

## DISRUPTION AND RESTORATION OF *EN ROUTE* HABITAT, A CASE STUDY: THE CHENIER PLAIN

WYLIE C. BARROW, JR., CHAO-CHIEH CHEN, ROBERT B. HAMILTON, KEITH OUCHLEY, AND TERRY J. SPENGLER

**Abstract.** Cheniers (relict beach ridges) and other habitats adjacent to ecological barriers may be critical linkages in the migratory pathways of long-distance migratory birds. It is important that these wooded habitats provide enough food and cover at the right time to support these birds' requirements. To date, little attention has been given to the conservation of coastal woodlands, habitats in which *en route* migrants tend to concentrate in large numbers during migration. Because about one-third of North America's human population lives within 80 km of the coast, many forest-dwelling landbird migrants now depend on degraded native woodlands and urbanized environments for survival during migration. Restoration or rehabilitation of coastal woodlands, such as the cheniers of southwest Louisiana and southeast Texas, is of particular importance because of historic anthropogenic modifications, their limited geographic extent, and the extraordinary abundance and species richness of migratory birds using them during migration. In this paper, we use the Chenier Plain as a case study to discuss the issue of land use changes and their consequences for maintaining suitable stopover habitat. Results from an ongoing field study in this ecosystem indicate that most forest-dependent migratory birds are tolerant of at least some degradation of chenier forest during migration. However, these results reveal that subtle differences in vegetation composition and structure beneath the canopy of these forests, primarily as a result of livestock grazing and white-tailed deer overbrowsing, can result in differential use by some *en route* migrants. Species that were most affected by disturbance to the forest understory were early-arriving migrants, dead-leaf foragers, frugivores, and nectarivores. Given that the understory structure and regeneration of chenier forests has been so greatly reduced, and that high densities of nearctic-neotropical migrants tend to concentrate in cheniers during migration, restoration and rehabilitation should be conservation priorities in the Chenier Plain.

**Key Words:** Chenier Plain, habitat degradation, habitat restoration, habitat use *en route*, migration, nearctic-neotropical migrant landbirds, plant species use.

The increasing international attention given to the nearctic-neotropical migratory bird system usually focuses on the hemispheric implications of deforestation, such as the clearing of tropical forests (Briggs and Criswell 1978, Terborgh 1980, Lovejoy 1983, Hagan and Johnston 1992, Rappole and McDonald 1994) and the fragmentation of temperate forests (Whitcomb 1977, Whitcomb et al. 1981, Wilcove and Whitcomb 1983, Hagan and Johnston 1992). Little attention is given to the disruptive events that may occur along the migration routes at important staging or stopover sites (Moore et al. 1993, Parker 1994). Due to the rapid expansion of human populations in the Western Hemisphere (Meyer and Turner 1992, Bongaarts 1994), migratory birds encounter an increasingly degraded landscape throughout their migration pathway each year.

Because *en route* migrants tend to concentrate in habitats adjacent to ecological barriers, several key landscape features have been identified as being stopover sites or staging areas of special concern to forest-dwelling birds. These landscape features include forests on and adjacent to mountain ranges; woodland patches in and adjacent to agricultural, grassland, and urban landscapes; coastal hardwoods near large

water bodies; and riparian vegetation and gallery forests in arid landscapes (Sprunt 1975, Moore et al. 1993). The degree to which the survival of long-distance migrants depends on strategically dispersed wooded stopover sites is unknown (Parker 1994). We do know, however, that these key stopover areas are precisely the locations that have received the greatest extent of anthropogenic modifications in the Americas, and are projected to be areas that will be receiving the greatest human population increases in the future. For example, coastal habitats (e.g., Atlantic and Gulf coasts) are known to be critically important stopover and staging areas (Sprunt 1975, McCann et al. 1993, Moore et al. 1993). In North America at present, about one-third of our population resides in coastal counties, and by the year 2010, as much as 75% of our population may live within 80 km of the coast (US Department of the Interior 1993). Nearctic-neotropical migrants now depend on degraded natural areas and urbanized environments for survival throughout their annual cycle (Morrison et al. 1994, Greenberg et al. 1995b). The fact that disturbed habitats will play an increasingly important role in the conservation of long-distance migrants accentuates the need for habitat restoration planning and implementation.

In this chapter we discuss the issue of land-use changes and their consequences, and we propose an approach to ameliorate rates of native woodland loss, namely the rehabilitation of damaged stopover sites and staging areas. Habitat rehabilitation provides a fundamental solution to current problems of woodland loss. We focus on the Chenier Plain of the Gulf of Mexico but believe that the principles described here apply to all key stopover areas.

We use the Chenier Plain as a case study to illustrate the various types of activities that produce damaged or degraded lands, provide results from an ongoing field study, discuss the ecological strategies for rehabilitating these lands, and conclude with a statement of directions for future work on the rehabilitation of *en route* habitat.

Conservation activities can be applied at several geographic scales. To be successful, restoration/rehabilitation of habitat should take place within the context of the conservation of an entire migration pathway. Unfortunately, exact migration routes (i.e., width, shape, orientation) for most species are unknown (Russell et al. 1994), especially those portions of the route that travel through the tropics (Parker 1994). At the next level of planning, decisions should be made within the context of the conservation of the entire landscape. Simons et al. (*this volume*) identify landscape-level factors to consider for conservation planning. We focus here on the local-level (i.e., within-habitat) features that may influence the suitability of a habitat to birds during migration.

## HISTORY AND IMPORTANCE OF THE CHENIER PLAIN

### DESCRIPTION OF THE CHENIER PLAIN

The geographic limits of the Chenier Plain are the Bolivar Peninsula and East Bay, Texas, on the west; the Gulf of Mexico on the south; Vermillion Bay, Louisiana, on the east; and the transition from plain to prairie and longleaf pine flatwoods on the north. The Chenier Plain comprises about 322 km of coastal landforms that lie perpendicular to the path of the trans-Gulf bird migration, and extends inland by distances ranging from 16 km to 64 km; total area is about 1,295 km<sup>2</sup> (Gosselink et al. 1979). The land area is approximately 750,000 ha, exclusive of water, and is comprised mostly of wetland habitats (i.e., marsh and coastal prairie). Wooded habitats occur as upland forest on salt domes and Pleistocene islands (1.2%); coastal hardwoods on relict beach ridges (i.e., cheniers), man-made levees, and spoil banks (4.5%); and bottomland hardwood and swamp forest along river systems (0.5%) (Gosselink et al. 1979).

The term "chenier" is French meaning "place of oak", referring to the upland areas occurring in the marshland of the Chenier Plain that are typically covered with a coastal live oak (*Quercus virginiana*) plant community. These ridges are of three basic origins: barrier islands, river mouth accretions, and relict beach ridges. The origins of the cheniers are explicable in terms of the fluctuation in Mississippi River delta sedimentation. Repeated occurrence of heavy sediment influx as the Mississippi River advanced westward, followed by lapses in the supply as the Mississippi River retreated eastward, created a series of cheniers as the shoreline periodically advanced gulfward. To a lesser extent, the Sabine, Calcasieu, and Mermantau rivers are contributors of sediment during chenier ridge formation (Taylor et al. 1995). Fluctuations of mud and sand supply to this region of the Gulf coast may also reflect periods of high and low floods in the Mississippi drainage, as well as delta shifts (Spearing 1995). Cheniers lie landward of primary beach dunes, up to a distance of about 20 km inland from the coast (Fig. 1). Ridges of southwest Louisiana generally trend east-west and have similar alignment as the present shoreline; some ridges have multiple crests and swales (Taylor et al. 1995). They range from 30–500 m in width, from a few centimeters to more than 3 m in elevation, and may extend coastwide for distances of 55 km or more without interruption (Russell and Howe 1935, Byrne et al. 1959).

In Louisiana, the associated plant community in its natural condition is most often a forest dominated by live oak and hackberry (*Celtis laevigata*). Chenier ridges in Texas, however, are often grasslands or shrub thickets that only locally support oak vegetation (Texas Bureau of Economic Geology 1976). According to Cocks (1904, 1907), Palmisano (1970), and W. Barrow (pers. obs.), other woody plant species that typically coexist on these ridges include water oak (*Quercus nigra*), red mulberry (*Morus rubra*), toothache-tree (*Zanthoxylum clava-herculis*), pecan (*Carya illinoensis*), green ash (*Fraxinus pennsylvanica*), common persimmon (*Diospyros virginiana*), bumelia (*Bumelia lanuginosa*), Chinese tallow (*Sapium sebiferum*), and honeylocust (*Gleditsia triacanthos*). The understory consists primarily of deciduous holly (*Ilex decidua*), yaupon (*Ilex vomitoria*), cherry laurel (*Prunus caroliniana*), sweet acacia (*Acacia farnesiana*), blackberry (*Rubus* sp.), swamp dogwood (*Cornus drummondii*), green hawthorn (*Crataegus viridis*), palmetto (*Sabal minor*), and Carolina wolfberry (*Lycium carolinianum*), and numerous vines such as greenbrier (*Smilax* spp.), grape vine (*Vitis cinerea*), Carolina moonseed



FIGURE 1. Aerial view of Hackberry Ridge, a forested chenier complex (relict beach ridges), in Cameron Parish, LA. Hackberry (*Celtis laevigata*) is the dominant canopy tree. Cattle ranching is the primary land use practice.

