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Conserving Migratory Land Birds in the New World: Do We Know Enough?

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Abstract. Migratory bird needs must be met during four phases of the year: breeding season, fall migration, wintering, and spring migration; thus, management may be needed during all four phases. The bulk of research and management has focused on the breeding season, although several issues remain unsettled, including the spatial extent of habitat influences on fitness and the importance of habitat on the breeding grounds used after breeding. Although detailed investigations have shed light on the ecology and population dynamics of a few avian species, knowledge is sketchy for most species. Replication of comprehensive studies is needed for multiple species across a range of areas.

Information deficiencies are even greater during the wintering season, when birds require sites that provide security and food resources needed for survival and developing nutrient reserves for spring migration and, possibly, reproduction. Research is needed on many species simply to identify geographic distributions, wintering sites, habitat use, and basic ecology. Studies are complicated, however, by the mobility of birds and by sexual segregation during winter. Stable-isotope methodology has offered an opportunity to identify linkages between breeding and wintering sites, which facilitates understanding the complete annual cycle of birds.

The twice-annual migrations are the poorest-understood events in a bird's life. Migration has always been a risky undertaking, with such anthropogenic features as tall buildings, towers, and wind generators adding to the risk. Species such as woodland specialists migrating

through eastern North America have numerous options for pausing during migration to replenish nutrients, but some species depend on limited stopover locations. Research needs for migration include identifying pathways and timetables of migration, quality and distribution of habitats, threats posed by towers and other tall structures, and any bottlenecks for migration.

Issues such as human population growth, acid deposition, climate change, and exotic diseases are global concerns with uncertain consequences to migratory birds and even less-certain remedies. Despite enormous gaps in our understanding of these birds, research, much of it occurring in the past 30 years, has provided sufficient information to make intelligent conservation efforts but needs to expand to handle future challenges.

Key words: breeding season management; conservation; en route bird conservation; global climate change; intratropical migration; land birds; migration; Partners in Flight; source–sink dynamics; winter population limitation.

INTRODUCTION

Prior to the 1970s, studies on the population ecology of Nearctic–Neotropical migratory land birds in the Western Hemisphere focused primarily on the breeding season. Ecology during the nonbreeding period was largely ignored, and the many studies on migration that existed focused on distribution and behavior, not species-specific demography. At that time, prevalent dogma was that North American breeders were temperate birds that spent the winter in warmer climates feeding on "excess" available resources. The infrequently expressed conservation concerns almost always focused on breeding success and its requisite habitats.

A major shift in the scientific approach to Nearctic–Neotropical migrant land birds occurred in 1977, when the Smithsonian Institution sponsored a symposium on migrant bird ecology (Keast and Morton 1980). The main lessons of this symposium were that many North American breeders spent much more time in the tropics than on the breeding grounds, that many played integral roles within tropical bird communities as members of mixed-species flocks or visitors at ant swarms, that many of these winter residents were territorial and very site faithful, and that some spent the nonbreeding season in mature forest habitats (Schwartz 1980), which were then being deforested at a rapid rate. After this symposium, our model of migration expanded from one of temperate land birds visiting the tropics to avoid harsh winters, to include birds with an evolutionary origin in the tropics using the temperate zone as a seasonal reproductive strategy. Tropical or subtropical origins for many of these land-bird groups have subsequently been supported by phylogeographic studies (Böhning-Gaese and Oberrath 2003, Steadman 2005, Milá et al. 2006, Kondo and Omland 2007, Bruderer and Salewski 2008; but see Zink 2002).

Few papers in Keast and Morton (1980) focused on conservation, but Terborgh (1980) noted that if migrant species were integral parts of tropical ecosystems rather than weedy opportunists, the destruction of the tropics through human activities could have a devastating effect on what temperate-zone ecologists had previously considered as "their" birds. He also concluded that because most of the migrants breeding throughout a vast area of North America wintered mainly in a much smaller area of Mexico and the West Indies, loss of an acre of wintering habitat could leave five to eight acres of breeding grounds devoid of migratory birds. The seed of winter limitation of migratory land-bird populations was planted.

The apparent occurrence of widespread declines of migratory bird populations in North America during the 1980s (Robbins et al. 1989) led to the development of the Neotropical Migratory Bird Conservation Plan, or Partners in Flight (PIF). It also led to a synthesis of old and new research, culminating in a broad new approach to our understanding of the demography of migratory birds (Finch and Stangel 1993, Martin and Finch 1995). In particular, the model of Sherry and Holmes (1995) showed how migratory bird populations could be regulated by factors occurring on the breeding grounds, the wintering grounds, or during migration between these sites (Fig. 1). Subsequent research has led to the realization that managers of migratory birds first must understand that migratory birds can be limited on a variety of spatial and temporal scales, and that understanding this complexity of habitat use is necessary for successful management of such wide-ranging species. This can be extremely challenging, because it involves breeding and wintering habitats that may be thousands of kilometers apart, plus the habitats needed during movements between such sites. Management of temperate-breeding migrants that winter in the Neotropics includes the entire area of a bird's annual cycle, and requires a large dose of international cooperation. This applies equally well to the lesser-studied species of the South American austral migrant system, which breed in the temperate latitudes of South American and over-winter closer to the equator (Chesser 1994, Joseph 1997, Jahn et al. 2004).

