Stopover Habitat and Its Importance in the Conservation of Landbird Migrants[1]

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Abstract: Conservation of neotropical landbird migrants will be compromised if attention is not focused on habitat requirements during migration. Habitat use during migration has profound consequences for a bird's (1) ability to satisfy energetic requirements, (2) vulnerability to predators, and (3) exposure to environmental stress. Largely correlative evidence indicates that landbird migrants select among available habitats on the basis of factors intrinsic to the habitat, such as food availability, habitat structure, and cover in relation to predation risk. Management decisions would be simplified if species could be grouped for the purpose of assessing en route habitat requirements, but our study of habitat use among neotropical landbird migrants along the northern coast of the Gulf of Mexico points to species-specific patterns of habitat use. On the other hand, many migrants display behavioral variability that may permit them to occupy different habitat types as well as respond to novel circumstances. It should be possible to evaluate the immediate consequences of such plasticity by measuring how effectively migrants satisfy energy demand during stopover in relation to habitat type.

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Approximately two-thirds of the bird species that breed in forests of eastern North America migrate from temperate breeding grounds to more tropical wintering areas in the Caribbean, Mexico, and Central and South America (Keast and Morton 1980). The conservation of neotropical[3] landbird migrants is complicated by the very life history characteristic that permits these birds to exploit seasonal

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[3]The term 'neotropical' pertains to those species that winter in the neotropical biogeographic realm, but breed in the nearctic realm. Our emphasis is on landbird migrants within the order Passeriformes.

environments, namely migration. Choice of habitat must be made in tropical wintering quarters, in temperate breeding areas, and repeatedly during migration. Each of the habitats encountered during the migrant's annual cycle faces different threats of degradation and destruction.

Although debate over causes of population decline among these intercontinental migrants will continue for some time, 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 the importance of habitat during migration (Moore and Simons 1992, Mabey et al. 1992, Moore et al. 1993). We know little about what types of habitats are most important a 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 very much about migrant-habitat relations.

Our objectives are twofold: (1) Recognize stopover habitat as an important link in the conservation of neotropical landbird migrants, and (2) emphasize that en route habitat use differs among species. We present data on migrant-habitat relations during spring and fall migration along the northern coast of the Gulf of Mexico. A prominent feature of the nearctic-neotropical bird migration system is the movement of individuals over the Gulf of Mexico each spring and fall (Buskirk 1980, Rappole et al. 1979, Ramos 1988). After the first week in April through mid-May, day-to-day consistency of migration across the Gulf of Mexico is rarely interrupted in spring, while fall movements occur regularly in September and October. Forested coastal habitats may be crucial to landbird migrants in fall because they provide a place to deposit energy (fat) reserves for a nonstop flight (18–24 hours) of >1,000 km and in spring by giving them a place to rest and replenish energy reserves following a trans-Gulf flight (Rappole and Warner 1976, Moore and Kerlinger 1987, Moore et al. 1990, Kuenzi et al. 1991).

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Methods

Spring

Spring data were collected on Horn Island (30°15'N, 88°40'W), a federally-designated wilderness area in the Gulf Island National Seashore. Located about 14 km from the Mississippi coast, the 1,400-ha island ranges in width from several hundred meters to just over 1 km and is 22 km long. Five plant habitats, considered potentially important to landbird migrants, were identified by Moore et al. (1990). The percent of the island occupied by a particular habitat, after excluding barren sand and open water (25% of total island area), is noted parenthetically in the following descriptions.

Primary dune (14.4%) borders the inter-tidal zone on both sides of the island and is dominated by *Uniola paniculata* and *Andropogon maritimus*. Marsh/meadow

(28.9%) habitat is dominated by large stands of *Juncus roemerianus*, *Spartina alternifora,* and *S. patens* in tidal flood areas, or *Fuirena scirpoidea*, *Panicum repens*, and *Andropogon virginicus* in fresh water areas, with occasional shrubs (*Baccharis halimifolia* and *Myrica cerifera*) and living and dead slash pines (*Pinus ellioti*) along the edges. Scrub/shrub (14%) consists of shrub thickets, which range to 5 m in height, that are dominated by *B. halimifolia* and *M. cerifera* on wetter sites and by yaupon (*Ilex vomitoria*), dwarf live oak (*Quercus geminata*), and *Serenoa repens* on drier sites. Relic dune (28.8%) refers to high, dry relic dune ridges characterized by sparse low shrubs, *Solidago pauciflosculosa*, *Ceratiola ericoides*, the rock-rose *Helianthemum arenicola*, *Opuntia* spp., and a few slash pine and dwarf live oak. Pine forest (13.9%) habitat consists of a slash pine canopy, with small numbers of *Quercus geminata* and an understory that ranges from open on drier sites to dense thickets of *Myrica*, *Baccaharis*, and *Ilex* on wetter sites.