(*Cocculus carolinus*), poison ivy (*Toxicodendron radicans*), rattan-vine (*Berchemia scandens*), trumpet-creeper (*Bignonia radicans*), virginia creeper (*Parthenocissus quinquefolia*), and ladies eardrop-vine (*Brunnichia cirrhosa*). Epiphytes such as Spanish moss (*Tillandsia usneoides*), resurrection fern (*Polypodium polypodioides*), and numerous species of mosses (e.g., *Cryphaea* spp. and *Thuidium* spp.) and lichens (e.g., *Usnea florida* and *Physcia* spp.) are patchily distributed and can be locally common (Cocks 1907, Reese 1984). As in other maritime forests, much of the plant species diversity is a result of the woody, smaller-statured species of the understory.

#### IMPORTANCE OF THE CHENIER PLAIN AS A STOPOVER AREA FOR NEARCTIC-NEOTROPICAL MIGRANTS

Historically, the landscape of this region has been recognized as one of the most important physiographic areas to migratory birds in North America (Gauthreaux 1971, Lowery 1974, Sprunt 1975, Bellrose 1976, Gosselink et al. 1979, Moore et al. 1993). Although forests were not originally extensive in the Chenier Plain, by reason of their geographic position they play a

key role in the nearctic-neotropical bird migration system. At least 63 species of migratory birds regularly use these wooded habitats prior to, or immediately after, crossing the Gulf of Mexico. The spring-migration period in the Chenier Plain extends from late February through May with peak numbers occurring between mid-April and early May (Fig. 2). Migrants are found in coastal forests somewhat erratically in March and then on a regular, almost daily basis in April and the first half of May (Gauthreaux 1971, Lowery 1974).

In spite of the difficulty in crossing an ecological barrier as large as the Gulf of Mexico, many trans-Gulf migrants continue flight inland and make landfall to the north of the Chenier Plain (Lowery 1945, Gauthreaux 1971). Intuitively, one would not expect the evolutionary strategies of trans-Gulf migrants to develop such that migrants would have to land along the coast since this would leave no room for error if the flight becomes difficult. The greater expanses of forest found farther inland would also appear to provide more suitable habitat for *en route* migrants than is available in the Chenier Plain. The "coastal hiatus" (Lowery 1945, 1951) and the days of few migrants encountered in the chen-

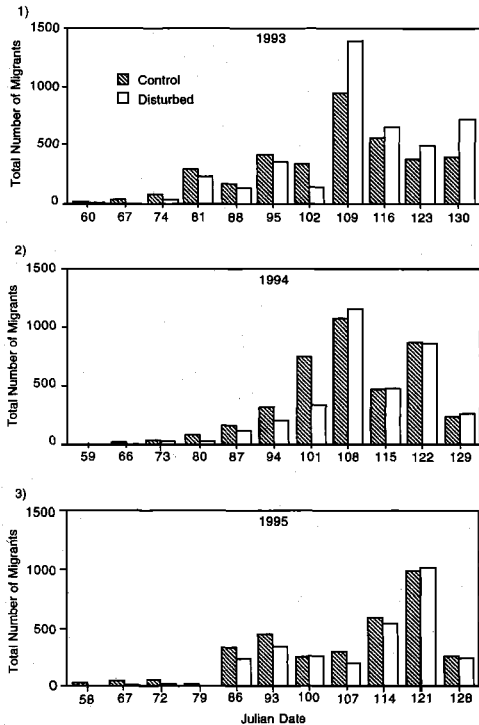


FIGURE 2. Comparison of total number of nearctic-neotropical migrants using control and disturbed plots during 12 weeks across three study sites in the Chenier Plain during 1993, 1994, and 1995.

iers, plus the few repeat birds between years (W. Barrow, unpubl. data), suggest that during the spring-migration period cheniers are crucial only at certain, rather infrequent occasions, and then only for individuals. However, due to the restricted spring-migration periods of some migratory species through the Chenier Plain (Lowery 1974; W. Barrow, unpubl. data), the infrequent occasions that migrants depend on cheniers could potentially impact large numbers of individuals of declining species. Furthermore, cheniers may be used to a greater extent by fall migrants, which travel southwest across the Chenier Plain (Able 1972), perhaps using cheniers as habitat corridors.

We can begin to determine the importance of cheniers as stopover habitat from radar technology, which provides the percentage of *en route* trans-Gulf migrants using cheniers. Gauthreaux (1971) revealed that during advantageous weather conditions (fair skies and southerly winds) about 10% of migrants flying across the Gulf of Mexico in spring land in the Chenier Plain at locations south of Lake Charles, Louisiana. However, during adverse weather conditions (hard rain and/or northerly winds), as many as

80% of individuals in a trans-Gulf flight alight in the wooded uplands of this region. Able (1972), also using radar facilities in Lake Charles, Louisiana, noted that trans-Gulf flights were less frequent during autumn migration, but the Chenier Plain was heavily used by birds moving southwest along the Louisiana and Texas coasts. These southwest flights across the Chenier Plain result in concentrations of fall migrants in chenier habitats that are similar to those observed during unfavorable weather conditions during spring migration (W. Barrow, unpubl. data).

Because of events that are occurring in the tropics, namely human population growth and subsequent development of the Gulf coastal plain, the Chenier Plain will likely play an even greater role in the conservation of the nearctic-neotropical migration system. Consider the following: nearctic-neotropical migrants need to accumulate large amounts of fat prior to crossing the Gulf, or any large ecological barrier. During the next decade, staging areas in Central America and Mexico will face an increasingly greater risk of degradation (Parker 1994). As key staging areas are disrupted, the effective width of the Gulf of Mexico will increase as a consequence of these land-use changes along the southern margins of the Gulf or at sites as yet unidentified. If migrants are prevented from depositing adequate fat stores prior to Gulf crossing, cheniers and human-created habitats may provide increasingly important feeding stations *en route*.

#### HISTORICAL CHANGES IN HABITAT STRUCTURE AND COMPOSITION

Habitats within the Chenier Plain have gained or lost area in response to natural processes, human-induced disturbances, or both. Wind and wave disturbance from hurricanes can reduce chenier habitat, especially when the vegetative cover has been altered. In addition, the forces that created the cheniers of Louisiana and Texas (sediment influxes and lapses due to a shifting Mississippi River delta) are no longer in effect today. Control structures were built during the 1950s to prevent further diversion of the river's main outlet and the subsequent westerly discharge of sediment. Without these control structures, it has been predicted that the Mississippi River would have changed its course to flow through the Atchafalaya River approximately twenty years ago (US Department of the Interior 1978). In addition, the net subsidence rate for the land in the Chenier Plain is about 1.7 cm per year (Gosselink et al. 1979). Subsidence of cheniers will likely proceed until their burial under marsh deposits becomes general everywhere



FIGURE 3. Aerial view of Peveto Woods, a chenier forest remnant, in Cameron Parish, LA. Disruptive land use practices evident on this chenier are private homesteads, sand mining pits, an industrial plant, highway and road development, and conversion of forest cover to pasture. Invasive exotic plants and coastal erosion are also a concern on this chenier.

to the north of coastal beaches. The exposure of water cover in the Chenier Plain increased 35% from 1956 to 1988 (National Wetlands Research Center Map 93-02-027). The subsidence and erosion normally associated with the northern Gulf coast are thus no longer being offset by the influx of sediment from the Mississippi River. Coastal lands, including cheniers, are or will be disappearing as long as subsidence and erosion continue to prevail along the northern Gulf coast.

Many recent changes in the Chenier Plain landscape have resulted directly from the influence of human settlement and exploitation (Fig. 3). Because cheniers are the only well-drained ground in the region, these areas are the most suitable for human development. The cheniers of Louisiana and Texas have been occupied by Europeans for over 200 years, and consequently, the factors that have affected the suitability of these habitats to nearctic-neotropical migrants are numerous. Some examples include residential and industrial development, recreational camps, conversion to croplands and pasture, oil and gas exploration and development (canals, levees, and spoil banks), water control structures, controlled burning, white-tailed deer

(*Odocoileus virginianus*) over-browsing (indirectly caused by humans), feral goat and cattle grazing, mosquito abatement programs, highway development, invasion of exotic plants, and coastal subsidence and sea-level rise.

The cumulative impact of the above factors have resulted in a disruption of the wooded habitat that originally occurred on the cheniers. Significant portions of most original chenier habitat have been cleared for agriculture (cotton), cattle production, and human settlement since the 1800s. Cattle ranchers prefer some tree cover for shade, although the understory vegetation remains altered. More recent losses are related to the population growth that is occurring throughout the Gulf coast region. Between 1952 and 1974 in the Chenier Plain, natural chenier forest, upland forest (primarily on salt domes), and swamp forest declined by approximately 1,250 ha, 1,250 ha, and 396 ha, respectively. Cropland (primarily rice) and urban areas had a net increase of 10,059 ha during the same period. Inland open water increased by 28,026 ha, representing the largest net area change during these 23 years (Gosselink et al. 1979). Continued expansion of the human population in this area will probably occur at the expense of the few re-

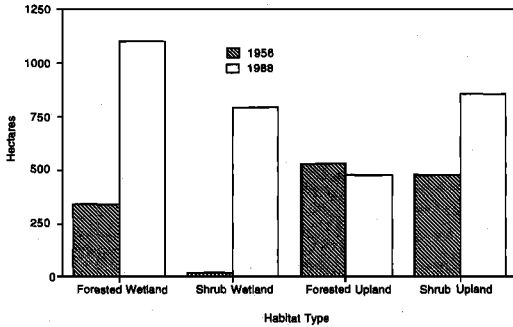


FIGURE 4. Changes in wooded habitats from 1956 to 1988 in the Chenier Plain. Data are from National Wetlands Research Center Map 93-02-027.

maintaining chenier forests and upland agricultural areas.