Major advances in our understanding of the ecology of migrant land birds have occurred in the past 20 years (Faaborg et al. 2010). Here we discuss how these advances may guide modern conservation practices for migratory birds and ask what questions need to be answered to improve such conservation guidelines. Because the various New World migration systems involve a thousand or more species, we recognize that
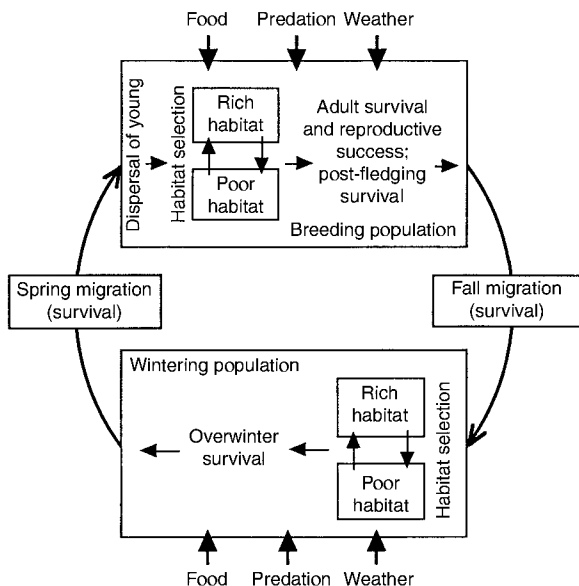
FIG. 1. The Sherry-Holmes model for understanding population limitation in migratory birds. Note that there are four major periods when populations may be limited (breeding, wintering, and two migration periods), with a number of possible limiting factors acting during each period. The figure is from Sherry and Holmes (1995), reprinted with permission of Oxford University Press.

our conservation efforts must focus on those species most in need of help. We assess PIF responses to the apparent decline in migrant birds, discuss methods of selecting target species, summarize research findings that relate to management in breeding and nonbreeding areas and while en route, and conclude by identifying critical information needs.

LESSONS FROM THE PIF RESPONSE

Like many ecological models, the model of Sherry and Holmes (1995) is both marvelously simple and unworkably complex. It shows clearly how a migratory bird population could be limited in size by factors related to the breeding season (particularly reproductive success and parental survival rates), the nonbreeding season (primarily individual survival), or during the migration between these two sites (also survival). Understanding the decline of a population as measured at a breeding site requires understanding the demographic situation at that site (Can the bird breed successfully or not?), the number of individual birds that move into and out of that site from the region where that species breeds (dispersal both to and from the study site), the factors that affect successful migration to and from the wintering grounds (including not only habitat conditions en route but factors such as tropical storms and the presence of cell towers or tall buildings), and the conditions on the wintering grounds (also involving quality and quantity of habitat, but additionally related to numbers of competing resident birds).

Even with knowledge of when and where populations are limited, applying the Sherry-Holmes model to design a conservation plan would still be complicated. For example, for nonbreeding patterns, the model assumes that we: know the wintering locations of the species in question (Remsen 2001); understand any habitat segregation by age, sex, or both (Marra et al. 1998, Marra and Holmes 2001); know the degree of mixing of populations from different breeding areas in winter sites (Rubenstein et al. 2002); and take into account the degree to which a species is site faithful from one winter to the next (Faaborg et al. 2007). A winter model also must account for variation in habitat quality, its effect on survival (Wunderle and Latta 2000, Latta and Faaborg 2001, 2002, Marra and Holmes 2001, Johnson et al. 2006), any carryover effects of the wintering grounds on reproductive success (Marra et al. 1998, Norris et al. 2004), or carryover from delayed breeding on winter survival (D. L. Morris, J. Faaborg, B. E. Washburn, and J. J. Millspaugh, *unpublished manuscript*). Studies during the breeding season have shown how conditions at a particular breeding site are affected by the surrounding landscape (Hunt 1998, Thompson et al. 2002). Additionally, information on patterns of natal dispersal of various age and sex categories of birds is necessary. En route ecology can be greatly affected by differences in weather patterns among years, so models must include climatic variation. Finally, the strength of any statements made about the causes of decline for a species within a region has a great deal to do with the linkages between regional breeding sites and wintering sites; without such linkage, it is difficult to affix regional cause and effect. Determining how and when a migratory bird species is limited is challenging but necessary when considering if conservation efforts should be made, or how to focus them.

With new data and analyses of populations done over the past 20 years, we believe that we have numerous lessons to determine which species are most in need of conservation efforts. For example, studies at the Manomet symposium (Hagan and Johnston 1992) reported diminished population sizes associated with the effects of forest fragmentation, indicating how species were lost from either a single isolated habitat block or from the smaller pieces in a series of habitat fragments (Robinson 1992), with long-distance migrants being the most sensitive to this habitat change. Birds in Rock Creek Park in Washington, D.C. (Robbins 1979), provide a classic example of how reducing the size of a forest and isolating it from other forests results in species loss. However, it was probably inappropriate to use studies covering a single or small set of sites to support the hypothesis of a global decline among migratory birds. In fact, Rock Creek Park may be more of an example of how urbanization affects birds than about fragmentation or migratory status per se.

The field of landscape ecology has provided great insight into how the landscape matrix affects conditions

in habitat fragments. However, the discovery of negative effects of habitat fragmentation concurrent with declining populations should not have resulted in acceptance of the assumption during the 1980s that migrants were showing global declines because of fragmentation. To be convincing, one must document an increase in regional fragmentation during a period of time that is concurrent with avian population declines. Additionally, one should document actual demographic patterns causing these declines and determine whether a species is declining globally or just in well-studied and often shrinking fragments. In some cases, the finding that migrants suffered most in fragmented habitats could be purely coincidental with findings of short-term declines in local populations. At the same time that many migratory birds were declining in New England (primarily due to loss of grassland and second-growth habitat but also due to maturation of fairly mature forest [Holmes and Sherry 1988]), Askins et al. (1990) suggested that forest fragmentation was becoming less of a problem in that region. While some believed that the lessons of the Manomet symposium were that we should be more objective and cautious about drawing conclusions from complex data sets (James et al. 1992), others seemed to ignore the complexity of the issues and became convinced that the proverbial sky was falling with regard to migrant land-bird populations.

The dominant evidence for widespread declines of migratory land birds came from the Breeding Bird Survey (BBS). BBS is a roadside survey throughout the United States and in parts of Canada containing roads conducted every June since 1966. BBS was designed to provide a basic index of population change over a vast area with relatively small investments in labor or materials, and BBS trends were and continue to be important information.

