use during migration compared to other times of the year, the habitat-specific benefits and costs that are associated with the probability of completing the migratory journey must weigh heavily in the evolution of habitat discrimination. Animals should exhibit an affinity to those habitats that offer the greatest fitness advantages (Wecker 1964, Fretwell and Lucas 1970, Charnov 1976).

Several authors recently have addressed the issue of why nearctic-neotropical migrants might occupy certain habitats, and not others, during migration (Kuenzi et al. 1991, Moore and Simons 1992a). This section provides a brief overview and evaluation of several of those hypotheses. Understanding the ecological and evolutionary basis for habitat selection will ultimately lead to better management of migratory stopover sites and of long-distance migratory birds.

The distribution of birds among habitats during migration may be influenced by four features: (1) food abundance or effectiveness in exploiting the food base, (2) competition with other species, (3) predation pressure or relative safety from predators, and (4) reproductive opportunities

FOOD ABUNDANCE OR AVAILABILITY

If birds are choosing habitats during migration based upon food abundance or the ease with which food can be harvested, several (non-exhaustive) predictions can be made.

Bird abundance across habitats should be correlated with food abundance

Several studies have documented correlations between fruit or insect abundance and density of migrating birds through major habitat types (Hutto 1985a, Martin 1985) and through different areas within the same habitat (Blake and Hoppes 1986, Martin and Karr 1986). Terrill and Ohmart (1984) found that autumn migratory movements of Yellow-rumped Warblers in riparian woodlands of the southwestern United States were "facultative" and related to local abundance of insects.

These studies suggest that migrating birds respond to abundances of arthropods and fruit once settlement within a habitat has occurred or when the northern limits of wintering ranges are established during autumn. However, because only Hutto's (1985a) work involved surveys across more than two habitat types, the extent to which site-based food abundance influences avian habitat use during migration needs further examination.

Species that have relatively similar diets or that forage in similar ways should co-occur in the same habitats

Because foraging behavior of woodland birds during the breeding season is related to local vegetative structure (Robinson and Holmes 1982, Petit et al. 1990), migrating birds also might choose habitats with vegetative or other environmental features, including food abundance, that allow efficient gathering of food. If habitat use during migration is driven primarily by abundance of particular food resources or the ease with which those resources can be harvested, one would predict close concordance between habitat use and diet or foraging behavior, respectively. Data from five studies (Parnell 1969, Hutto 1985a [spring and autumn], Moore et al. 1990, Mabey et al. 1993) were used to test the hypotheses that dietary habits and foraging behavior are related to habitat types used during migration. Species were categorized by diet (omnivore or insectivore) and foraging location (canopy, shrub/understory, or ground gleaner, or aerial forager). Omnivores were defined as those species that include fruit or nectar as a major component of their diet (Ehrlich et al. 1988; pers. obs.).

To examine the above hypotheses, the relative use of the array of habitats was summarized for each species into a single index. For each study, principal component analysis (PCA; PROC PRINCOMP, SAS Institute 1990) was used to ordinate bird species by their proportional use of surveyed habitats. Scores on each principal component axis were derived for each species and were used to characterize habitat use by that species relative to all others. Thus, species with comparable patterns of habitat had similar scores along an axis. Only scores from the first two principal components were used in analyses as those two components accounted for more than half of the variation within all datasets ($\bar{x}$ = 67%, range = 53–85%). These scores were then used as dependent variables in a three-way analysis of variance (ANOVA) to evaluate differences (α = 0.10) in habitat use between the two dietary guilds and among the four foraging guilds. Scores from the first PCA component were analyzed separately from the second component.

In addition to diet and foraging behavior, a third factor, breeding season habitat (each species categorized as breeding in either coniferous forest, deciduous forest, shrub, or edge/open habitats), was included in the ANOVA model. Although the relationship between habitat use during migration and the breeding season is evaluated separately below, foraging behavior was not independent of breeding season habitat (log-likelihood ratio [G] test; P < 0.05 in four of the five studies). Thus, inclusion of breeding season habitat use in the ANOVA models was appropriate to control for spurious relationships, and to provide a more comprehensive analysis of the correlates of habitat use during migration. Only main effects in the ANOVA model were relevant to testing of the above hypotheses (i.e., interactions were not examined).

Species that eat the same general type of food did not consistently co-occur in similar habitats during migration (Table 1, Fig. 6). However, data from the mid-Atlantic coast (Mabey et al. 1993, McCann et al. 1993) and Arizona highlands (Hutto 1985a) during autumn and along the Gulf coast (Moore et al. 1990) during spring provided some evidence that birds selected general habitat types based upon the types of food that were found there. In two of those studies (Moore et al. 1990, Mabey et al. 1993), omnivorous species tended to be overrepresented in scrub habitats and underrepresented in coniferous habitats. Insectivorous species exhibited varied responses to habitats across the five studies.