Despite the loss of chenier forests, there has been an overall increase in woody vegetation since 1956 (Fig. 4). This increase in woody vegetation can be primarily attributed to the creation of human-made levees and spoil banks that support woody vegetation and the natural succession of abandoned agricultural fields. Canals form an extensive network throughout the marshland of the Chenier Plain. Levees and spoil banks (20–75 m in width) associated with these canals support upland vegetation previously absent from the coastal marsh landscape. The total length of canal networks in the Chenier Plain is greater than 8,715 km (Gosselink et al. 1979). As of 1979, these habitats already occupied more than 2% of the total area of the Chenier Plain, an area greater than that of the beach, swamp-forest, upland-forest, and salt-marsh habitats combined (Gosselink et al. 1979). The vegetation on the levees and spoil banks is largely comprised of an exotic species, Chinese tallow. The shrub (dominated by sapling tallow trees) and forested wetland (dominated by older tallow tree thickets) categories in Fig. 4 illustrate the rapid expansion of this exotic plant during the past 40 years.

Of particular interest is the ability of Chinese tallow to invade the coastal prairie even though native trees in the area are restricted to relict beach ridges and riparian sites. The greater ability to survive occasional droughts on the heavy clay soil of the Chenier Plain is thought to be an important factor to its successful invasion (Bruce 1993). Tallow trees can facilitate the creation of new woodlands (Bruce et al. 1995). Bruce (1993) found that tallow trees improve germination conditions for other woody plant species in the coastal prairie. Depending on the age of the woodland, the understory and co-dominates of tallow woodlands in the Chenier

Plain typically consist of dense stands of tallow saplings, wax myrtle (*Myrica cerifera*), yaupon, hackberry, oak species, groundsel bush (*Baccharis halimifolia*), and various species of vines. It remains uncertain whether colonization of tallow woodlands by native species will eventually replace tallow, or if tallow will retain dominance (Bruce et al. 1995).

The remaining "natural" coastal forest is suffering from reduced overstory regeneration, elimination of understory vegetation, altered plant species composition, and spread of exotic plants. This is, in part, the result of cattle ranching. Essentially all (>95%) cheniers in Louisiana are grazed by cattle (M. Mattox, Soil Conservation Service, pers. comm.), causing the forested landscape on cheniers to be comprised of a structurally non-diverse mosaic of forested habitats that is park-like in appearance. Although cattle density and grazing schedules vary among cheniers, the general ranching system that has developed over the past two centuries is one of seasonal movement of cattle between cheniers/marshland and the coastal prairies to the north. Cattle graze cheniers and adjacent marsh from about 15 October through 15 May. The cattle are then transported to the coastal prairies north of the cheniers and marshland to graze during the summer months, where insects are less of a problem. Cattle movement among the cheniers is facilitated by more than 400 km of cattle walkways that traverse marshland and connect or nearly connect the isolated, parallel ridges. These walkways are small earthen levees about 1–3 m in elevation that were constructed across marshland during the 1920s and continue to be maintained today (Gosselink et al. 1979). Cattle grazing and pasture development have been shown to negatively affect breeding (Mosconi and Hutto 1983, Taylor 1986, Taylor and Littlefield 1986; J. Rappole, unpubl. report to USFWS), *en route* (Mueller and Sears 1987), and wintering nearctic-neotropical migrants (Saab and Petit 1992). However, in the absence of American Bison (*Bison bison*; Newcomb 1961), cattle may be instrumental in maintaining the dispersal and distribution (through differential grazing) of certain plant species important to migrants, such as honeylocust and *Acacia* spp. (Vines 1960, Fowells 1965).

A natural disturbance that may influence plant distribution is fire. Although not well-documented, chenier forests may have been subject to frequent fires. Fire played an important role in the maintenance of the adjacent plant communities, coastal prairie and marshland. How alteration of the historic fire regime, by use of controlled burning programs, has influenced

plant species composition in chenier forests is not known to us.

On the more heavily disturbed cheniers, plant species composition usually shifts to a habitat dominated by nonindigenous species. Examples include chickasaw plum (*Prunus angustifolia*), cherokee (*Rosa laevigata*) and McCartney roses (*Rosa bracteata*), prickly pear cactus (*Opuntia lindheimeri*), chinaberry (*Melia azedarach*), Japanese honeysuckle (*Lonicera japonica*), privet (*Ligustrum* spp.), Chinese wisteria (*Wisteria sinensis*), lantana (*Lantana camara*), salt cedar (*Tamarix sallica*), and Chinese tallow (Cocks 1904, Palmisano 1967; W. Barrow, pers. obs.). All of these species are exotic except prickly pear cactus and chickasaw plum. How the encroachment of these exotic plants have affected the native plant species is unknown.

Restoration efforts to create historic plant communities in the Chenier Plain may be impractical because we are not even certain of the true pre-settlement plant species composition and relative abundance. A review of the trees recorded in the original land surveys of the Chenier Plain needs to be investigated (see Sicama 1971, Delcourt and Delcourt 1974). One species that apparently was common in the past is the toothache-tree (Hine 1906, Cocks 1907, Billings 1909). Hine (1906:68) considered this species "a common tree that grows in the locality" (referring to the Chenier Plain). Billings (1909:1) described a chenier in Cameron Parish, Louisiana, as "partially covered with a growth of stunted trees, principally *Xanthoxylum clava-herculis*." Cocks (1907:6) described the region of the Chenier Plain in the vicinity of the Calcasieu river as "practically treeless, with the exception of some thickets of *Bumelia lanuginosa* and *Xanthoxylum clava-herculis*, and a few stunted specimens of hackberry on the ridges." The toothache-tree may have been a "keystone species" in the Chenier Plain. For instance, Hine (1906:68) described an insect outbreak specific to this plant: "a scale insect, *Ceroplastes cirripediformis*, is abundant on this tree, in fact, some trees are literally covered with it. The scale is rather large and must secrete a great deal of honeydew, for insects of different orders were attracted in large numbers. Many species not seen anywhere else were plentiful enough here to make them appear common." The large and diverse insect community associated with the toothache-tree would make it quite valuable to insectivorous birds during migration (Hine 1906). Many *en route* migrants also eat the fruit of toothache-trees in the fall (Vines 1960). An investigation into the apparent demise of this plant species seems warranted.

## MICROHABITAT USE BY *EN ROUTE* MIGRANTS

Extrinsic benefits, such as wind conditions and location along evolutionarily programmed migration routes, will initially determine the use of some stopover habitats (Hutto 1985b, Moore and Simons 1992a, Moore et al. 1993). Although numerous studies have examined habitat use and foraging ecology of nearctic-neotropical migrants on their temperate breeding grounds, relatively few studies have examined the patterns of resource exploitation during migration. The quality of stopover habitats affects the physiological, behavioral, and population ecology of Rufous Hummingbirds (*Selasphorus rufus*), and perhaps other species as well (Russell et al. 1994). Selections between habitats at stopover sites have largely been attributed to food availability (Bibby et al. 1976, Martin 1980, Bairlein 1983, Bibby and Green 1983, Graber and Graber 1983; Hutto 1985a,b; Martin 1985, Lindström 1990b, Winker et al. 1992a). Previous *en route* studies suggest that migrants select among habitats during stopover (Hutto 1981, 1985a,b; Moore et al. 1990, 1993; Moore and Simons 1992a, Winker et al. 1992a), especially for structurally complex habitats (Moore et al. 1993). Parnell (1969) reported that several species of migrants in North Carolina during spring migration exploit sites similar to those of their breeding grounds. Parnell (1969) concluded that, for certain species, the selection of certain areas within a habitat (microhabitat use) might be more important than habitat choice.

Within-habitat selection during stopover is poorly understood (Moore et al. 1993), but food availability appears to also determine microhabitat use (Hutto 1985b). Graber and Graber (1983) studied foraging movements and food availability of spring-migrant warblers in Illinois. They found that differences in migrants' foraging patterns depended on the abundance of available arthropods. At stopover sites with low prey abundance, migrants foraged rapidly and were unsuccessful in finding enough food to permit weight gain. Most birds departed low-prey sites after one day. It may be critical for migratory birds to find one or more stopover sites with high prey availability along the migratory pathway (Graber and Graber 1983, Myers et al. 1987).

Loria and Moore (1990) demonstrated that fat-depleted Red-eyed Vireos (see Appendix for scientific names of all birds) in the Chenier Plain following trans-Gulf migration diversified their foraging behavior and expanded their use of microhabitat space. In another study at the same site, Moore and Yong (1991) used a predator-

exclosure experiment to demonstrate that trans-Gulf migrants can depress prey abundance during stopover in chenier forests. Migrants foraging during periods of high migrant abundance were not able to replenish energy reserves as rapidly as migrants using the woodlands during periods of low migrant abundance (Loria and Moore 1990). If species that typically forage in the understory are forced to shift to the canopy or ground for food because of understory alterations, how does the increased abundance of potential competitors in these different microhabitats affect their ability to replenish energy reserves?