Point counts were used to estimate the number of avian species stopping on the island and to provide an index of abundance. No effort was made to estimate the absolute density of the migrants that stopover on the island. Sampling points were established at 50-m intervals along 3 transects that passed through each of the 5 habitats. A point within each habitat type along the 3 transects was selected randomly (3 points per habitat) and counts conducted daily (0730–1000 hours) in each habitat type. The order of daily visitation to habitat types was randomized. At each stop, the observer recorded all birds seen within that habitat type during a 10-minute period, although only individuals perched, foraging, or displaying aggressive behavior were included in the analysis of habitat use. Observations were made daily 10 April to 9 May 1987 in primary dune, marsh/meadow, pine forest, relic dune, and scrub/shrub habitats.

Fall

Use of coastal habitat by fall landbird migrants was studied by censusing birds on Bon Secour National Wildlife Refuge (30°10'N, 88°00'W), located on Ft. Morgan peninsula about 15 km west of Gulf Shores, Alabama. The peninsula was mostly covered by scrub habitat, characterized by scattered slash pines interspersed among hummocks of sand live oak and yaupon. However, areas on the south side of the peninsula and towards the western tip were occupied by marsh/meadow habitats, and the eastern portion was characterized by mixed evergreen/deciduous areas. We censused 4 habitats available to fall migrants during their stopover on Bon Secour National Wildlife Refuge.

Deciduous forest consisted largely of southern magnolia (*Magnolia grandiflora*), pignut hickory (*Carya glabra*), laurel oak (*Quercus hemisphaerica*), and loblolly pine (*Pinus taeda*) with a more open understory of yaupon and highbush blueberry (*Vaccinium elliottii*). Pine/shrub forest habitat was dominated by a slash pine canopy with a dense understory of yaupon, redbay (*Persea borbonia*), and saw palmetto. Scrub/shrub habitat was dominated by thickets of sand live oaks 2–4 m in height, but includes some rosemary and some saw palmetto. Marsh/meadow habitat was characterized by *Andropogon* spp. and *Spartina* spp. grasses with a few was scattered 1–2 m slash pines and *Baccharis*.

Appendix A Alphabetical list of common names of neotropical landbird migrants and number of individuals detected while censusing birds during spring (21 Mar–9 May 1987) on Horn Island and fall (1 Sep–21 Oct 1992) on Ft. Morgan peninsula.

Species	Horn Island	Ft. Morgan
American redstart	11	36
Bay-breasted warbler	3	—
Barn swallow	—	35
Black-and-white warbler	26	8
Black-throated green warbler	7	16
Blackburnian warbler	—	10
Blackpoll warbler	8	—
Blue grosbeak	47	11
Blue-gray gnatcatcher	3	286
Blue-winged warbler	2	—
Bobolink	2	1
Broad-winged hawk	—	4
Canada warbler	—	5
Cape May warbler	2	—
Cerulean warbler	3	—
Chestnut-sided warbler	—	3
Chimney swift	—	13
Chuck-Will's-widow	—	11
Common yellowthroat	—	39
Eastern kingbird	174	57
Eastern wood-peewee	—	15
Empidonax sp.	—	9
Gray catbird	13	369
Gray-cheeked thrush	4	—
Great-crested flycatcher	84	8
Hooded warbler	26	11
House wren	—	7
Indigo bunting	119	21
Least flycatcher	—	1
Magnolia warbler	7	13
Nashville warbler	—	1
Northern Oriole	20	9
Northern Parula	12	—
Northern Rough-winged swallow	—	2
Northern Waterthrush	1	1
Orchard Oriole	96	—
Ovenbird	8	—
Painted bunting	1	—
Palm warbler	2	3
Philadelphia vireo	—	4
Prairie warbler	43	18
Prothonotary warbler	—	3
Red-eyed vireo	111	62
Rose-breasted grosbeak	38	1
Ruby-throated hummingbird	128	6
Scarlet tanager	70	2
Summer tanager	64	11
Swainson's thrush	55	5
Tennessee warbler	52	3
Tree swallow	—	89
Veery	40	5