Other studies (e.g., Blake and Hoppes 1986, Martin and Karr 1986) identified food preferences as a strong correlate of habitat selection during autumn migration. One explanation for lack of a general relationship between diet and

TABLE 1. ECOLOGICAL CORRELATES OF HABITAT USE DURING MIGRATION

Study	Dependent variable	Source of variation	F	df	P
Parnell 1969	PC1	Overall	1.98	5, 13	0.15
		Diet	0.02	1, 13	0.88
		Forage	1.11	2, 13	0.36
		Nest	0.95	2, 13	0.41
	PC2	Overall	3.66	5, 13	0.03**
		Diet	0.01	1, 13	0.91
		Forage	1.83	2, 13	0.20
		Nest	7.77	2, 13	<0.01**
Hutto 1985a (Spring)	PC1	Overall	14.73	3, 18	<0.01**
		Diet	0.22	1, 18	0.64
		Forage	4.84	1, 18	0.04**
		Nest	7.11	1, 18	0.02**
	PC2	Overall	1.38	3, 18	0.28
		Diet	2.13	1, 18	0.16
		Forage	0.87	1, 18	0.36
		Nest	2.23	1, 18	0.15
Hutto 1985a (Autumn)	PC1	Overall	13.38	3, 22	<0.01**
		Diet	3.49	1, 22	0.08*
		Forage	0.71	1, 22	0.41
		Nest	13.74	1, 22	<0.01**
	PC2	Overall	0.35	3, 22	0.79
		Diet	0.71	1, 22	0.41
		Forage	0.28	1, 22	0.60
		Nest	0.28	1, 22	0.60
Moore et al. 1990	PC1	Overall	3.18	7, 12	0.04**
		Diet	0.20	1, 12	0.66
		Forage	2.60	3, 12	0.10*
		Nest	2.93	3, 12	0.08*
	PC2	Overall	6.38	7, 12	<0.01**
		Diet	3.53	1, 12	0.09*
		Forage	3.40	3, 12	0.05**
		Nest	1.23	3, 12	0.34
Mabey et al. 1993	PC1	Overall	3.43	7, 24	0.01**
		Diet	0.46	1, 24	0.50
		Forage	1.20	3, 24	0.33
		Nest	2.23	3, 24	0.11
	PC2	Overall	2.57	7, 24	0.04**
		Diet	6.03	1, 24	0.02**
		Forage	0.53	3, 24	0.67
		Nest	2.84	3, 24	0.06*

* P ≤ 0.10; ** P ≤ 0.05.

Note: For each of five studies, a three-factor analysis of variance (ANOVA) model was used to evaluate the effects of diet, foraging location (Forage), and habitat use during the breeding season (Nest), on habitat use during migration (PC1 and PC2). Only main effects are presented. See text for additional details.

habitat use in this analysis was that data from most of these studies were collected during spring migration when comparatively little fruit is available in North America. Mabey and co-workers (1993) collected their data in autumn, although Hutto (1985a) also worked during autumn in the Arizona desert and documented no obvious pattern of fruit-related habitat use (Fig. 6), at least at the scale at which habitat was measured. Stevens et al. (1977) found that the distribution of spring migrants moving through Ar-

izona was closely related to insectivorous and granivorous food habits.

Foraging behavior was significantly related to habitat use in three of the five studies (Table 1, Fig. 7). Generally, species that glean insects from foliage in the shrub layer were underrepresented in pine-dominated forests, but were relatively abundant in shrubby habitats of low stature. Canopy foragers typically were most common in tall coniferous and broad-leaved forests. Thus, insect-gleaning species used those habitats that offered
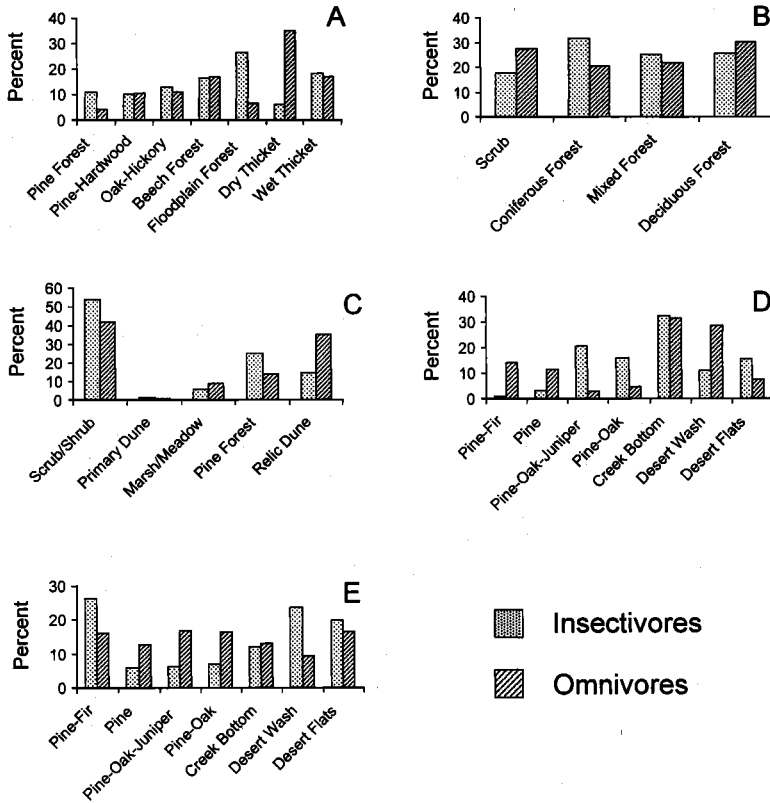
FIGURE 6. Distribution of omnivorous and insectivorous bird species among different habitat types during migration. Bars represent the average percentage of individuals for each species that was surveyed in each habitat type (thus all bars for each dietary category total 100%). Data are from (a) North Carolina (Parnell 1969), (b) mid-Atlantic coast (Mabey et al. 1993), (c) Mississippi coast (Moore et al. 1990), and southeastern Arizona (Hutto 1985a) in (d) spring and (e) autumn.

the densest foliage at preferred foraging heights. Ground foragers tended to use the tallest broadleaved vegetation available, whereas the few flycatching species represented in the data sets exhibited wide variability in habitat use.