#### FIELD STUDIES OF HABITAT USE IN CHENIER FORESTS

We studied *en route* landbird migrants at three locations situated approximately 60 km apart in the Chenier Plain: (1) Grand Chenier, Cameron Parish, Louisiana; (2) Hackberry Ridge, Cameron Parish, Louisiana; and (3) Smith Point, Chambers County, Texas. The study areas at each site consisted of a "disturbed" plot with reduced understory (i.e., structure, species composition, or both) primarily due to cattle grazing, paired with an adjacent "control" plot, where the understory had not been as affected. The fact that plots were adjacent is important, because adverse weather conditions or depleted energy reserves may restrict the movements, and thus the range of habitats available to migrants during stopover (Moore et al. 1993). Plots were 1.5 ha in size and were flagged at 25-m intervals to facilitate the running of strip transects and the collection of behavioral observations. A stratified random sampling scheme was used to identify differences in habitat structure between disturbed and control plots at each site. At each sampling location, we recorded the presence or absence of four habitat types within an imaginary cylinder with a diameter of 1 m: near-ground (0–0.5 m), understory (>0.5–2 m), subcanopy (>2–10 m), and canopy (>10 m). Control plots at Hackberry Ridge and Grand Chenier had a higher proportion of vegetation in the understory and subcanopy; proportion of canopy vegetation was similar between plots (Fig. 5). At Smith Point, no difference in understory structure occurred between plots; proportion of subcanopy vegetation was greater in the control plot (Fig. 5). Occurrence of grass and herbaceous cover was greater in the disturbed plot at Grand Chenier, greater in the control plot at Smith Point, and similar in the two plots at Hackberry Ridge (Fig. 5). Plant species diversity was reduced at all three disturbed plots (W. Barrow, unpubl. data).

To investigate how structural differences in

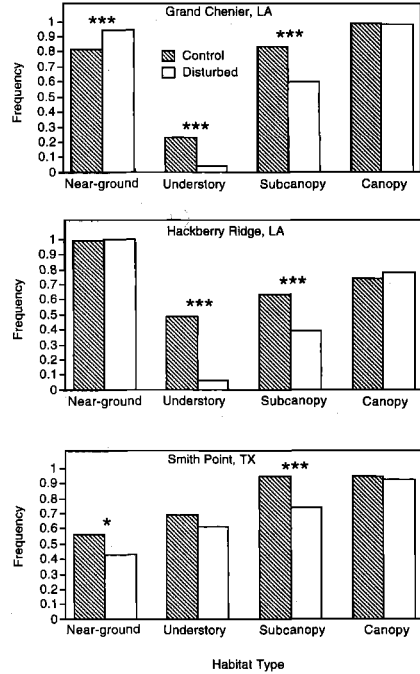


FIGURE 5. Comparison of proportion of habitat types between control and disturbed plots at three study sites. Significant differences of Z tests are indicated by asterisks (\* =  $P < 0.05$ , \*\*\* =  $P < 0.001$ ). Sample sizes in control and disturbed plots at Grand Chenier, Hackberry Ridge, and Smith Point are 213, 184; 336, 336; and 149, 165, respectively.

vegetation affect nearctic-neotropical migrants during stopover, migrants were first collectively examined and then separated into height guilds (ground, understory, and subcanopy/canopy) and substrate guilds (fruit/flower, air space, leaf litter, live foliage, suspended dead foliage, and bark). Height guild composition was determined by examining the height distributions of each species from the transect data sets in "control" plots. If at least 50% of the observations of a species were 0 m, 0–2.5 m, or >2.5 m from the ground, the species was placed in the ground, understory, or subcanopy/canopy guild, respectively (Appendix). Substrate guild composition was determined from observations on foraging migrants. Species predominantly foraging on one type of substrate (i.e., having at least 50% of their foraging observations on one substrate) were placed into their appropriate guild (Appendix). Classification into the "suspended dead foliage" guild required at least 50% of leaf-directed prey attacks to be on suspended dead leaves. Using strip transect data, Wilcoxon signed-rank tests were performed to compare the abundance of all migrants, early migrants, and



TABLE 1. COMPARISON OF MIGRANT USE OF CONTROL AND DISTURBED FOREST PLOTS (MEAN  $\pm$  SD PER 1.5 HA) IN THE CHENIER PLAIN DURING SPRING 1993, 1994, AND 1995

Migrants	Grand Chenier		Hackberry Ridge		Smith Point	
	Control	Disturbed	Control	Disturbed	Control	Disturbed
1993	N = 74		N = 74		N = 69	
All migrants	9.7 $\pm$ 10.8*	6.5 $\pm$ 8.8	10.5 $\pm$ 12.4	18.1 $\pm$ 30.1	8.0 $\pm$ 10.0	10.5 $\pm$ 13.5*
Early migrants	4.4 $\pm$ 4.2*	2.9 $\pm$ 5.4	4.4 $\pm$ 4.7*	3.6 $\pm$ 5.4	7.6 $\pm$ 10.3	9.7 $\pm$ 14.5
1994	N = 67		N = 67		N = 75	
All migrants	9.5 $\pm$ 10.6*	4.2 $\pm$ 6.6	11.2 $\pm$ 14.8	13.1 $\pm$ 20.3	10.6 $\pm$ 13.8	16.4 $\pm$ 22.0*
Early migrants	2.4 $\pm$ 2.9*	0.4 $\pm$ 0.8	2.7 $\pm$ 2.6*	1.5 $\pm$ 2.7	4.2 $\pm$ 6.7	6.4 $\pm$ 9.8*
1995	N = 73		N = 73		N = 75	
All migrants	9.6 $\pm$ 14.2*	4.6 $\pm$ 8.1	11.1 $\pm$ 14.1	12.2 $\pm$ 18.3	3.0 $\pm$ 5.0	6.6 $\pm$ 10.6*
Early migrants	4.7 $\pm$ 8.4*	1.6 $\pm$ 3.7	6.7 $\pm$ 10.6*	4.3 $\pm$ 8.5	1.8 $\pm$ 3.7	4.5 $\pm$ 10.0*

\* =  $P \leq 0.05$ 

substrate guilds in control versus disturbed plots at each site for spring migration 1993–1995. The high daily turnover rate of migrants using chenier forests (mean recapture rate = 7.6%;  $N = 5,146$  initial captures in 1993) enabled differences in bird abundances between contrasting plots to be calculated on a daily basis. Significance was defined as  $P < 0.05$  for all single tests of hypotheses. To avoid simultaneous inference from multiple tests of hypotheses, alpha levels were adjusted for each guild using the sequential Bonferroni method (Rice 1989, Beal and Khamis 1991). Family-wide alpha levels for the substrate guilds was thus  $P < 0.008$ .

Foraging studies were conducted at all sites to supplement abundance data. The frequencies with which birds used plant species on the Chenier Plain were obtained from quantified data on their foraging behavior. Plots were traversed systematically, and foraging maneuvers according to Remsen and Robinson (1990) were recorded. A variety of other habitat parameters, including the height, substrate, and plant species on which the last maneuver occurred, were also recorded. To ensure that foraging data were gathered from separate individuals, we did not collect data on two consecutive individuals of the same species and sex in a given 25-m<sup>2</sup> grid during a data gathering period (1–3 hrs per d).

Plant species use versus availability comparisons were made to determine which plant species were preferred by migrants. Vegetation was randomly sampled to obtain relative frequency and relative basal area coverage for each plant species at each site. We made these comparisons only in the control plots because they most closely resemble natural conditions; our interest here was to make recommendations for restoration of chenier forests.

#### ABUNDANCE OF MIGRANTS IN DEGRADED VERSUS INTACT HABITAT

Two of the questions this study seeks to answer that relate to restoration planning are: (1) what does the impact of understory degradation have on the abundance of trans-Gulf migrant landbirds using chenier forests, and (2) which plant species and structural features of chenier forests are preferred by migrants during stop-over.

#### All migrants

No consistent trends were detected across sites for all migrants (Table 1). All migrants were more abundant in control plots each year at Grand Chenier and in disturbed plots each year at Smith Point (Table 1). Grand Chenier control plots had greater vegetation in the understory and less grass/herbaceous ground cover compared to Smith Point. The reduced vegetation near the ground may have afforded better foraging opportunities for those species that search for prey living in the leaf litter, whereas greater understory vegetation provided perch sites for migrants that forage within this stratum. Factors determining the greater use of the disturbed plots at Smith Point remain unclear. Understory vegetation structure was similar between plots; however, the species composition was different: cherry laurel dominated the control plot, and yaupon and *Rubus* sp. were dominant understory plants in the disturbed plot. Because of secondary compounds present in the foliage of cherry laurel, this plant harbors few leaf-chewing insects (W. Barrow, unpubl. data). This may account for the greater use of the disturbed plots at Smith Point when all migrants were combined.