Unfortunately, such a massive data set can be inappropriately interpreted. Early in the discussion about migrant declines, for example, major arguments developed over how BBS data should be analyzed, with important differences in results depending upon method of analysis (James et al. 1996). Summarizing declines on various spatial scales was problematic; obviously, a 2% annual population decline that occurs throughout a species' range should be interpreted differently from the same annual decline composed of large declines in only a few regions and stable or even increasing populations elsewhere. In most declining situations, we lacked details on when and where declines occurred (Robbins et al. 1989). In many cases, declines were observed in birds that favor second-growth or early-successional vegetation; these declines presumably were a result of forest regeneration in many regions of the Eastern United States. While this is potentially problematic, the restoration of forest across New England and other regions favors many species but obviously works against all early-succession birds (Askins 2000, Hunter et al. 2001). Other analyses identified decreases in populations

during the period 1980–1988, even though those declines brought populations back to the levels that had occurred earlier (Faaborg 2002). For declines of winter residents that breed in the eastern United States (Faaborg and Arendt 1989), drought on their breeding grounds during the 1980s seemed to provide a simple explanation (Faaborg and Arendt 1992). Recent work showing correlations between long-term declines in populations of the Yellow-billed Cuckoo (*Coccyzus americanus*) and such broad climatic measures as the North Atlantic Oscillation and the El Niño Southern Oscillation suggests that climatic patterns broader than short-term drought may be important for some species (Anders and Post 2006).

Certainly, the lessons with regard to interpretation of BBS data include: (1) necessity of spatial and temporal precision about the declines that are occurring; (2) care in generalizing patterns and grouping species together; and (3) recognition that the BBS is not a good monitoring tool for all species. Interestingly, Rich (2006) showed that many experts think that only 46% of North American land-bird species are adequately censused by the BBS. Many of the species not covered by BBS are boreal birds, whose breeding range does not include enough roads for this survey technique. Others suffer from problems with breeding phenology or detectability during the June census period.

Considering these caveats, can BBS data tell us the current abundance of migrant bird populations on the breeding grounds? Given the percentage annual decline occurring for some species during the 1980s, a continuing trend would have meant these species would soon be approaching extinction. Instead, a realistic evaluation of migrant bird species on the BBS website shows only a few species with continued widespread declining populations across most or all of their ranges; most species exhibit complex patterns geographically, with regions where populations are increasing and others where decreases occur. The BBS patterns of decline in migrant forest birds were probably overstated; subsequent analyses have shown that grassland birds have the most consistent and widespread declines of any avian group over the life of BBS (Peterjohn and Sauer 1999). The BBS data are what they are, and in many ways BBS served its purpose by providing evidence of large-scale patterns, even if humans sometimes misinterpreted them. On a more philosophical note, ecologists have started to accept that changes in abundance and distribution are part of nature; however generated, they are inevitable. This does not mean that we should shrug them off for all species. The challenge is to focus conservation efforts where they are most needed and most likely to be effective.

PIF identifies species of conservation concern through species prioritization scores. Population trends are only one of four or five criteria contributing to a species' global or regional prioritization score; the higher of two threat scores based on breeding (from the BBS) or

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┌──────────────────────────────────────┐
│ Large-scale, biogeographic           │
│ effects                              │
│                                      │
│ Abundance and demographics of        │
│ songbirds, cowbirds, and predators vary│
│ at a geographic scale.               │
│    ┌───────────────────────────────────┐
│    │ Landscape-level effects          │
└────│                                  │
     │ Land cover and use affect the abundance│
     │ of breeding birds, predators, and nest │
     │ predation, and cowbirds and      │
     │ brood parasitism.                │
     │    ┌──────────────────────────────────┐
     │    │ Habitat and local effects       │
     └────│                                 │
          │ Habitat type, patch size, proximity│
          │ to edge, and forest management affect│
          │ predator and cowbird activity, nest│
          │ predation, and brood parasitism.│
          │    ┌─────────────────────────────┐
          │    │ Nest-site effects          │
          └────│                            │
               │ Characteristics such as nest type,│
               │ height, and concealment affect the│
               │ probability of predation and parasitism.│
               └─────────────────────────────┘
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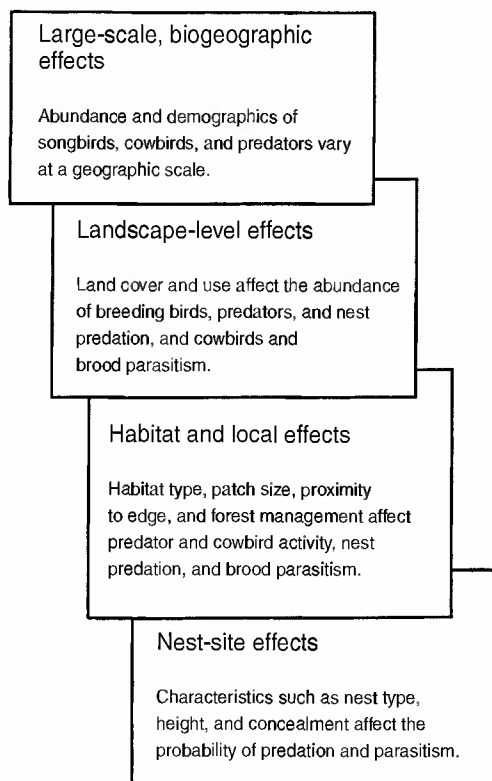
FIG. 2. Conceptual model of factors at multiple spatial scales that affect reproductive success in songbirds. This highlights the complexity of modern management decision-making, as one must take into account all spatial factors in making local management decisions. (The figure is adapted from Thompson et al. [2002: Fig. 1].)

nonbreeding is used in the prioritization. Because we know little quantitatively about winter habitat use for most migrant species, we are concerned about the information used to assign nonbreeding season priority scores as part of the PIF assessment process (Rich et al. 2004). This requires knowledge of where a bird actually spends the winter and what habitats are required. In general, one would expect that species using disturbed winter habitats might suffer less than those that require primary forests (Stotz et al. 1996, Latta and Baltz 1997), although this has yet to be adequately tested.