Migratory species that breed in similar habitat types during the summer also occur together in a restricted set of habitats during migration (Table 1, Fig. 8). In all five studies, one of the principal components summarizing habitat use was significantly related to the patterns of habitat used during the breeding season. Thus, this analysis provides support for the assertion that long-distance migrants should occur in similar habitat types (if available) year-round because they are most effective in exploiting only a subset of environmental conditions (Morse 1971, Greenberg 1984c). It also supports the predictions of others that morphological constraints predispose species to select certain habitats over others. Several authors have demonstrated the relationship between morphology and use of habitat (includ-

ing foraging behavior) during the breeding season (e.g., Miles and Ricklefs 1984, Leisler and Winkler 1985). Because morphology of a species is related to habitat use during the breeding season and remains relatively constant throughout the year, species that breed in similar habitats may also be found together at other times of the year, such as during migration. Bairlein (1992a) documented a close relationship between morphological characteristics and habitat distributions of neotropical migrants along the Gulf of Mexico coast during early spring, indicating that morphological constraints may influence habitat selection during migration (Berthold 1988).

Although habitat use during migration appears to be most closely related to vegetative characteristics of habitats used during the breeding season (Fig. 8), diet (Fig. 6) and foraging behavior (Fig. 7) may also influence habitats used during migration. The significant energetic demands of migration are believed to exert a
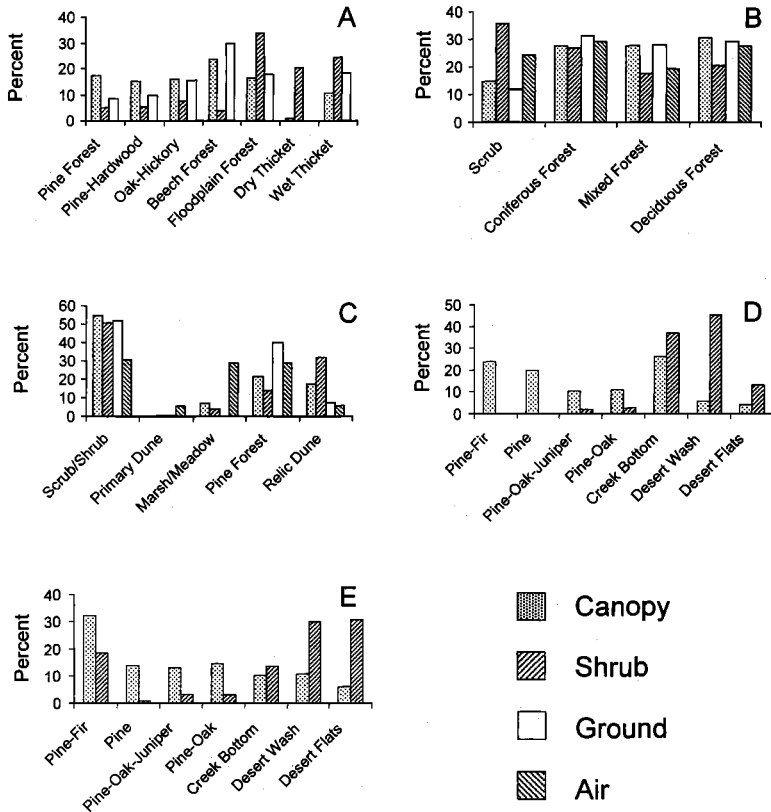
FIGURE 7. Distribution of canopy, shrub, ground, and air foragers among different habitat types during migration. Bars represent the average percentage of individuals for each species that was surveyed in each habitat type (thus all bars for each foraging category total 100%). Data are from (a) North Carolina (Parnell 1969), (b) mid-Atlantic coast (Mabey et al. 1993), (c) Mississippi coast (Moore et al. 1990), and southeastern Arizona (Hutto 1985a) in (d) spring and (e) autumn.