(continued on next page)

Appendix A *(continued)*

Species	Horn Island	Ft. Morgan
White-eyed vireo	46	28
Wilson's warbler	—	3
Wood thrush	25	18
Yellow warbler	29	1
Yellow-billed cuckoo	45	—
Yellow-breasted chat	1	1
Yellow-throated vireo	16	2
Yellow-throated warbler	7	3
Total *N* individuals	1,451	1,321
Total *N* species	41	48

To estimate the number of species stopping over on the peninsula and to determine migrant-habitat relations, we established 50-m × 500-m transects in each habitat type. We quantified distributions by walking the transects (30- to 40-minute pace) and recording detections of migrants within 25 m on either side of the transect. Detections beyond 25 m were separately recorded and were not included in this analysis. Censuses were conducted in all 4 habitats each morning (0630–1130 hours). The order by which habitat were visited was systematically changed to avoid time-of-day effects. Migrants were censused 1 September–21 October 1992 in the 4 designated habitat types.

Results

Spring

We detected 41 species of forest-dwelling neotropical migrant (N = 1,451) on Horn Island during censuses in 1987 (Appendix A). Migrants were distributed unequally among the 5 habitats. A 1-way ANOVA of individuals of all species indicated significant variation in the mean number of detections ($F_{0.05(1)4,76} = 11.30$, $P < 0.05$) and a Tukey's multiple range test (Zar 1984) separated scrub/shrub habitat from the other habitat types. Scrub/shrub habitat, which represented 14% of available habitat, was characterized by the greatest number of species, the highest species diversity, and the largest number of individuals. Of the 41 species observed, 93% were seen in scrub/shrub, 82% in pine forest, 68% in relic dune, 32% in marsh/meadow, and only 10% in primary dune. Of the 1,451 individuals detected, 47% were in scrub/shrub, 20% in both pine forest and relic dune, 11% in marsh/meadow, and 2% in primary dune.

Habitat use for 4 selected species are shown in Fig. 1. Hooded Warblers (*Wilsonia citrina*) showed a preference for scrub/shrub where they were observed gleaning insects from the foliage. Blue grosbeaks (*Guiraca caerulea*) were frequently detected in relic dune habitat, where they were often observed on patches of bare sand apparently foraging for insects. The selection of open habitats by eastern kingbirds (*Tyrannus tyrannus*) is likely related to the birds' propensity to hawk