As we assess how management for migratory birds should proceed and what further research is needed, we must accept the difficulty associated with managing the (literally) moving targets that are migrant land birds. In many cases, the decision about where population limitation occurs for a species is just an educated guess. We believe that more reliable knowledge is needed on what is limiting populations of migrant land birds to have an acceptable level of confidence in our management decisions. However, we acknowledge that conservation planning and day-to-day management decisions must proceed with current knowledge. So, in the next section, we review how current knowledge can help

guide breeding, wintering, or en route management activities, whether we have a clear understanding of which part of the annual cycle is limiting a species, or we are making a hypothesis about such limitation.

RECENT RESEARCH IMPLICATIONS
FOR BREEDING-SEASON MANAGEMENT

Conservation strategies

The current era of non-game bird management began in the 1970s with a focus on understanding and providing the proper vegetative structure for breeding. As such, bird management has always focused primarily on habitat management. Each species has a particular habitat type that it chooses from among those available; provision of such preferred or high-quality habitat is necessary to support the species. However, what we have learned in the past three decades is that providing the proper vegetation structure in the proper landscape context may be critical to certain demographic processes and to providing enough habitat regionally to maintain a viable population. Building from the idea of minimum areas of occurrence in fragmented environments, we now know that management must take into account factors on a variety of spatial scales to be successful.

The idea that landscape-level habitat patterns could affect management was proposed long before PIF (Wiens 1973, Johnson 1980). More recently, Thompson et al. (2002) provided a multiscale perspective on how a modern management approach can be developed for a species (Fig. 2). It builds from nest-site effects, which involve nest-site selection and possible predation and parasitism, to habitat and local effects, which involve such factors as patch size, proximity to edge, and characteristics of the matrix between habitat patches. These local effects are influenced by landscape-level factors that deal with regional patterns of habitat cover and how these affect predators and brood parasites (Chalfoun and Martin 2007). Finally, they suggest that large-scale biogeographic factors are important, as these are related to distribution and abundance of a species, and its predators and parasites, across its range. The actual habitat area parameters that are suitable for a species depend upon a variety of factors related to location within the species range, dispersal patterns, susceptibility to predation and/or parasitism, and other factors.

Thompson et al. (2002) present their model as a hypothesis based on existing studies, but the components of the model have been accepted by most conservationists. However, there still are many unknowns involved in this approach (Faaborg et al. 2010). In fact, most of the model's parameters have not been quantified for any species across its breeding range. Certainly, at least in North America, there are good measures of reproductive success for many species, showing that locations are producing young at a rate that exceeds parental mortality, qualifying these locations as potential source populations. Unfortunately,

most young disperse from their natal area, which makes their survival and future reproduction difficult to study. As far as we know, there are no good field data verifying an actual source–sink dynamic. Even information about dispersal distances is limited. Tittler et al. (2006) estimated dispersal distances in the Wood Thrush by looking for lagged (one-year) spatial autocorrelations of bird abundances on BBS routes over time, but their model is based on unproven assumptions about the effect of dispersal patterns on regional populations, and lacks measurements of actual bird movement. In addition, survival rates of juveniles that are dispersing are very difficult to track; while some studies of post-fledging behavior have recorded survival rates of young as high as 0.70 up to the time of fall migration (Fink 2003), most show much lower rates. This still leaves several periods (autumn migration, first winter survival, and spring migration) that must affect first-year survival.

We also know that habitat edge effects can be critical on a local scale, but that responses to edge vary by species and can be heavily dependent upon landscape composition. The Ovenbird (*Seiurus aurocapilla*) seems to show strong edge avoidance in much of the Midwestern United States, with individuals avoiding edge by as much as 300 m in habitat fragments (Van Horn et al. 1995) and by well over 100 m in heavily forested landscapes (Wallendorf et al. 2007). On the other hand, some species that appear to be sensitive to patch size also respond positively to edge, perhaps because of the increased vegetation density that characterizes edge. Edge responses also vary regionally, such that Ovenbirds in central Canada are found in much smaller forest fragments and closer to the edge than elsewhere in their range (Burke and Nol 2000, Mazerolle and Hobson 2003). Obviously, knowledge of response to edge must be incorporated into management goals.

As we attempt to understand recent avian population trends in fragmented habitats, we need to think about the timing of events important to populations. Although many researchers seem comfortable with regional source–sink scenarios, we have little information supporting the actual existence of such dynamics in almost all species. For example, recent work on the persistence of forest birds in fragments has shown that the birds often are successful later in the breeding season (Fink 2003; D. L. Morris, J. Faaborg, B. E. Washburn, and J. J. Millspaugh, *unpublished manuscript*), so that source-based "rescue" of populations is less needed. Whereas these species often have shown widespread negative responses to habitat fragmentation such that they may occur only in relatively large habitat patches, it is important to understand how these populations maintain themselves. For most species, we have no idea what size of habitat is required to reach the threshold of source population.

Finally, recent work has shown that some species spend a major part of the breeding season in a habitat other than that used for nesting. In the eastern United States, fledglings of a variety of species move into different habitat upon attaining independence (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006), and sometimes adults use different habitats during or after nesting (Vega Rivera et al. 1998, 1999, Pagen et al. 2000). In western North America, the occurrence of molt-migration in some species results in migration from the nesting grounds to a molting area farther south but still in the temperate zone (Pyle 1997, Carlisle et al. 2005). Recent work suggests that some of these apparent molt-migrants actually breed in two locations, with a first brood produced in the known breeding area of temperate North America, then a second brood produced in the western Mexico sites that were previously thought to be only for molt (Rohwer et al., *in press*). To develop breeding season management plans, we must be aware of the full geographic scale of both breeding and post-breeding habitat.