strong influence on the ecology, behavior, and evolution of migrating birds (Rappole and Warner 1976; Berthold 1975, 1993:92–106; Blem 1980, Moore 1991a). Thus, the lack of a close relationship between general dietary characteristics of species and habitat use during migration was unexpected. Many of the previous studies that have found a relationship between frugivorous behavior of migrating birds and habitat use have focused on microhabitat preferences within one habitat type (Blake and Hoppes 1986, Martin and Karr 1986), an analysis that was not possible using the data derived from the published reports used in this study. Other research has documented major patterns of habitat use during migration that were related to diet (Stevens et al. 1977, Martin 1985). Thus, although selection of habitats that offer the best foraging opportunities may partially account for the observed distributions of species during migration (Raitt and Pimm 1976, Martin 1980, Blake 1984, Hutto 1985a, Moore and Yong 1991), the analysis presented here suggests that affinities to broad habitat types used during the breeding season or other factors (e.g., predation pressure, morphological and energetic constraints, surrounding land-use patterns) may exert significant control over habitat selection (Hutto 1985b, Ward 1987, Moore et al. 1990). Distribution of individuals *within* those habitat types, however, may be more closely associated with abundance of insect and fruit resources (e.g., Blake and Hoppes 1986, Martin and Karr 1986). For example, Smith et al. (1998) suggested that Black-throated Green Warblers (*Dendroica virens*) foraging in forests within three kilometers of Lake Huron during spring migration used microhabitats (those closest to the water) that supported the greatest numbers of emerging aquatic insects.

COMPETITION

When settling into stopover habitats, migrating birds may respond to the combined effects of food abundance and the number of potential
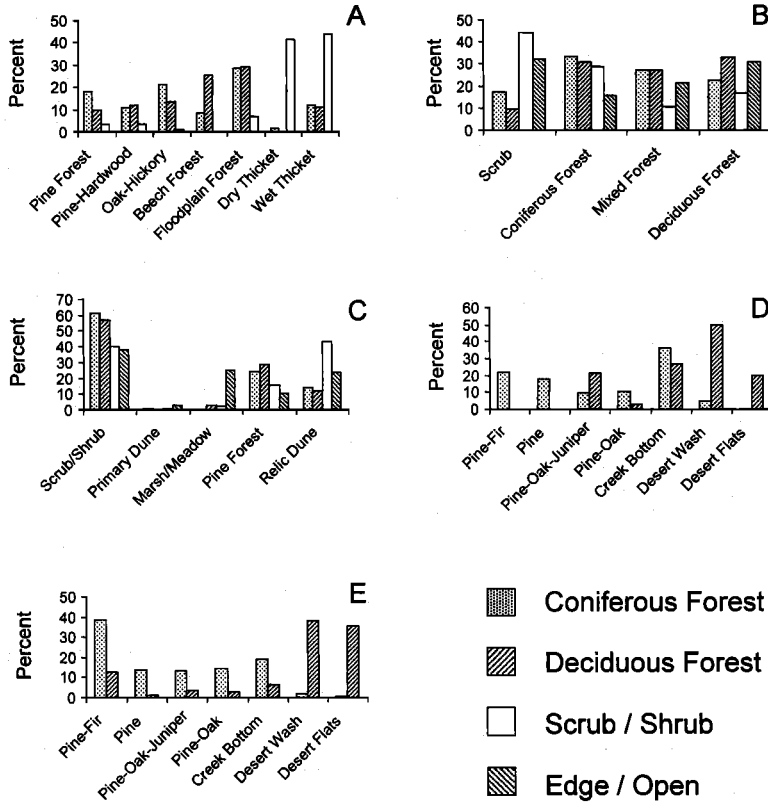
FIGURE 8. Distribution of coniferous forest-, deciduous forest-, scrub/shrub-, and edge/open-nesting species among different habitat types during migration. Bars represent the average percentage of individuals for each species that was surveyed in each habitat type (thus all bars for each nesting category total 100%). Data are from (a) North Carolina (Parnell 1969), (b) mid-Atlantic coast (Mabey et al. 1993), (c) Mississippi coast (Moore et al. 1990), and southeastern Arizona (Hutto 1985a) in (d) spring and (e) autumn.

competitors (both heterospecifics and conspecifics). Two facets of this hypothesis need to be verified. First, does competition among species or among individuals of the same species occur? And, second, if competition does exist, does it influence the distribution of individuals across broad habitat types?

Food-based competition occurs only when already limited resources are depleted by foraging individuals (Martin 1986). Abramsky and Safriel (1980) suggested that competition may have influenced the evolution of migration periods among Mediterranean species. Studies in Europe (e.g., Hansson and Petterson 1989; but see below) and North America (e.g., Martin 1980, 1981) have concluded that use of different habitat patches by transient species was determined (at least) partially through competitive interactions. Data on within-habitat resource use from several studies in Europe were consistent with expectations of interspecific competition (Ormerod 1990, Pambour 1990). Moore and Yong

(1991) presented a brief synopsis of several studies that offered circumstantial evidence for interspecific and intraspecific (also see Greenberg 1986) competition among North American birds during migration. In perhaps the most convincing demonstration of *en route* competition, Moore and Yong (1991) found that, after having just crossed a 1,000-kilometer expanse of the Gulf of Mexico, the rate of mass gain by spring migrants on the Louisiana coast was influenced by the density of other small songbirds.