### Early migrants

When transect data from all sites were combined, distributions of migrants shifted from control to disturbed plots during the migratory season (Fig. 2). Early migrants, individuals detected before the second week of April (primarily Ruby-throated Hummingbird, White-eyed Vireo, Yellow-throated Vireo, Northern Parula, Yellow-throated Warbler, Black-and-white Warbler, Louisiana Waterthrush, and Hooded Warbler), were significantly more abundant in control plots at the two sites having significantly more understory vegetation in control plots (Fig. 2; Table 1). Food may be especially limiting during early spring and late fall migration (Martin and Karr 1990), suggesting that undisturbed habitats may be critical for early migrating species. Disturbed plots were predominantly used when migrants reached their greatest densities (Fig. 2). High concentrations of energy-depleted birds may cause competition for food resources at stopover sites (Moore and Yong 1991). Competition would explain the increased densities of birds in disturbed plots during the peak of migration, but not the greater use of disturbed habitats than intact habitats, as occurred in 1993. The cause of this apparent switch in proportional use of disturbed versus control plots during spring migration is unclear, but it may be due to reduced bird detectability in control plots after leaf-out; to the late influx of ground foraging birds (e.g., thrushes), which may prefer more open habitats (see below), or to short-term changes in environmental conditions (e.g., food resources). We feel the latter may play an important role at our study sites. If food became more abundant in the disturbed (vs. control) plots during the late migration period, then the change in bird abundance can be explained fairly well. Disturbed plots at two of our sites may provide more food resources during the time that migrant numbers were greater in the disturbed plots. At Hackberry Ridge, the disturbed plot had a higher density of hackberry trees than the control plot; at Grand Chenier, the disturbed plot had a greater density of honeylocusts than control plots (W. Barrow, unpubl. data). Both tree species can provide an extraordinary abundance of food resources from middle April through early May. An annual outbreak of lepidopteran (Geometridae) larvae occurs on Hackberry Ridge and is specific to hackberry trees (Moore and Yong 1991; W. Barrow, pers. obs.). The flowers of honeylocust are used by several nectarivorous species; the foliage apparently harbors an abundance of insects (e.g., honeylocust pod gall midge larvae [*Dasineura gleditchiae*]; W. Barrow, unpubl. data), as it is a preferred

plant by feeding migrants (see below). The relations between food resource phenology, abundance, and habitat switching by *en route* migrants at our study sites provide an excellent opportunity for further research.

### Foraging substrate guilds

Species that are specialists on certain foraging substrates are affected by alterations to vegetation of stopover habitats. Abundance of nectarivorous and frugivorous migrants was significantly greater in control plots versus disturbed plots at Grand Chenier (1993 and 1994) and Hackberry Ridge (all years; Table 2), the two sites with a reduced understory (Fig. 5). Grazing has been shown to negatively affect frugivores and nectarivores in temperate regions (Bock et al. 1984, Taylor 1986, Knopf et al. 1988) as well as tropical areas (Saab and Petit 1992). Because very few birds breed on cheniers (Moore and Yong 1991), nectarivorous and frugivorous migrants may play key roles in pollination and seed dispersal (Herrera 1984, Saab and Petit 1992). Species foraging on suspended dead leaves also were more abundant in control plots at Grand Chenier (all years) and Smith Point (1993 and 1994; Table 2). This would be expected because the denser understory and subcanopy vegetation in control plots would be more likely to trap dead leaves as they fall from the canopy. Ground foraging migrants that feed on insects and arthropods of the forest's leaf litter were more abundant on the control plot at Grand Chenier all years (Table 2). The reduced amount of grasses and herbs near the ground was apparently more suitable for those species that rummage through the leaf litter on the forest floor at this site. No consistent significant trends were observed across sites for the remaining substrate guilds (Table 2). Canopy vegetation remaining in the disturbed sites apparently provided sufficient foraging substrates for bark and live-foliage gleaners.

### BIRD MOVEMENTS WITHIN AND BETWEEN HABITATS

We can use measures other than bird density to evaluate habitat quality during the nonbreeding season (Winker et al. 1995). Based on observations of arriving trans-Gulf migrants in coastal woodlots, Moore et al. (1993) suggested that migrants "rank" alternative habitats during an initial exploratory phase shortly after arrival. Our results support this hypothesis. Nets were randomly placed in 25 m × 25 m blocks throughout the study sites. Number, arrangement, size, height and orientation of the nets were the same in control and disturbed plots and remained the same among years. Each day, we

TABLE 2. COMPARISON OF MIGRANT USE IN CONTROL AND DISTURBED FOREST PLOTS (MEAN  $\pm$  SD PER 1.5 HA) IN THE CHENIER PLAIN DURING SPRING 1993, 1994, AND 1995

Substrate guilds	Grand Chenier		Hackberry Ridge		Smith Point	
	Control	Disturbed	Control	Disturbed	Control	Disturbed
1993	N = 74		N = 74		N = 69	
Leaf litter	2.2 $\pm$ 3.4*	1.8 $\pm$ 3.7	1.2 $\pm$ 2.7	4.4 $\pm$ 10.4*	1.4 $\pm$ 2.8	2.6 $\pm$ 4.4
Dead foliage	0.5 $\pm$ 1.0*	0.2 $\pm$ 0.5	0.2 $\pm$ 0.3	0.2 $\pm$ 0.4	0.4 $\pm$ 0.9*	0.3 $\pm$ 0.7
Bark	0.2 $\pm$ 0.5	0.2 $\pm$ 0.6	0.3 $\pm$ 0.5	0.4 $\pm$ 1.1	0.4 $\pm$ 0.8	1.0 $\pm$ 2.0
Live foliage	1.1 $\pm$ 2.0	1.3 $\pm$ 2.8	0.6 $\pm$ 1.4	1.5 $\pm$ 3.3	0.5 $\pm$ 1.2	0.9 $\pm$ 2.3
Fruit/flower	0.8 $\pm$ 1.8*	0.2 $\pm$ 0.8	3.1 $\pm$ 6.1*	1.4 $\pm$ 3.0	0.2 $\pm$ 0.5	0.1 $\pm$ 0.4
Air space	0.1 $\pm$ 0.3	0.3 $\pm$ 0.7	0.2 $\pm$ 0.8	0.4 $\pm$ 1.3*	0.1 $\pm$ 0.2	0.2 $\pm$ 0.9
1994	N = 67		N = 67		N = 75	
Leaf litter	1.9 $\pm$ 2.7*	1.0 $\pm$ 2.4	1.6 $\pm$ 2.9	2.4 $\pm$ 4.7	1.2 $\pm$ 2.3	2.7 $\pm$ 6.2
Dead foliage	0.6 $\pm$ 1.2*	0.0 $\pm$ 0.2	0.3 $\pm$ 0.7	0.3 $\pm$ 0.8	1.2 $\pm$ 2.5*	0.8 $\pm$ 2.2
Bark	0.3 $\pm$ 0.6*	0.1 $\pm$ 0.2	0.2 $\pm$ 0.5	0.3 $\pm$ 0.6	0.8 $\pm$ 1.5	1.0 $\pm$ 1.8
Live foliage	1.8 $\pm$ 3.3*	0.7 $\pm$ 1.7	0.9 $\pm$ 2.3	1.5 $\pm$ 3.3	0.7 $\pm$ 2.0	1.6 $\pm$ 3.6
Fruit/flower	0.9 $\pm$ 2.0*	0.2 $\pm$ 0.6	2.5 $\pm$ 4.1*	0.7 $\pm$ 1.6	1.0 $\pm$ 2.1	1.6 $\pm$ 4.0
Air space	0.1 $\pm$ 0.3	0.3 $\pm$ 0.6	0.2 $\pm$ 0.4	0.3 $\pm$ 0.5	0.1 $\pm$ 0.4	0.7 $\pm$ 1.3*
1995	N = 73		N = 73		N = 74	
Leaf litter	1.3 $\pm$ 2.3*	0.3 $\pm$ 0.9	1.5 $\pm$ 2.8	1.5 $\pm$ 3.0	0.5 $\pm$ 1.2	1.5 $\pm$ 2.9*
Dead foliage	0.4 $\pm$ 0.7*	0.1 $\pm$ 0.3	0.3 $\pm$ 0.7	0.2 $\pm$ 0.4	0.1 $\pm$ 0.3	0.1 $\pm$ 0.4
Bark	0.4 $\pm$ 0.7*	0.1 $\pm$ 0.4	0.3 $\pm$ 0.5	0.3 $\pm$ 0.7	0.2 $\pm$ 0.4	0.7 $\pm$ 1.6
Live foliage	1.9 $\pm$ 4.0	1.2 $\pm$ 2.8	1.2 $\pm$ 2.8	1.5 $\pm$ 2.9	0.4 $\pm$ 1.4	0.7 $\pm$ 1.7
Fruit/flower	1.1 $\pm$ 2.3	0.9 $\pm$ 2.0	2.2 $\pm$ 4.0*	1.3 $\pm$ 3.7	0.2 $\pm$ 0.8	0.2 $\pm$ 0.7
Air space	0.3 $\pm$ 0.7	0.3 $\pm$ 0.7	0.2 $\pm$ 0.6	0.3 $\pm$ 0.7	0.1 $\pm$ 0.5	0.4 $\pm$ 0.9

\* =  $P \leq 0.008$ .

attempted to have the same net exposure in both control and disturbed plots. Capture data were standardized to captures per 500 net hours. At Smith Point, 63% of birds known to have moved between plots (based on recaptures and observations of color-marked individuals) switched from the disturbed to control plot (one-tailed binomial test,  $P = 0.01$ ,  $N = 87$ ). Worm-eating Warblers, specialists on suspended dead leaves, and Hooded Warblers, subcanopy foragers, frequently moved from disturbed plots to control plots (75%,  $P = 0.07$ ,  $N = 12$ ; and 64%,  $P = 0.21$ ,  $N = 14$ , respectively). In contrast, Black-and-white Warblers, bark specialists, moved between plot types with equal frequency (47%,  $P = 0.81$ ,  $N = 17$ ). At Grand Chenier, 67% of migrants in 1993 (only year with sufficient sample size) known to have moved between plots settled in the control plot (one-tailed binomial test,  $P = 0.01$ ,  $N = 31$ ). These data are further evidence that birds use the disturbed and control plots differently. The Hackberry Ridge site was not included in this analysis because the plots along this ridge were separated by nearly 1 km.