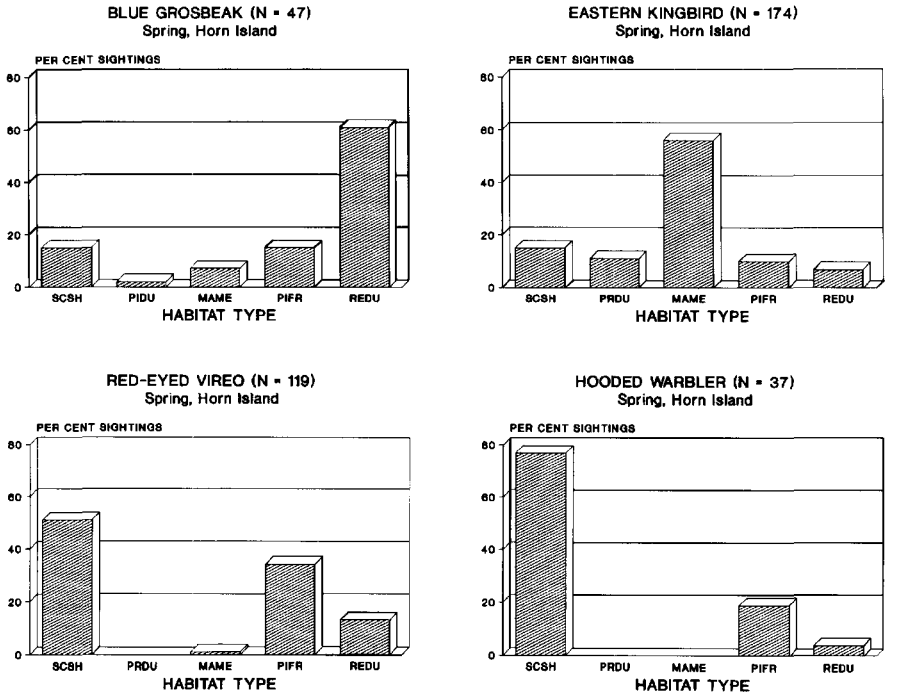

Figure 1. Habitat associations of 4 species detected during daily censuses on Horn Island, spring 1987. Note species-specific habitat preferences. SCSH = scrub/shrub habitat; PRDU = primary dune; MAME = marsh-meadow; PIFR = slash pine forest; REDU = relic dune.

food items. Whereas red-eyed vireos (*Vireo olivaceus*) were often observed gleaning prey from foliage in scrub/shrub, they were also detected flycatching from pine forest canopy during the afternoons.

Fall

A total of 1,321 individuals of 48 neotropical migrant species were detected during fall censuses in 1992 (Appendix A). Migrant abundance and species richness varied with each habitat type. Migrant abundance and species richness were greatest in scrub/shrub and pine/shrub forest habitats. Individual species were strongly associated with particular habitats (Fig. 2). For example, barn swallows (*Hirundo rustica*) were detected most often foraging over the marsh/meadow habitat catching flying insects. This relationship is not surprising given that barn swallows are aerial insectivores. With the exception of barn swallows and tree swallows (*Tachycineta bicolor*), few landbird migrants (5 species) were associated with marsh/meadow habitat. American redstarts (*Setophaga ruticilla*) were most often detected in scrub/shrub where they were observed gleaning insects from the

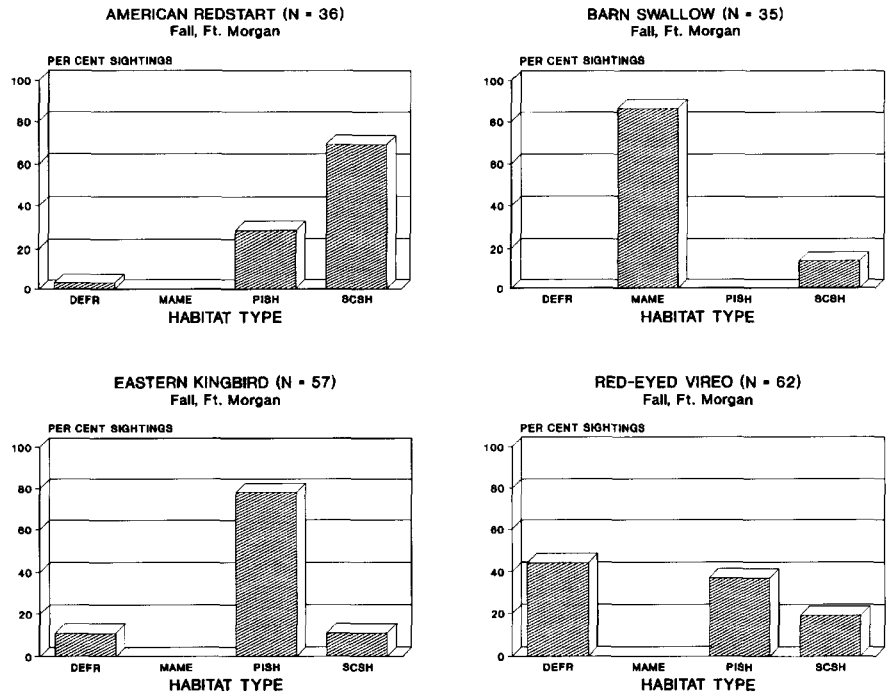

Figure 2. Habitat associations of 4 species detected during daily censuses at Bon Secour National Wildlife Refuge on Ft. Morgan peninsula, Alabama, fall 1992. Note species-specific habitat preferences. DEFR = deciduous forest; MAME = marsh-meadow; PISH = slash pine/shrub; SCSH = scrub/shrub habitat.

foliage. Eastern kingbirds were seen most often in the shrub layer of pine forest feeding on ripening fruit.