Other studies (e.g., Power 1971, Bairlein 1983, Fasola and Fraticelli 1990), however, have found that the distribution of migrating individuals was not consistent with the predictions of competition theory. In fact, Lovei (1989) concluded that competition for food resources among Palearctic-African migrants was minimal. Competition is most likely to occur at those locations where large numbers of migrants congregate near significant physical barriers, such as large bodies of water or small habitat patches

surrounded by inhospitable habitat. Indeed, much of the evidence for competition among individuals has been generated at sites of relatively high avian density (e.g., Rappole and Warner 1976, Laursen 1978, Martin 1980, Moore and Yong 1991), while most of those studies not detecting competitive interactions have been conducted in areas where lack of physical barriers allow a more dispersed distribution of individuals (e.g., Power 1971, Fasola and Fraticelli 1990). Density-dependent intraspecific (Brown 1969, Fretwell and Lucas 1970) and interspecific (MacArthur 1972) interactions are believed to influence the distributions of birds among habitats. High relative densities of potentially competing species, such as on habitat "islands" or close to physical barriers, increase the probabilities that "interference" and "exploitation" competition (Schoener 1974) will occur.

These results have important ramifications for conservation of habitats along migratory routes. If migrating birds are most stressed after long flights over unsuitable habitats and in areas of high density, particular emphasis needs to be made for maintaining the ecological integrity of isolated stopover sites and sites near ecological barriers. Indeed, both ecologists (e.g., Rundle and Fredrickson 1981) and legislators (e.g., Public Law 99-645, the "Energy Wetlands Resources Act of 1986") have long recognized the importance of isolated stopover sites in the population dynamics of shorebirds, waterfowl, and rails. Conservation of large habitat patches in coastal areas, agricultural regions, and desert zones may serve to mitigate the detrimental effects of increased competition for resources in these areas.

PREDATION

Predation has been given very little attention as a factor shaping habitat use by migrating landbirds (Lovei 1989), largely because of the difficulties in documenting relatively rare predation events. However, in some situations bird-eating hawks and falcons, the principal predators of migrating birds, can cause substantial mortality (e.g., Lindström 1989, Moore et al. 1990, Alerstam 1993:343–344). Many birdwatchers also have observed a relationship between the timing of small landbird migration and that of their avian predators (e.g., Alerstam 1993:343).

The sparse data on predation in different habitat types makes difficult an evaluation of the hypothesis that habitat use or other behaviors of migrating landbirds is influenced significantly by predation pressure. Circumstantial evidence by Lindström (1990b) indicated that habitat use by migrating Bramblings (*Fringilla montifringilla*) in Sweden was a tradeoff between food abundance and predation pressure, a conclusion also supported for other species during the breeding and wintering seasons (Schneider 1984, Lima et al. 1987).

Several predictions can be made from the hypothesis that the behavior of migrants is influenced by predators along migration routes. If landbirds choose habitats or behave in ways that minimize the risk of predation, then one or more of the following relationships should be evident (data were extracted from Moore et al. 1990, the only published report that allows direct assessment of these hypotheses).

Either a negative or a positive relationship could exist between raptor and landbird abundance across local habitat types

Although Moore and Simons (1992a:351) stated that a positive relationship existed between predation pressure and migrant density, data from Moore et al. (1990) suggest that, in fact, the relationship is inconclusive ($r_s = -0.40$, $P = 0.60$, N = 4).

Migrants should exhibit disproportionate use of those habitats that afford the greatest protection from predators

Dense cover probably affords the greatest protection to small birds (e.g., Morse 1973, Grubb and Greenwald 1982; but see Lima et al. 1987). Thus, the shrub/scrub habitat in Moore et al.'s (1990) study probably offers the safest environment from predatory hawks, followed by pine forest, dune, and marsh/meadow. Data from Moore et al. (1990) support the above prediction ($r_s = 1.0$, $P < 0.05$, N = 4), although the value of these habitats as foraging sites may confound this relationship.

Species that make the greatest use of habitats that harbor high densities of raptors should exhibit more pronounced flocking behavior

By forming flocks, group members are believed to reduce their probability of predation (Pulliam 1973). Data from Moore et al. (1990; their Tables 2 and 4) provided little support for the prediction above. In the habitat with the highest relative density of bird-eating raptors, results opposite to the prediction were observed. That is, in pine forests, where raptor densities were greatest, a *negative* relationship ($r = -0.84$, $P < 0.01$, N = 17) was observed between percent overall use of that habitat and percentage of individuals of each of the 17 species that occurred in flocks. In contrast, migratory species that frequented scrub habitats (few raptors present), showed no relationship ($r = 0.17$, $P = 0.49$) between use of that habitat and propensity to join flocks.

Clearly, a simple relationship between predation pressure and habitat use does not exist. Rather, as other authors have noted, the primary consideration for birds during migration may be meeting energetic demands (Loria and Moore 1990, Moore 1991a). This does not imply that the risk of predation has not been important in the evolution of habitat selection by migrating birds, only that its potential importance is imbedded in a tradeoff between energetic gain and the risk of predation (or other factors). Furthermore, exact predictions are difficult to test using data that currently are available and, by lumping all migratory species together, important relationships between predators and prey may be obscured. Nevertheless, researchers need to continue to evaluate testable predictions in this area to fully understand habitat selection during migration.

REPRODUCTIVE OPPORTUNITIES

Several species of neotropical migrants are known to copulate while migrating in the spring, despite being up to 1,500 km from breeding areas (Quay 1985, 1989; Moore and McDonald 1993). Extra-pair copulation clearly could be beneficial to both sexes (Møller 1988, Westneat et al. 1990), although these benefits have not been empirically documented for birds that copulate during migration. Alternatively, *en route* copulation could occur between already paired birds (e.g., Greenberg and Gradwohl 1980), thus potentially minimizing the time required to lay a full clutch of eggs, and thereby maximizing the time to raise offspring on the breeding grounds. Female passerines can store sperm for more than 2 weeks and still produce viable eggs (Birkhead 1988).