Research priorities for the breeding season

The problems discussed above support and augment the general research goals noted by the PIF Research Working Group (Donovan et al. 2002). This group advocated the need for experimental habitat manipulations, long-term studies, and regional studies that are well replicated in both time and space. We concur, but note that the current funding climate makes development of such studies difficult. The general science funding agencies for the federal governments of the United States and Canada will support research that has conservation implications only if the work also constitutes cutting-edge science. Many management studies require tests of the conservation relevance of recently discovered ecological patterns across spatial or temporal scales; the repetitive nature of such studies often reduces their novelty and chances of federal support, particularly with low overall science funding rates. It is also worth noting that the U.S. National Science Foundation once announced a panel that was to focus only on proposals related to conservation biology, but this panel never was able to gain its own funding and quickly disappeared. A new effort is needed to develop funding from private, state, and federal agencies for the kinds of research we advocate here, i.e., long-term, replicated studies of migratory species during the different phases of their annual cycle.

The regional subdivisions of federal agencies sometimes inhibit research approaches focused across the extent of species breeding ranges. At least one model program that would have accomplished the goals of consistency in protocol and extensive coverage of the breeding grounds, both spatially and temporally, was developed by a federal science agency, the BBIRD program of the USGS, but this poorly funded program was terminated after agency review several years ago. Few states are large enough to have the distribution of habitats that would allow landscape-level approaches,

and few state agencies have funding for research. Canada supports the majority of populations of many Nearctic–Neotropical migrant songbirds and shorebirds, and has landscape patterns extensive enough to successfully allow for the evaluation of broad-scale questions there (Bayne and Hobson 1997, Hobson and Bayne 2000, Hobson et al. 2002, Schmiegelow and Mönkkönen 2002, Hannon and Drapeau 2005, Rempel et al. 2007). We strongly encourage major evaluation and advocacy for funding priorities focused on breeding and post-breeding North American migrant birds so that we can provide the best science-based conservation possible.

Conservation of Wintering Habitat

Conservation strategies

Management of wintering habitat for migratory birds must focus on maintenance of sites that support high annual survival and abundance of these birds. Ideally, the provisioning of enough such sites will ameliorate problems associated with low habitat quality that delay the initiation of spring migration and potentially reduce survival during migration and reproductive success on the breeding grounds (Marra et al. 1998).

To identify high-quality sites, ideally one must measure long-term survival rates and physical condition of wintering birds in differing habitats. This requires an intensive study over several years and has been done for only a few species (Holmes et al. 1989, Wunderle 1995, Wunderle and Latta 2000, Latta and Faaborg 2001, 2002, Latta 2003, Johnson et al. 2006). The American Redstart (*Setophaga ruticilla*) provides a model system for winter ecology based on studies in Jamaica by Richard Holmes, Tom Sherry, Peter Marra, and others starting in 1986. These researchers have shown how male dominance forces females into lower-quality habitats (Marra et al. 1998, Marra 2000), which results in delayed initiation of spring migration, which, in turn, has a reproductive cost for females (Marra et al. 1998, Marra and Holmes 2001, Reudink et al. 2008). The fact that females are forced into the lowest-quality habitat could help explain skewed sex ratios in breeding populations (Sherry and Holmes 1996), especially if there is not enough habitat to support wintering females and facilitate successful spring migration. Many studies of warbler species show some evidence of sexual habitat segregation on the wintering grounds (Lynch et al. 1985, Lopez Ornat and Greenberg 1990, Parrish and Sherry 1994, Wunderle 1995, Sherry and Holmes 1996, Marra et al. 1998, Wunderle and Latta 2000, Latta and Faaborg 2001, 2002, Komar et al. 2005), and for these species aspects of the redstart model probably apply. Yet, many species have not been adequately studied and others do not show sexual dimorphism on the wintering grounds, show little or no evidence of sexual segregation by habitat, or have wintering strategies that are not as site-based as those of the territorial redstart. For these

hard-to-track species, researchers must develop alternative models.

Some species seem to be exceedingly mobile either within or between winters. For example, the Chestnut-sided Warbler (*Dendroica pensylvanica*) moves throughout the winter, tracking changes associated with seasonality within the tropics (Greenberg 1984). Other species, such as Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Yellow-rumped Warbler (*Dendroica coronata*) may be abundant in a particular site some years, but absent in others (Latta et al. 2003, Faaborg et al. 2007). Such an opportunistic strategy makes determination of possible limiting conditions for such species very difficult for the researcher or manager. Because banding is integral to understanding patterns of long-term habitat selection in the winter, to date we have been able to make statements about habitat selection and quality in the winter only for those species that are site faithful enough to allow us to track individuals within their habitats and to estimate survival rates (Wunderle 1995, Latta and Faaborg 2001, 2002, Dugger et al. 2004, Johnson et al. 2006). In at least one case, roosting behavior may allow such measures (Smith et al. 2008).

As information becomes available on the demography of wintering migrants, we must better understand linkages that occur between breeding and wintering grounds (Fig. 3). Recent progress with such information through the use of stable isotopes has been made, although it is possible that this technique will not achieve the precision desired (Hobson 2005). However, Rubenstein et al. (2002) showed how Black-throated Blue Warblers (*Dendroica caerulescens*) from northern breeding populations tended to winter in Cuba and Jamaica and those from southern breeding populations wintered in Hispaniola and Puerto Rico. Similarly, Kelly et al. (2002) demonstrated leap-frog migration among western breeding populations of the Wilson's Warbler (*Wilsonia pusilla*). Isotopic connectivity maps have also recently become available for American Redstart (Norris et al. 2006) and Yellow Warbler (*Dendroica petechia*; Boulet et al. 2006). These studies indicate that the patterns of linkage between breeding and wintering sites are fairly general (eastern breeding birds use the eastern part of the wintering range, etc.). However, one study, using isotopes, has shown that Black-throated Blue Warblers in local habitats in winter have come from widely separated parts of the breeding range, suggesting considerable mixing of populations (Rubenstein et al. 2002). Similarly, Hobson et al. (2004) used isotopic techniques to identify Bicknell's Thrush (*Catharus bicknelli*) in wintering populations in the Dominican Republic from previously unknown breeding sites.