Discussion

Suitability of En Route Habitat

When migrants stopover, they must adjust their foraging behavior to unfamiliar habitats, resolve the conflicting demands of predator avoidance and food acquisition, compete with other migrants and resident birds for limiting resources, respond to unpredictable and sometimes unfavorable weather, and correct for orientation errors (see Alerstam 1990, Moore and Simons 1992). These problems are magnified when migrants cross geographical barriers, such as the Gulf of Mexico, and often arrive at stopover sites with depleted energy stores (e.g., Loria and Moore 1990; see Alerstam 1981).

The probability a migrant will meet its nutritional requirements and achieve safe passage is correlated with the intrinsic suitability of stopover habitat. Suitability of en route habitat depends largely on 3 factors: (1) foraging opportunities, (2)

competition with other migrants and with resident birds, and (3) shelter against predators and adverse weather (see Hutto 1985*b*, Moore and Yong 1991, 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 that must overcome geographic barriers (e.g., Biebach 1990, Moore 1991). Several studies conducted at disparate locations and with different species stress the importance of food availability in relation to the use of different habitats (Bibby et al. 1976; Martin 1980, 1985; Bibby and Green 1983; Graber and Graber 1983; Hutto 1985*a*; Lindström and Alerstam 1986).

Other factors besides food availability *per se* may influence the suitability of stopover habitat and affect habitat use. Physical structure (cf. Holmes and Robinson 1981, Robinson and Holmes 1982, 1984) such as plant species composition and foliage structure may influence how birds move through the habitat and how they see and capture prey. Habitat extent or patchiness (cf. Robbins et al. 1989) may be an important factor because migrants may require different threshold levels of habitat area below which they find habitat unsuitable. Suitable habitat associated with ecological barriers, for example, are often fragmented and many woodlands average only a few hectares in area. If fragments are widely dispersed, the opportunity to gain access to conditions wherein fat stores can be safely replenished would be restricted. Dehydration and water economy (Haas and Beck 1979, Biebach 1990) might constrain migratory range. Lean migrants that have mobilized carbohydrate or protein sources in response to increased energy demand might experience a serious water balance problem. Predation (Lindström 1989, Kerlinger 1989, Wiedner et al. 1992, Aborn 1994) may play a role because stopover habitats undoubtedly vary in predation risk. When the best areas for depositing fat are also the most dangerous, the migrant must trade off energy gain against mortality risks. Despite high oxidative capacity, migratory birds may experience muscular fatigue (cf. Lundgren and Kiessling 1988, Piersma 1990) during sustained flights over ecological barriers and stopover to metabolize lactate and "repay" an oxygen debt, regardless of how much fat remains. Stopover would also be required for tissue repair if migrants are forced to catabolize muscle tissue to offset unexpected energy demands or if muscle fibers are damaged during sustained, long-distance flight.

Differential Habitat Use

Although we might expect migrants to settle in habitats on the basis of relative suitability (*sensu* Fretwell and Lucas 1970, see Moore and Simons 1992), that outcome is not assured. Over the course of a season's migration a red-eyed vireo, for example, encounters a variety of habitats, most of them new habitats with associated new food, new competitors, and new predators. After a night's passage it finds itself in a habitat that may be very different from the one occupied the previous day, let alone the previous year. Moreover, favorable en route habitat, where migrants can rapidly accumulate energy reserves, is probably limited in an absolute sense (Sprunt 1975, Hutto 1985*a*, Martin and Karr 1986), or effectively so because migrants have limited time to search for the "best" stopover site.

Nevertheless, correlative evidence indicates that migrants prefer certain habitats and select among alternatives during stopover (e.g., Bairlein 1983, Moore et al. 1990, Winker et al. 1992, Mabey et al. 1992), presumably in response to differential suitability (Hutto 1985*a*, Moore and Simons 1992). The patterns of habitat use revealed in this study are consistent with en route habitat selection and emphasize the species-specific nature of habitat use during often brief periods of migratory stopover. Why certain habitats are attractive to migrants is open to speculation. The selection of open habitats by eastern kingbirds on Horn Island in spring, for example, is probably related to the bird's propensity to hawk prey items, whereas their use of pine/shrub during fall is likely related to a diet shift to frugivory. Scrub/shrub habitat was attractive for foliage-gleaning species such as hooded warblers, red-eyed vireos, and American redstarts possibly because it offered adequate food as well as refuge from predators. Barn and tree swallows probably find marsh/meadow habitats suitable because an abundance of airborne prey occur in these open areas, which is conducive to their mode of feeding.