The length of time that migrants stay in an area is another method to evaluate habitat quality. A comparison of recapture rates between contrasting habitats is a way to measure this (Winker et al. 1995). The paired plots situated along Hackberry Ridge had the greatest contrast

in vegetative structure between disturbed and control plots. Woody vegetation at the Hackberry Ridge disturbed plot is essentially nonexistent below the canopy layer (primarily hackberry trees). Several subcanopy-height trees are present (mostly honeylocusts), leaf litter is reduced, and grass/herbaceous cover is abundant. The structure is not unlike an urban "park." At Hackberry Ridge, the proportion of birds recaptured on the control plot was higher than the disturbed plot for ground guilds in 1993 and 1994 and subcanopy/canopy guilds for all years; recapture rates were similar between the plots for understory birds (Fig. 6). Apparently, most species in our understory guild were able to shift their foraging activity down to the ground (e.g., Gray Catbird, Kentucky Warbler, Common Yellowthroat, and Hooded Warbler) or up to the canopy (e.g., Canada Warbler and Yellow-breasted Chat); others may have moved to more suitable habitat (e.g., Worm-eating Warbler; Chen 1996). No differences in recapture rates were found between contrasting plots at the other two study sites; this is not very surprising because the sample sizes were low and the habitat differences were much less than at Hackberry Ridge.

Future research on the suitability of chenier forests as stopover sites should focus on rates of

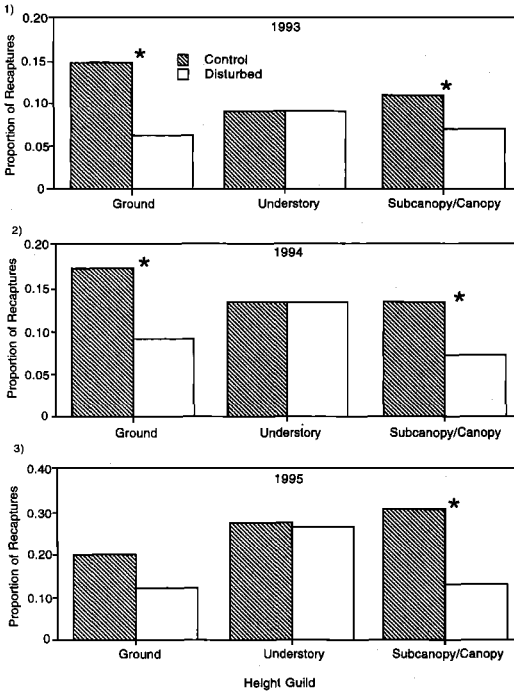


FIGURE 6. Comparison of proportion of recaptures per 500 net hours between control and disturbed plots at Hackberry Ridge. Significant differences of G-tests are indicated by asterisks (\* =  $P < 0.05$ ). Sample sizes of initial captures in control and disturbed plots for ground, understory, and subcanopy/canopy guilds for (1) 1993: 290, 315; 301, 147; and 785, 402; (2) 1994: 285, 243; 173, 87; and 662, 421; (3) 1995: 104, 78; 100, 27; and 215, 135, respectively.

weight gain for *en route* migrants during their stay in these contrasting vegetation conditions.

#### IMPORTANT FOOD PLANTS

Land managers interested in restoring or rehabilitating habitat for *en route* nearctic-neotropical migrants need to know which plant species are important for these birds. From observations taken on foraging migrants, plant species use versus availability comparisons were made to determine which plant species would be most beneficial for *en route* nearctic-neotropical migrants.

Chi-square goodness-of-fit tests, performed on all plant species constituting more than 5% of the available vegetation at each site, indicated that the use of plant species by migrants differed significantly from the availability of plant species at each site ( $P < 0.001$  for all sites). Following Neu et al. (1974), Bonferroni confidence intervals were calculated to determine significant preference or avoidance of individual plant

species by migrants. All foraging analyses are from 1993 data only.

#### Understory vegetation

Shrubs common enough (i.e., constituted at least 5% of total plants on the control plots) to test statistically included yaupon (Smith Point) and deciduous holly (Grand Chenier), which were used in equal proportion to their availability by all migrants (Table 3). Yaupon was significantly preferred by understory species at Smith Point ( $P < 0.05$ ,  $N = 92$ ). Green hawthorn (Grand Chenier) was the only small tree used significantly more than available (Table 3). Cherry laurel (Smith Point) and Chinese tallow (Smith Point) were both significantly avoided by all migrants (Table 3). Understory species used cherry laurel in equal proportions to its availability ( $P > 0.05$ ), and significantly avoided Chinese tallow ( $P < 0.05$ ). Preliminary results from a study on arthropod-plant relations indicate that densities of arthropods are much lower in cherry laurel and Chinese tallow than in live oak, hackberry, and yaupon (W. Barrow and T. Spengler, unpubl. data). Cherry laurel is known to have a secondary chemical compound, prussic acid, in its foliage to deter herbivory (Vines 1960). Not surprisingly, 30% of the foraging observations occurred on the bark rather than the foliage of this tree. The mechanism deterring insects from associating with Chinese tallow is unknown, but apparently effective.

#### Canopy vegetation

Hackberry was used in larger proportion than any other plant species at both sites in which it occurred, and was significantly preferred at Grand Chenier (Table 3). However, hackberry was significantly avoided by understory species at Hackberry Ridge ( $P < 0.05$ ,  $N = 50$ ). Live oak was used in proportion to its availability at two sites, but was significantly avoided by all migrants (Table 3) at Grand Chenier and by understory species at Smith Point ( $P < 0.05$ ,  $N = 92$ ). The avoidance of both hackberry and live oak by understory species may be due to the lack of regeneration of these species. Because few live oak and hackberry saplings occur on these cheniers, foliage of these species are available only in the subcanopy/canopy stratum of the forest. The distribution of plant species on cheniers may also affect their use by foraging birds. When a habitat is primarily comprised of a single species, such as hackberry at Hackberry Ridge or live oak at Smith Point (Table 3), the benefits of foraging on the less abundant plant species may be outweighed by the costs associated with searching for uncommon or rare species. When plants are more evenly distributed

TABLE 3. SIMULTANEOUS CONFIDENCE INTERVALS FOR THE USE OF PLANT SPECIES BY NEARCTIC-NEOTROPICAL MIGRANTS AT THREE CONTROL PLOTS IN THE CHENIER PLAIN

	Expected proportion of use, $P_0$	Actual proportion of use, $P_1$	Bonferroni intervals for $P_1$
Grand Chenier N = 442			
Deciduous holly	0.070	0.088	$0.051 \leq P \leq 0.125$
Green hawthorn	0.098	0.149	$0.103 \leq P \leq 0.196^*$
Hackberry	0.151	0.253	$0.197 \leq P \leq 0.310^*$
Honeylocust	0.062	0.075	$0.040 \leq P \leq 0.109$
Live oak	0.254	0.133	$0.089 \leq P \leq 0.178^*$
Vine	0.092	0.145	$0.098 \leq P \leq 0.192^*$
Other	0.178	0.085	$0.049 \leq P \leq 0.123^*$
Hackberry Ridge N = 303			
Hackberry	0.446	0.429	$0.354 \leq P \leq 0.504$
Honeylocust	0.020	0.109	$0.062 \leq P \leq 0.156^*$
Live oak	0.057	0.053	$0.019 \leq P \leq 0.087$
Red mulberry	0.186	0.119	$0.070 \leq P \leq 0.169^*$
Vine	0.173	0.211	$0.149 \leq P \leq 0.273$
Other	0.119	0.079	$0.038 \leq P \leq 0.120$
Smith Point N = 274			
Cherry laurel	0.140	0.086	$0.043 \leq P \leq 0.133^*$
Chinese tallow	0.101	0.040	$0.009 \leq P \leq 0.071^*$
Live oak	0.464	0.460	$0.380 \leq P \leq 0.539$
Yaupon	0.263	0.325	$0.250 \leq P \leq 0.400$
Vine	0.013	0.066	$0.026 \leq P \leq 0.105^*$
Other	0.017	0.022	$0.000 \leq P \leq 0.045$

N = Total number of foraging migrants recorded.

\*  $P < 0.05$ .

throughout a habitat, such as at Grand Chenier (Table 3), avian foraging preferences may become more readily apparent.

Plants producing fruit or flowers during the spring migration season appear to be especially important to several migrant species. For instance, although red mulberry was significantly avoided at Hackberry Ridge when all species were combined (Table 3), some species fed almost exclusively on the fruit of this tree. Red mulberry fruit was eaten in 35 out of 50 independent foraging observations taken on Gray Catbirds and 14 of the 31 observations on Rose-breasted Grosbeaks. The flowers of the honeylocust tree appeared to be especially important to nectarivorous species, as well as many insectivorous species. Honeylocust was the only tree significantly preferred by migrants at Hackberry Ridge (Table 3). Although honeylocust only comprised 2% of the plant community at Hackberry Ridge, more than 48% of the foraging observations for Tennessee Warblers ( $N = 103$ ), and more than 70% of the foraging observations for Baltimore Orioles ( $N = 18$ ) and Orchard Orioles ( $N = 20$ ) occurred on the flowers of this tree.