The distribution of individuals among available habitats during the breeding season is believed to be based primarily on reproductive opportunities, while during migration replenishing energetic stores or protection from predators may be the primary selective force driving habitat selection (see above). However, given that some birds copulate during spring, habitat selection during migration also could be associated with potential reproductive benefits. If the "best" males are able to secure the highest quality stopover sites through an ideal dominance (i.e., despotic; Brown 1969) or other type of competitive interaction, females may reap reproductive benefits (in addition to food or predation benefits) by also occurring in those habitats. (A parallel argument also could be made, whereby males are attracted by the presence of females.) If territoriality or aggression (e.g., Rappole and Warner 1976, Bibby and Green 1980, Sealy 1988) among migrating males forces subordi-

nate birds into lower quality habitats, and if *en route* copulation is beneficial to females, a basis for female (or male) preferences of certain stopover sites over others can be hypothesized. Although many males apparently are not physiologically capable of successful copulation during migration (e.g., Jones and Norment 1998), additional study is necessary to fully investigate the above ideas.

ARE GUIDELINES FOR MANAGEMENT OF SPECIES DURING THE BREEDING SEASON APPROPRIATE FOR MIGRATION PERIODS AS WELL?

Successful conservation of migratory species requires that temporal variation in habitat requirements be incorporated into management plans. The literature review and analyses above indicate that while many long-distance migratory species use superficially similar types of habitats during different stages of their annual cycles, substantial variation exists in this general theme. Specifically, many species appear to be more dispersed among available local habitats during migration than they are during the breeding season. This level of behavioral plasticity suggests that the same rigid guidelines (e.g., Robbins 1979, Faaborg et al. 1993) for conservation and management of breeding habitats may not be applicable to stopover habitats. These issues are reviewed below.

Recent bird conservation efforts in North America have focused on development of large-scale habitat management and conservation strategies (e.g., L.J. Petit et al. 1995). Thus, in addition to the historical approach of identifying important local habitat needs of species, the new strategies also incorporate landscape- and regional-level issues into local management directives. Wildlife managers now know that local populations cannot persist in isolation from the surrounding landscape (e.g., Rodiek and Bolen 1991). In this context, several issues are relevant to management of migration stopover habitats.

FRAGMENT SIZE

Habitat fragmentation has detrimental effects on *breeding* bird populations (e.g., Lynch and Whigham 1984, Robbins et al. 1989a, Wilcove and Robinson 1990, Vickery et al. 1994), but a much less severe impact on overwintering nearctic-neotropical migrants (D. R. Petit et al. 1995). Unfortunately, little is known about the relative values of small and large habitat patches to *migrating* birds.

Yahner (1983) found no significant relationship between patch area and number of migratory species using small shelterbelts during spring in Minnesota. The sizes and range (0.2–

0.8 ha) of shelterbelts in Yahner's (1983) study, however, were small. In addition, few individual migratory species (e.g., Northern Oriole [*Icterus galbula*], Common Grackle [*Quiscalus quiscula*]) showed a preference for larger patches. In southern Wisconsin, Howe (1984) found that species richness and total density within small (<7 ha) survey plots in large forest tracts were similar to that recorded in nearby, small (<7 ha) forest fragments during spring and autumn migrations. Howe (1984), however, did not present information on species-specific responses to fragmentation.

Martin (1980) recorded a positive relationship between area and the number of species in shelterbelts that ranged from 0.1–3 ha in area. Density, however, was inversely related to fragment size. Individual species' distributions were not examined. Willson and Carothers (1979) found a strong positive correlation between island size and numbers of species migrating through isolated riparian forest patches along the Colorado River. In another study in southwestern United States, the number of species of springtime migrants was inversely related to area (and length) of woodland riparian corridors, although that relationship was not evident when total abundance of birds was examined (Skagen et al. 1998). Unfortunately, in this latter study several confounding factors such as elevation, isolation, and vegetative structure, may have obscured the true relationship between species use of woodlands of different size.

Several species migrating through northeastern Florida exhibited preferences for small (<5 ha) or large (>20 ha) maritime hammocks (Cox 1988). Long-distance migratory species that breed only in large forest tracts were detected disproportionately in larger patches, suggesting that species that are area-sensitive (sensu Robbins 1979) during the breeding season also prefer the largest available forest tracts during migration. For short- and long-distance migrants moving through the coastal plain of Maryland during spring, D.R. Petit et al. (unpubl. data) found mixed patterns for species that are considered area-sensitive or that typically nest in extensive forest tracts. For example, Ovenbirds and Yellow-rumped Warblers were more abundant in large (>300 ha) forest patches, whereas Black-throated Blue Warblers (*Dendroica caerulescens*) exhibited no such pattern (Fig. 9). Blackpoll Warblers (*D. striata*) were found most often in small (<150 ha) fragments. In Petit et al.'s study, habitat use during migration apparently did not reflect a simple relationship with patch size, but instead also appeared to be influenced by microhabitat characteristics and surrounding landscape (see below).
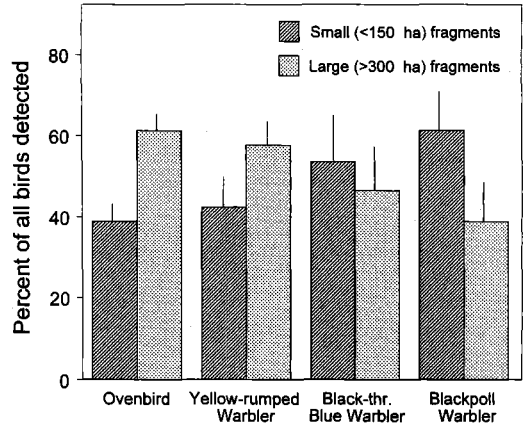