Finally, management and conservation of winter habitat for Nearctic–Neotropical migrants could preserve breeding habitat for tropical residents and intratropical migrants, and, in South America, winter habitat for austral migrants. Such multifold benefits to man-
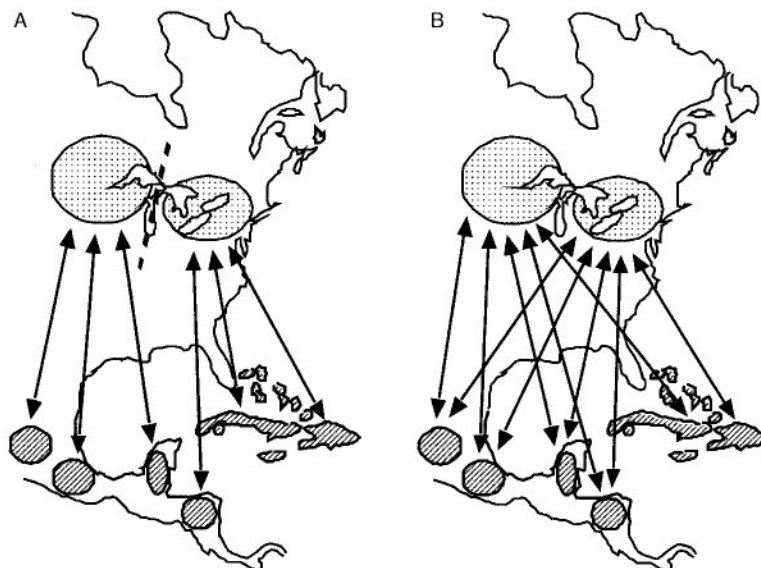
FIG. 3.   Hypothetical patterns of migratory connectivity for a long-distance migrant that breeds in eastern North America and winters in Mexico, Central America, and the West Indies. In panel (A), migratory connectivity is moderately high, whereas in panel (B) connectivity is low and breeding populations are highly mixed on the wintering grounds. The figure is from Webster and Marra (2005), reprinted with permission of Johns Hopkins University Press.

agement efforts are not always highlighted to potential funding agencies, yet are attractive and tangible arguments for funding such management efforts or refuge preservation.

Research priorities during the winter season

Most recent work on migrant land birds on their wintering grounds was done during the 1990s, mainly in the West Indies. The only sustained long-term, community-wide monitoring program we know of is that of Faaborg, Arendt, and Dugger in Puerto Rico (Faaborg et al. 2007). Latta and collaborators work in a variety of natural and anthropogenic habitats in Hispaniola, at cenotes in the Yucatan Peninsula, and in riparian habitats of Mexico. The Holmes-Sherry-Marra group continues its long-term Jamaican research focusing on American Redstart, but also on Black-throated Blue Warbler and Ovenbird (Holmes et al. 1989, Marra et al. 1998, Marra and Holmes 2001, Norris et al. 2004, Studds and Marra 2005, 2007, Brown and Sherry 2006a, b, 2008, Johnson et al. 2006, Studds et al. 2008). Other studies in the Caribbean, such as those in Cuba (Wallace et al. 1996), the Virgin Islands (Askins et al. 1992), Puerto Rico (Smith et al. 2008), and the Bahamas (Currie et al. 2005a, b) have been of shorter duration. Less work has been done on a community-wide basis on the Central and South American mainland, notwithstanding important early studies published in Keast and Morton (1980), a community-wide survey by Gram (1998) in Mexico, and some recent work on the wintering grounds of threatened/endangered species such as the Golden-cheeked Warbler (Rappole et al. 1999, 2003), Cerulean Warbler (*Den-*

droica cerulea; Hamel et al. 2004, Colorado et al. 2008), Southwestern Willow Flycatcher (*Empidonax trailli extima*; Koronkiewicz et al. 2006, Sogge et al. 2007), Kirtland's Warbler (*Dendroica kirtlandi*; Wunderle et al. 2007), and Bicknell's Thrush (Rimmer and McFarland 2001).