#### Vine tangles

Vines are an important habitat feature for migrants. Vines were preferred at all three sites,

with a significant preference for vines by migrants occurring at two of the three sites (Table 4). When just vine species were compared to each other, Virginia creeper was the only vine that was used significantly less than expected by migrants (Table 4). The only vine significantly preferred to other vines was Japanese honeysuckle, an exotic species (Table 4). Although grape vine was not significantly preferred by all migrants, it was used more than any other vine species. Because vines easily entrap falling dead-leaf clumps, they are also important food patches for the Worm-eating Warbler and several species in the genus *Vermivora*. Vine tangles have been previously noted as an important foraging substrate in bottomland hardwood forests for at least some species of breeding migrants (Barrow 1990, Moser *et al.* 1990, Pashley and Barrow 1992), and appear to be important for *en route* migrants as well.

#### Exotic plants

All nonindigenous trees and shrubs such as chinaberry, Chinese tallow, cherokee rose, and lantana were used less than expected by migrants. At Smith Point, the only site in which an exotic was abundant enough to test statistically, Chinese tallow was used significantly less than expected by migrants (Table 3). Invasion of ex-

TABLE 4. SIMULTANEOUS CONFIDENCE INTERVALS FOR THE USE OF VINE SPECIES BY NEARCTIC-NEOTROPICAL MIGRANTS AT THREE CONTROL PLOTS IN THE CHENIER PLAIN

Vine species	Expected proportion of use, $P_{10}$	Actual proportion of use, $P_i$	Bonferroni confidence intervals for $P_i$
Grape vine	0.529	0.451	$0.356 \leq P \leq 0.545$
Greenbrier	0.049	0.052	$0.009 \leq P \leq 0.094$
Japanese honeysuckle	0.080	0.164	$0.094 \leq P \leq 0.235^*$
Lady's eardrop	0.004	0.019	$0.000 \leq P \leq 0.045$
Poison ivy	0.016	0.047	$0.007 \leq P \leq 0.087$
Rattan vine	0.189	0.207	$0.129 \leq P \leq 0.284$
Trumpet creeper	0.042	0.056	$0.012 \leq P \leq 0.100$
Virginia creeper	0.089	0.005	$0.000 \leq P \leq 0.018^*$

N = Total number of foraging migrants recorded.

\*  $P < 0.05$ .

otic plants may pose one of the most serious threats to the integrity of chenier forests. Once permanently established, exotic organisms have only been successfully eradicated in a few expensive and labor-intensive instances (Coblentz 1990, Westman 1990). While some scientists argue that all exotics should be removed (Coblentz 1990), others suggest that the contribution of exotic species to wildlife communities should first be examined, and only those shown to severely degrade native habitats be removed (Westman 1990).

Due to their low abundance on our sites, Cherokee rose, chinaberry, and lantana need further investigation before substantive results on migrant use of these exotic species can be obtained. We have only preliminarily examined exotic plant/avian/insect relationships, and that has been restricted to the spring migration season. Exotic plants (e.g., Chinese tallow), and native plants (i.e., cherry laurel and palmetto) that are avoided by spring migrants may provide important food sources (fruit pulp, waxy epicarp) or cover for birds using these habitats in fall and/or winter.

#### SUMMARY FOR THE CHENIER PLAIN FIELD STUDY

Because the majority of forested habitats in the Chenier Plain were altered close to a century ago, the effects that this loss of stopover habitat had on neotropical landbird migrants cannot be determined. The conservation value of a chenier should thus not be compared to the original intact chenier forest type, but to the land presently surrounding them. Clearly, a disturbed forest, even one intermingled with exotic plants, is more desirable than pasture or cotton fields. As revealed in these analyses, most forest-dependent migratory birds are tolerant of at least some degradation of chenier forests during migration. However, these results show that subtle differences in vegetation composition and structure of

the understory layer of these forests can result in differential use by some *en route* migrants. Because of species-specific habitat requirements, the effect of understory reduction is not similar for all nearctic-neotropical migrants, and each condition may provide benefits for at least some species.

Cheniers with a disturbed understory were less frequently used by early migrants, dead-leaf foragers, frugivores and nectarivores, but had little or no effect on most other nearctic-neotropical migrant species. However, our study may have underestimated actual differences in habitat use by migrants. Bird detectability was greater in the open, disturbed plots, and most cheniers in the region were more heavily grazed than the treatment plots used in this study. Thus, the results from this study are probably conservative in their estimation of the effects habitat degradation has on *en route* nearctic-neotropical migrants.

Hackberry, red mulberry, honeylocust, green hawthorn, vine tangles, and other plants that fruit or flower during the spring-migration period appear to be important microhabitat features for *en route* nearctic-neotropical migrants in the Chenier Plain. Our foraging data indicate that the structure and floristics of these forests may influence the foraging opportunities available to migrants and therefore affect how successfully they can exploit these stopover habitats. Because species may specialize on different foraging substrates, stopover habitats with diverse plant communities that are able to produce a variety of nectar, catkins, fruits, and seeds, should be best equipped to produce sufficient food resources for all migratory species (Moore and Simons 1992a, Moore et al. 1993).

The decision to rehabilitate a forested stopover site depends on several factors, such as funding levels and land ownership. Otherwise, the two most important considerations are: (1)

the relative status of forest conditions in the migration pathway or landscape under consideration, and (2) the relative status of birds that may be negatively impacted by habitat disruption in the landscape under consideration. Given that the understory structure and regeneration of chenier forests has been so greatly reduced, and that several species considered here to be sensitive to understory degradation are believed to have declining population trends (Robbins et al. 1989b), restoration and rehabilitation should be a priority.

#### RESTORATION RECOMMENDATIONS AND DIRECTIONS FOR FURTHER WORK

Ultimately, the goal is to rehabilitate *en route* habitat at key stopover locations in a manner that ensures their suitability to the birds that depend on these wooded sites for food, rest, and shelter each year during spring and fall migration periods. Because of species-specific microhabitat preferences, no single restoration or rehabilitation plan will have a similar effect on all nearctic-neotropical migrants, and each management practice will provide benefits for at least some species. However, because understory vegetation is the most degraded, restoration/rehabilitation projects should concentrate their efforts on this habitat component.

#### RECOMMENDATIONS OF SPECIFIC MANAGEMENT ACTIONS FOR THE CHENIER PLAIN

Rehabilitation of coastal woodlands will depend on local involvement. Private citizens own 95% of the cheniers of Louisiana and Texas. We recommend establishment of working relationships with the Cameron Parish, Louisiana, and Chambers County, Texas, Cattlemen's Associations to discuss opportunities to modify grazing schedules that will encourage vegetative regeneration while still meeting the economic needs of ranchers. It will be important for conservationists to keep in mind that if it were not for the cattle ranching industry of southwest Louisiana, the forest remnants that are so important today may otherwise be private homesteads or petrochemical plants.

On cheniers where landowners want to restore woodlands for migratory landbirds, we recommend the following:

1. On cheniers where little or no understory exists, or where little or no regeneration is occurring, grazing pressure should be reduced until vegetation recovers. Once a chenier recovers, grazing may be allowed under constraints, preferably low-density, winter-only grazing (November 1–March 31). If the lack of understory is a result of overbrowsing by deer, the deer population should be reduced.

2. Portions of each chenier, especially the remaining, relatively intact chenier forests, should be permanently protected from deer, cattle and goats. These reserves, if strategically dispersed, could serve as seed sources as well as provide structurally complex and diverse habitat for *en route* nearctic-neotropical migrants.

3. The suitability of recent, human-created habitats (e.g., tallow woodlands, levees, and spoil banks) in the Chenier Plain needs to be evaluated. Maintenance of the vegetation types on levees and spoil banks would not replicate historic conditions, but it would provide woody vegetative cover that may compensate for upland sites that can no longer be restored or rehabilitated.

4. On degraded cheniers, we recommend re-seeding or planting trees such as live oak, hackberry, honeylocust, and red mulberry; shrubs such as yaupon, sweet acacia, deciduous holly, and green hawthorn; and vines such as poison ivy, rattan, trumpet creeper, grape, and greenbrier. Studies of habitat and plant species use during fall migration need to be conducted before a complete list of beneficial plants can be compiled.

5. Although rehabilitation is recommended for the forested cheniers, it may not be as feasible for native grasslands (i.e., coastal prairie). Most of this habitat has been converted to agriculture, pasture, or is now dominated by tallow woodlands. Research focused on habitat relations of migrants requiring grassland/prairie habitat during migration is needed.

#### RECOMMENDATIONS FOR RESTORATION AND REHABILITATION OF STOPOVER HABITATS FOR NEARCTIC-NEOTROPICAL MIGRANTS

1. Inventory all key stopover locations. Determine vegetation characteristics (i.e., plant community type) and level of disturbance.