FIGURE 9. Distribution of Ovenbirds, Yellow-rumped Warblers, Black-throated Blue Warblers, and Blackpoll Warblers in 8 large (>300 ha; typically >500 ha) and 8 small (<150 ha; typically <80 ha) mature forest fragments in Maryland and Washington, DC, during spring migration. Bars represent the average percentage of all individuals for each species detected on a given day. Vertical line indicates one standard error.

Taken together, these studies suggest that maintenance of large tracts of relatively homogeneous, but structurally diverse, habitat is important for some species of landbirds during migration. However, constraints on habitat selection appear to be much more pronounced during the breeding season for most species. This suggests that habitat management guidelines developed for breeding birds will meet the requirements of most species during migration periods as well.

ISOLATION

By definition, habitat fragmentation results in isolation. The detrimental effects of isolation on animal populations has been both theoretically (MacArthur and Wilson 1967) and empirically evaluated (Shafer 1990, and references therein). However, for landbirds occupying terrestrial habitat islands (as opposed to oceanic islands), studies of the effects of isolation from similar types of habitat patches only recently have been investigated. Those studies conclude that some species are most likely to occupy forest fragments that are in close proximity to other, larger forest blocks (Lynch and Whigham 1984, Askins et al. 1987, Robbins et al. 1989a).

Little information exists to address this issue for migrating birds, however. Yahner (1983) detected an effect of isolation on birds migrating through agricultural shelterbelts of the upper Midwest. However, most species were more abundant in shelterbelts that were farther away

from other woodlots. Martin (1980) concluded that degree of shelterbelt isolation was not related to species richness or abundance once habitat features and shelterbelt area were considered. Skagen et al. (1998) found that more species were detected in isolated oases compared to larger riparian woodlands in southeastern Arizona, although this pattern may have resulted from other, confounding factors (see above).

Corridors that connect fragments to larger habitat blocks have been suggested as remedies for decreased immigration and emigration often associated with wildlife breeding in isolated fragments (MacClintock et al. 1977, Wegner and Merriam 1979, Noss 1987). Several authors, however, have identified potentially serious ecological problems associated with presence of corridors (Whitcomb et al. 1981, Simberloff and Cox 1987).

During migration, corridors may provide a means by which individuals can readily find alternative stopover sites, as well as being "shunted" into appropriate breeding habitat during spring. D.R. Petit and co-workers (unpubl. data) surveyed more autumn transients in small forest fragments (<100 ha) that were connected via corridors than in similar-sized fragments that were isolated from surrounding woodlands. This same pattern was not observed during spring migration or for large (>300 ha) forest blocks in either season. These conclusions, while preliminary, suggest that wildlife corridors may enhance migratory bird use of small, isolated habitat fragments in some situations.

Given the wide diversity of results noted above with respect to the relationship between isolation and bird abundance, additional research is needed to evaluate the value of corridors to migrating (as well as breeding and overwintering) birds.

LOCAL HABITAT DIVERSITY

Maximization of regional species diversity, as opposed to local diversity, is a guiding principle of conservation biology (Murphy 1989). For management of migratory birds, this typically means maintaining large habitat blocks necessary for sustaining viable populations of area-sensitive species and species susceptible to harmful edge effects (Faaborg et al. 1993). However, this rule may not need to be so strictly interpreted in management of habitats for landbirds during migration periods for three reasons: (1) migratory birds exhibit diverse patterns of habitat use during migration, so more species might be accommodated through local (landscape-level) habitat diversification; (2) many species appear to be capable of using a wide variety of habitats (compared to that used during

the breeding season); and (3) the detrimental effects associated with small habitat fragments and edges (Wilcove and Robinson 1990) may not be applicable to transient individuals. Moore et al. (1993) also recommended that a diverse set of local habitats be maintained for birds during migration.

The contradiction between this recommendation and that suggested above for maintaining large habitat blocks for migrating birds is obvious. The solution, however, is to develop regional and local priorities for habitat types and species. For example, in regions where important breeding populations exist (e.g., Robinson et al. 1995), breeding season habitat requirements should be emphasized in local priorities. On the other hand, in locations where suburban or agricultural development has consumed all large blocks of habitat, conservation of existing small, interspersed patches might be promoted because of their benefits to migrating birds (Whitcomb et al. 1976). In addition, in regions where migrating birds may face particularly severe stress, such as areas bordering large physical barriers (e.g., Gulf of Mexico), local planners may desire to focus efforts on providing large blocks of high quality habitat, while not losing sight of the fact that a diverse set of stopover habitats would benefit a greater suite of species. Conservation benefits derived from local strategies and actions can be maximized only if developed within a larger, regional context.