We need widespread assessment of which species spend the winter in which habitats and what the demographic consequences are of that habitat occupancy across the wintering range. Intensive studies using color-marked birds have the potential to tell us much about the conservation value of many types of native and anthropogenic habitats, and offer opportunities to simultaneously determine population trends for permanent resident species that often also are of great concern (Latta et al. 2005). Collections of feathers from captured birds for genetic and stable isotope studies could provide information on potential linkages between breeding and wintering range (or the lack thereof; Smith et al. 2003). Such assessment must be of sufficient intensity and of long enough duration to deal with the annual variation that may be inherent in migratory birds. The Institute of Bird Populations (IBP) recently has developed a wintering monitoring and assessment scheme called Monitoreo de Sobrevivencia Invernal (MoSI) that is designed to answer many of these questions, including the linkage problem, but because it depends on scarce mist-net recaptures, results are likely to be of value only when pooled across regions, decreasing greatly its applicability to local sites, local conditions, and species conservation. There is concern that MoSI results will present us with many of the problems associated with BBS data, in particular an inability to identify the
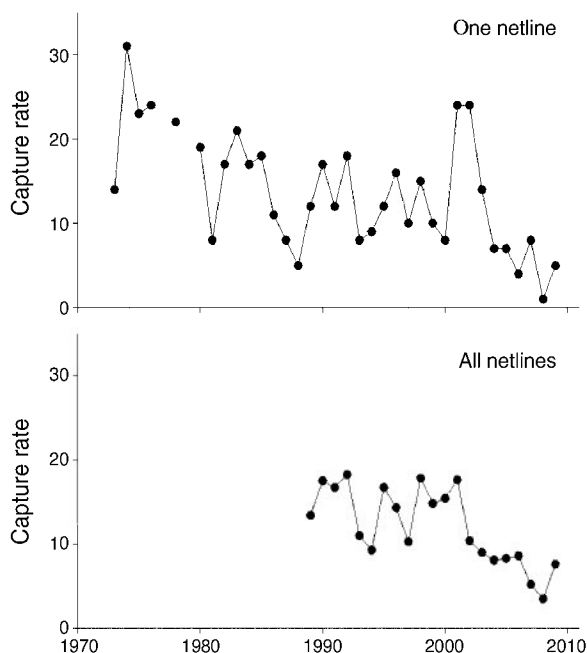
FIG. 4. Long-term declines in capture rates of winter resident birds (primarily winter resident warblers) from Guánica Forest, Puerto Rico. All netlines involved sixteen 12-m nets erected end-to-end and operated for three consecutive days from dawn to dark in the same location in January. The top figure shows capture rates for a single netline operated from 1973 through 2009 (except for 1977 and 1979); the lower figure shows the mean capture rate per netline for seven netlines (1989), eight netlines (1990), and nine netlines (1991–2009), all operated in the same location during this period. For details on methodology, see Dugger et al. (2004) or Faaborg et al. (2007). Over 75% of captures were Black-and-white Warbler, Ovenbird, and American Redstart, all of which showed population declines over this period.

habitats and geographic areas where problems are occurring when negative population trends are revealed.

Details of winter habitat use by austral migrants in South America are still poorly understood. Indeed, if the winter ecology of most Nearctic–Neotropical migrants has and continues to be a "black box," that of austral migrants is much more so; information for austral migrants lags decades behind that of most Nearctic–Neotropical migrants. Even without detailed information, however, it is intuitive that preservation and management of winter habitat for Nearctic–Neotropical migrants can often have simultaneous benefits for nonmigratory tropical species and austral migrants.

Doing extensive research across the wintering range of Nearctic–Neotropical migrants will require a major investment of funds for research. In recent years, several million U.S. dollars have been invested annually in the Neotropical Migratory Bird Conservation Act through the U.S. Fish and Wildlife Service, with 75% of this targeted for Latin American projects. This fund has recently become available for Canadian researchers. The U.S. funds currently have to be matched 3:1 with funds

or in-kind support from other nonfederal sources. Although research and monitoring are listed within the guidelines as activities that are supported by the Act, an examination of the funded proposals suggests little funding in the area of basic research (information available online).[24] This is disappointing and paradoxical given the vast effort and funds devoted to other conservation and management programs throughout Canada and the United States, and the simultaneous advances in capacity building and community education that often accompany field research activities in the tropics (Latta and Faaborg 2009). The U.S. Fish and Wildlife Service and the Canadian Wildlife Service should consider funding a short but intensive (and geographically extensive) assessment of winter migrant distributions, over-winter survival, habitat quality, and stable isotope studies, so that we can determine winter distributions, optimal habitats, and migratory connectivity between breeding and wintering populations of Neotropical migrants.

We need numerous studies on the ecology of wintering migrants that equal the quality of those listed earlier, but we need them to cover a broader range of species, habitats, and geography. The long-term monitoring study of Faaborg, Arendt, and Dugger (Faaborg et al. 2007) has shown some frightening patterns of decline in captures of winter residents (almost exclusively warblers), including a general decline in a single netline operated since 1973 and a major decline over the past eight years in samples including nine netlines annually (Fig. 4). The two most common species (Black-and-white Warbler (Mniotilta varia) and Ovenbird) have declined to <20% of their original abundances. Documenting these declines is much easier than trying to explain them. While some of the decline for migrants may be correlated with rainfall on their breeding grounds (Dugger et al. 2004), the decline of many permanent resident Puerto Rican bird populations suggests that general ecological conditions in the Guánica Forest are deteriorating. The strongest decline in recent years coincides with the spread of West Nile Virus (WNV) across the breeding range of these birds, but warblers in general are not considered to be sensitive to WNV. Perhaps Global Climate Change has moved the winter range of these species closer to the breeding range, which would be most pronounced in Puerto Rico because it is the eastern limit of wintering birds in the Caribbean (Terborgh and Faaborg 1980). Without similar studies across the wintering grounds it is difficult to understand if the Puerto Rico declines are due to local or range-wide factors. Of course, if these declines have occurred range wide, any studies initiated after the year 2000 are of questionable value because they may not show the natural abundance of these wintering birds before recent declines.
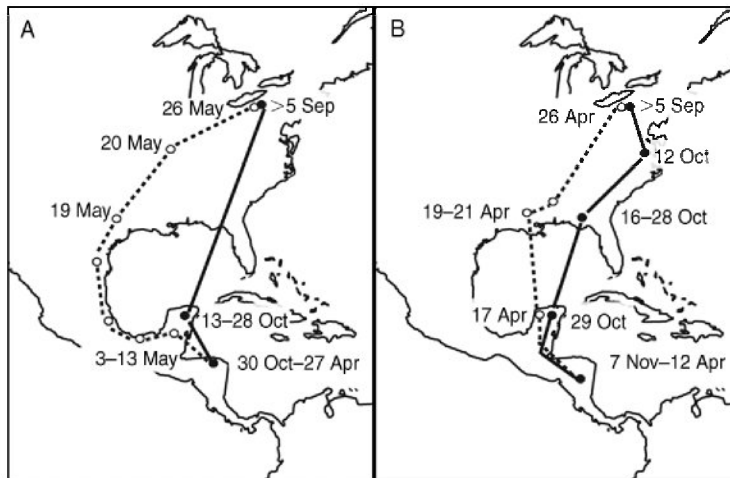
FIG. 5. Movement patterns and movement rates for two Wood Thrush individuals, as determined by geolocators carried by these birds from their breeding grounds to their wintering grounds and back (Stutchbury et al. 2009). These figures were provided by Bridget Stutchbury and are reprinted with her permission.