2. Collaboration among restorationists, conservationists, researchers, and landowners is essential. Technology for restoration/rehabilitation of coastal forested habitats, including exotic plant species control, is in its infancy. Due to the considerable time, expense, and effort associated with restoration projects, we suggest that information and technological advancement from previous restoration projects be exchanged among agencies, organizations, and landowners.

3. Many questions concerning the habitat requirements of migratory birds during stopover, especially during fall, remain unanswered. A recent study by Leberg et al. (1996) suggests that water may be a limiting factor for *en route* migrants that have just crossed the Gulf. Further studies examining the importance of water sources in stopover habitats to *en route* migrants

are needed. In addition, the response of migratory birds to various restoration practices and exotic species, as well as the importance of staging areas near ecological barriers in Mexico and Central America (Parker 1994), still need to be determined.

4. Work with state and local mosquito abatement programs to develop a plan that would lessen the possibility of indirect impacts on the non-target arthropod/insect community inhabiting wooded habitats. Avoidance of aerial spraying immediately prior to and during migration is recommended.

5. Because nearctic-neotropical migrants are so diverse in their foraging strategies, structurally complex and diverse plant communities able to provide sources of both fruit and nectar during the migration seasons should be protected or established wherever possible. Encourage local communities situated in key stopover locations to landscape with native plants indigenous to the region.

6. Restoration and rehabilitation of stopover habitats depend on the development of partnerships with landowners of the region; their understanding and cooperation is essential.

In conclusion, restoration and rehabilitation of stopover habitat in the Chenier Plain, as well as

at other key stopover locations, will require the introduction of new technology, insights, and most importantly, enlightened management techniques through cooperative efforts with the local people.

#### ACKNOWLEDGMENTS

We are grateful to the Stream family in Louisiana for permission to do research on their property. Permission to do research in Texas was granted by Texas Parks and Wildlife Department through T. Tourney, Candy Abshier WMA. Stream Property Management Co., Rockefeller Wildlife Refuge, Louisiana Department of Wildlife and Fisheries, and Tennessee Gas Co. provided invaluable assistance with this study. The fieldwork was supported by Houston Audubon Society and U.S. Fish and Wildlife Service. Bill Goulet photographed and provided the aerial images of the cheniers. This study would not have been possible without the capable help of our 23 field assistants. J. Lind and S. Lind assisted with all phases of the study, especially data entry and management. V. Moseley provided several obscure reports that were cited in the manuscript. We thank F. Moore for many insightful discussions of the topic. C. Cordes, G. Gomez, R. Greenberg, K. Gutzwiller, F. Moore, D. Pashley, D. Richard, B. Vairin, and an anonymous reviewer provided many useful comments on the manuscript. We are especially grateful to N. and S. Baughman, J. and W. Erbelding, G. Nunez and family, D. Richard, and T. Tourney for use of their facilities and help with logistics.



APPENDIX. SPECIES COMPOSITION AND TOTAL NUMBER OF MIGRANTS DETECTED ON TRANSECTS AT THREE STUDY SITES FOR SPRING MIGRATION SEASONS 1993–1995

	1993	1994	1995
Black-billed Cuckoo ( <i>Coccyzus erythrophthalmus</i> ) <sup>c</sup>	8	2	0
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> ) <sup>c</sup>	105	194	161
Common Nighthawk ( <i>Chordeiles minor</i> ) <sup>c</sup>	1	1	2
Ruby-throated Hummingbird ( <i>Archilochus colubris</i> ) <sup>c,d</sup>	102	246	133
Eastern Wood-Pewee ( <i>Contopus virens</i> ) <sup>c,e</sup>	125	121	168
Acadian Flycatcher ( <i>Empidonax virens</i> ) <sup>c</sup>	29	31	10
Great Crested Flycatcher ( <i>Myiarchus crinitus</i> ) <sup>c</sup>	23	45	19
Eastern Kingbird ( <i>Tyrannus tyrannus</i> ) <sup>c,e</sup>	46	72	48
White-eyed Vireo ( <i>Vireo griseus</i> ) <sup>c</sup>	347	265	253
Yellow-throated Vireo ( <i>Vireo flavifrons</i> ) <sup>c</sup>	31	23	70
Warbling Vireo ( <i>Vireo gilvus</i> ) <sup>c</sup>	4	0	3
Philadelphia Vireo ( <i>Vireo philadelphicus</i> ) <sup>c</sup>	15	14	23
Red-eyed Vireo ( <i>Vireo olivaceus</i> ) <sup>c,g</sup>	519	424	511
Blue-gray Gnatcatcher ( <i>Poliopitila caerulea</i> ) <sup>c</sup>	216	222	120
Veery ( <i>Catharus fuscescens</i> ) <sup>a,f</sup>	84	174	91
Gray-cheeked Thrush ( <i>Catharus minimus</i> ) <sup>a,f</sup>	47	127	47
Swainson's Thrush ( <i>Catharus ustulatus</i> ) <sup>a,f</sup>	444	246	147
Wood Thrush ( <i>Hylocichla mustelina</i> ) <sup>a,f</sup>	774	501	234
Gray Catbird ( <i>Dumetella carolinensis</i> ) <sup>b</sup>	782	612	357
Blue-winged Warbler ( <i>Vermivora pinus</i> ) <sup>c,h</sup>	56	139	47
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> ) <sup>c,h</sup>	14	17	12
Tennessee Warbler ( <i>Vermivora peregrina</i> ) <sup>c,d</sup>	277	291	341
Nashville Warbler ( <i>Vermivora ruficapilla</i> ) <sup>c</sup>	1	4	0
Northern Parula ( <i>Parula americana</i> ) <sup>c</sup>	231	143	84
Yellow Warbler ( <i>Dendroica petechia</i> ) <sup>c</sup>	22	22	55
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> ) <sup>c,g</sup>	63	70	71
Magnolia Warbler ( <i>Dendroica magnolia</i> ) <sup>c,g</sup>	132	335	258
Cape May Warbler ( <i>Dendroica tigrina</i> ) <sup>c</sup>	2	3	2
Black-throated Green Warbler ( <i>Dendroica virens</i> ) <sup>c</sup>	32	87	44
Blackburnian Warbler ( <i>Dendroica fusca</i> ) <sup>c</sup>	34	16	17
Yellow-throated Warbler ( <i>Dendroica dominica</i> ) <sup>c</sup>	18	4	19
Bay-breasted Warbler ( <i>Dendroica castanea</i> ) <sup>c</sup>	45	219	121
Blackpoll Warbler ( <i>Dendroica striata</i> ) <sup>c</sup>	10	26	6
Cerulean Warbler ( <i>Dendroica cerulea</i> ) <sup>c</sup>	12	8	17
Black-and-white Warbler ( <i>Mniotilta varia</i> ) <sup>c,i</sup>	279	292	226
American Redstart ( <i>Setophaga ruticilla</i> ) <sup>c</sup>	92	181	150
Prothonotary Warbler ( <i>Protonotaria citrea</i> ) <sup>c,g</sup>	84	44	110
Worm-eating Warbler ( <i>Helmitheros vermivorus</i> ) <sup>b,h</sup>	152	224	102
Swainson's Warbler ( <i>Limnithlypis swainsonii</i> ) <sup>a</sup>	1	12	8
Ovenbird ( <i>Seiurus aurocapillus</i> ) <sup>a,f</sup>	246	291	209
Northern Waterthrush ( <i>Seiurus noveboracensis</i> ) <sup>a,f</sup>	130	119	66
Louisiana Waterthrush ( <i>Seiurus motacilla</i> ) <sup>a,f</sup>	45	6	66
Kentucky Warbler ( <i>Oporornis formosus</i> ) <sup>b</sup>	120	133	81
Mourning Warbler ( <i>Oporornis philadelphia</i> ) <sup>c</sup>	1	3	3
Common Yellowthroat ( <i>Geothlypis trichas</i> ) <sup>b</sup>	83	61	43
Hooded Warbler ( <i>Wilsonia citrina</i> ) <sup>b</sup>	464	428	296
Canada Warbler ( <i>Wilsonia canadensis</i> ) <sup>b</sup>	52	25	6
Yellow-breasted Chat ( <i>Icteria virens</i> ) <sup>b</sup>	13	3	15
Summer Tanager ( <i>Piranga rubra</i> ) <sup>c</sup>	79	63	150
Scarlet Tanager ( <i>Piranga olivacea</i> ) <sup>c</sup>	65	116	87
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> ) <sup>c,d</sup>	86	111	134
Blue Grosbeak ( <i>Guiraca caerulea</i> ) <sup>c</sup>	10	13	73
Indigo Bunting ( <i>Passerina cyanea</i> ) <sup>a</sup>	961	677	644
Painted Bunting ( <i>Passerina ciris</i> ) <sup>c</sup>	49	28	25
Orchard Oriole ( <i>Icterus spurius</i> ) <sup>c,d</sup>	301	119	157
Baltimore Oriole ( <i>Icterus galbula</i> ) <sup>c,d</sup>	77	57	92

<sup>a</sup> Ground Guild.<sup>b</sup> Understory Guild.<sup>c</sup> Subcanopy/Canopy Guild.<sup>d</sup> Fruit/Flower Foraging Guild.<sup>e</sup> Air Space Foraging Guild.<sup>f</sup> Leaf Litter Foraging Guild.<sup>g</sup> Live Foliage Foraging Guild.<sup>h</sup> Suspended Dead Leaf Foraging Guild.<sup>i</sup> Bark Foraging Guild.