CONSERVATION IMPLICATIONS

The discussions presented above clearly demonstrate the numerous sources of variation that are related to habitat use by migrating birds, including intraspecific, interspecific, geographic, behavioral, and seasonal elements. The complex nature of habitat selection, along with a paucity of well-designed studies to evaluate habitat use during migration, precludes formulation of firm management recommendations at the present time. However, by identifying some of the components influencing, or at least correlated with, habitat use, robust patterns are beginning to emerge. Documentation of these patterns is a critical step in development of detailed management plans in the future. The above analyses have several broad implications for management and conservation of migration stopover habitats.

(1) *The quality and importance of an area as a migration stopover site must recognize geographic location,* in addition to its vegetative, topographic, and other ecological characteristics. Specifically, habitat conservation and management for migrating birds must be given special attention in areas and along routes of heavy migratory bird movements (e.g., Atlantic coast),

and in areas adjacent to formidable ecological barriers (also see Moore et al. 1993, Petit et al. 1993, Cox 1995), such as large bodies of water (e.g., Gulf of Mexico, Great Lakes), and arid and highly agricultural regions.

(2) *Habitat patches surrounding ecological barriers must be of particularly high quality* because high densities of migrants at these sites may create a competitive environment with limiting resources. Habitat enhancement and restoration efforts need to focus on those concentration points to ensure sufficient food and shelter for prolonged occupancy by individual birds. Specifically, more extensive, undisturbed habitat should be maintained near barriers compared to areas where migrants are more spatially and temporally dispersed (Agard 1995). Where that may not be possible because of development, for instance, small landowner and backyard habitat programs may be effective in providing migratory birds critical habitats both before and after long flights over inhospitable barriers.

(3) *Habitat management and conservation priorities established in North America during the breeding season usually will be sufficient for providing the types, physical characteristics (e.g., patch sizes), and spatial arrangements (e.g., landscape connectivity) of habitats required by landbirds during migration periods.* Indeed, the behavioral plasticity exhibited by migratory birds during the spring and autumn, suggests that these species are able to effectively exploit widely divergent environmental conditions along migration routes. While any management generality will not apply to all species in all circumstances, these types of generalities offer land managers and planners a basis from which to begin to develop management plans. Needless to say, all conservation generalities need to be adapted to local situations.

(4) *Maintenance of relatively tall and structurally diverse forest types should be a high priority in stopover habitat management plans* because structurally diverse habitats generally support greater numbers of migratory species than habitats of low stature or vegetative complexity. Again, while this type of recommendation may be appropriate for most species, certain species may require different management actions.

(5) *Landscape-level and regional conservation plans should ensure a diversity of habitats for migrating landbirds.* The above recommendation notwithstanding, managers must also consider species with habitat requirements that do not include taller forests. During migration, early successional and grassland species appear to be more confined to habitat types that mimic those used during the breeding season, than are species that nest in mature forests. Thus, grass-

land and scrub habitats should be closely managed and positioned in ways that do not diminish their own quality or that of adjacent forests; for example, creation of a "checkerboard" of small habitat patches is not recommended.

(6) *Although the quality of small habitat fragments probably is inferior to large patches, small parcels should be protected as "migration stepping stones" (Date et al. 1991) when possible, especially in the absence of large habitat patches (e.g., shelterbelts, suburban parks).* In addition to the ecological benefits, parks offer an opportunity for people to view (and hear) the grand phenomenon of migration.

(7) *Local planning for management of migratory bird stopover habitats must consider and integrate both landscape- and regional-level issues.* Decisions for site-level conservation actions should not be made without consideration of landscape-level processes (e.g., plant and animal population dynamics) or patterns (e.g., composition and spatial distribution of landscape elements). Furthermore, optimal site-level conservation strategies can be achieved only by viewing objectives and biological targets in a regional context.

FUTURE RESEARCH

Good management decisions cannot be made in the absence of sound biological information. The lack of attention by scientists to migratory landbird habitat use during spring and autumn has severely hindered the ability of land managers to preserve the ecological integrity of migration stopover habitats. For research to contribute fully to management and conservation of migratory birds, a comprehensive strategy must be devised to understand the complexities of migration, including the underlying evolutionary, behavioral, and ecological components associated with the migration phenomenon. Moore (1991b) identified three broad arenas that require more in-depth study: (1) the evolutionary correlates of bird migration; (2) the energetic and ecological costs associated with travelling long distances over hostile environments and through unfamiliar habitats; and (3) the factors regulating the population dynamics of migratory birds, not only during the breeding and overwintering seasons, but also during migration. In addition, more thorough investigation of the seven main questions addressed in this review paper is urgently needed. Habitat requirements of individual species, as well as season-, age-, or sex-related variability in those patterns, need to be evaluated through rigorous surveys and habitat association studies. And finally, for conservation planners to establish a regional framework for preservation of critical migration stopover hab-

itats, research ecologists must establish criteria by which important sites can be identified and managed. Without rigorous, biologically based standards, important stopover sites will "slip through the cracks," and with those habitats will go migratory birds.