Management Implications

Recognizing the Importance of Stopover.— The 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 (Moore et al. 1994). The complexity of this issue, and the fact that the abundance of migrants found at individual stopover sites varies from year to year, tends to devalue the migratory period when developing conservation programs. Because neotropical landbird migrants spend more of their lives in breeding and wintering habitats, these areas become natural targets for conservation efforts. Nevertheless, if the persistence of migrant populations depends on the bird's 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 the development of a comprehensive conservation "strategy" for Neotropical wintering landbird migrants (Moore and Simons 1992).

Consider the consequences of en route habitat loss on landbird migrant populations. The density of landbird migrants 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, not to mention increasing predation pressure. Increased competition may also redistribute birds among habitats, with younger, less experienced migrants forced into poorer sites where mortality rates are expected to be higher.

If mortality is concentrated in the migratory period, then factors that increased 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 do not have

the luxury of selecting alternative habitats. Therefore, a lack of suitable stopover habitat will result in death or reproductive failure for migrants and contribute substantially to future population declines.

Species-specific Habitat Needs.— The designation "landbird migrant" applies to a heterogenous assemblage of species. Even among New World warblers, most of which are insectivorous foliage gleaners, several examples of ecological and morphological convergence toward unrelated species are well known (see Morse 1989): the ovenbird (*Seiurus aurocapillus*) and waterthrushes (*S. noveboracensis* and *S. motacilla*) have adopted a thrushlike existence, the black-and-white warbler (*Mniotilta varia*) resembles a nuthatch when foraging, and the American redstart is essentially a flycatcher. Moreover, landbird migrants use en route habitat for different reasons; some birds try to deposit lipid stores, others use the site as a molting ground, and still others simply rest until nightfall.

The migrant-habitat associations evident in our study may reflect species-specific needs during migration. If so, caution should be exercised when grouping species for the purpose of assessing en route habitat requirements and making management recommendations (see Hutto 1989, Moore et al. 1993). Accordingly, planners should prefer a diverse array or mosaic of habitats. Floristic and structural diversity is desired (e.g., mixed forest and scrub/shrub habitats "attract" more individuals and are characterized by greater species richness). Mixed communities should be maintained in urban and agricultural landscapes as well as managed forests. A variety of foods, including insects and fruit, is important both spring and fall migration, while management practices that reduce food (insect, fruit) abundance should be scrutinized (e.g., pesticide application). Efforts to restore habitat within areas known to be important to migrating birds, such as coastal cheniers in Louisiana and oak motts in coastal Texas, should incorporate these broad recommendations.

We also must recognize that flexibility in the use of habitat is to be expected during migration (see Morse 1971, 1989). Landbird migrants make repeated and temporary use of stopover habitats that normally differ in vegetation structure, resource quality and quantity, and competitive pressures; circumstances that undoubtedly select for behavioral plasticity. For example, red-eyed vireos (Loria and Moore 1990) and *Catharus* thrushes (Moore 1992) alter foraging behavior in response to heightened energy demand during migration, thereby increasing the likelihood they will satisfy energetic requirements and minimize migration time. Similarly, migrants may adjust their behavior to compensate for variation in the suitability of habitats encountered en route.

Although it would be difficult to measure directly the effect of en route events on survival or reproductive success, it is possible to evaluate the immediate consequences of differential fat deposition during migration. Individuals in migratory disposition become hyperphagic and deposit lipid reserves which are mobilized to offset energetic requirements. As lipid stores are depleted during migration, free-living birds should replenish stores as fast as possible (Alerstam and Lindström 1992). Rate of fat deposition could serve as a fitness surrogate when evaluating

migrant-habitat relations. Features that characterize "better" habitats could be incorporated in management plans and efforts to restore degraded stopover habitat. Clearly, there is a pressing need for more information on stopover ecology and habitat requirements of long-distance, landbird migrants.

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