CONSERVATION ALONG MIGRATION ROUTES

Conservation strategies

In late summer or early autumn, most of the forest-dwelling species in North America leave temperate breeding grounds, traveling thousands of kilometers in uncertain weather over ecological barriers (e.g., the Gulf of Mexico), stopping at intervals to rebuild energy stores in unfamiliar habitats, and finally arriving at destinations in tropical habitats often drastically different from those left behind in the temperate zone. After surviving for five to eight months in tropical communities, they return north again to their breeding areas. Each of the habitats encountered during the migrant's annual cycle faces different threats of degradation and destruction resulting from human activities. Unless habitat requirements during migration are met, conservation measures focused on temperate breeding grounds and/or Neotropical wintering areas will be compromised. Moreover, fitness of migrants is not all or none, but can be influenced by the delays before or during migration that decrease subsequent reproductive output (Marra et al. 1998).

Although much of the focus of our discussion in this paper has been on migrant songbirds, the classic example for en route limitation of a migratory bird involves the Red Knot (*Calidris canutus rufa*), a sandpiper, in Delaware Bay. This species winters in Tierra del Fuego, Argentina, with portions of the population possibly wintering in northeastern Brazil, and breeds in the Arctic. Its migration route involves several traditional stops where the bird regains body fat before moving onward (González et al. 1996, Harrington 2001). In Delaware Bay, the knot times its spring migration with the egg-laying season of the native horseshoe crab (*Limulus polyphemus*; Castro and Myers 1993). In the past, egg-laying by thousands of crabs

provided a seemingly unlimited food supply for knots and other shorebirds. Recent severe declines in horseshoe crab numbers resulted in fewer egg-laying individuals, dramatically reduced food for knots, and greatly reduced knot populations. For a species with distinct stop-over sites across a vast migration range, this "chain is only as strong as its weakest link" example serves as a model for the potential conditions facing all migratory birds.

Shorebirds may be particularly vulnerable because they often have traditional movement patterns that take advantage of unusually food-rich locations as staging areas during migration; depletion of resources in these sites can show the immediate effects of en route limitation on populations. Shorebirds are also advantageous to study because they are large enough to track individually with radio transmitters. Observations of birds with transmitters can help estimate stopover length at particular sites (Farmer and Durbian 2006), a potential surrogate of site quality, with longer stopovers (preferably in combination with condition indices and measures of food availability) indicating more time required to build reserves for further migration. Geolocators are another type of device that promises to provide detailed information on migration paths and stopovers. Stutchbury et al. (2009) provided spectacular data on movements of Purple Martin (*Progne subis*) and Wood Thrush from their breeding grounds to their wintering grounds and back (Fig. 5); unfortunately, the weight of such geolocators (1.5 g) still limits their use to larger migratory birds, and the bird must be recaptured to get access to the information, but this methodology may allow for rapid advances in our knowledge of movements for some species.

Most Nearctic–Neotropical migrant species do not travel as far, do not travel in groups, and do not require such specialized food as Red Knot. For most land-bird

migrants, stop-over habitat is widely spaced across their migratory path, although this habitat may vary in quality. Under extreme conditions, migrants can stop anywhere on the ground until conditions ameliorate. Obviously, trans-Gulf and other oceanic migrants must deal with a major geographic barrier. The work of Frank Moore and colleagues with regard to migration ecology, and Sidney Gauthreaux and colleagues with regard to the use of wind patterns for trans-Gulf migration has shown that it is usually not a dangerous journey, although extreme weather events can be disastrous (Moore et al. 1995, Gauthreaux and Belser 1998).

In South America, most (>90%) austral migrants have overlapping breeding and wintering ranges (Stotz et al. 1996), such that the migration period of these species in many regions is characterized by a mix of migrants and local breeding or wintering individuals. The ability to distinguish between migratory and resident populations is a prerequisite to understanding the ecology and management requirements of austral migrants.

Research priorities during migration

The science behind understanding en route ecology is difficult because it is challenging to track birds and quantify the effects of individual factors on overall population trends. These problems make management recommendations difficult, even though it is obvious that en route population limitation is possible. Understanding how habitats vary in the quality of resources and protection they provide for migrants is valuable, as is the understanding of preferred pathways and timetables of movements for migrants. Recent work using Doppler radar has provided valuable data on sites used by nocturnal migrants, data that can help focus habitat protection or restoration efforts (Bonter et al. 2009). Minimizing the effects of such obviously detrimental factors as cell phone and other towers, wind farms, and buildings is valuable, although measuring how these factors affect the overall demography of migrant populations is difficult. It is clear that the provision of good habitats well distributed across the landscape in preferred migratory pathways seems like a safe strategy to protect en route migrants, with the addition of sites in areas where larger barriers to migration may exist, such as along the Gulf of Mexico or Great Lakes. The need of many species of shorebirds or marshbirds to use a dwindling number of coastal or inland wetlands en route provides a compelling reason for strict conservation of wetlands generally. Obviously, migratory birds need habitat during migration, and any little fragment of forest, field, or wetland may be valuable on occasion (Rodewald and Brittingham 2004, Rodewald and Matthews 2005). Determining when enough habitat is available in a region will be difficult, but well-designed studies may determine when and where migration bottlenecks occur.

Concepts of en route ecology for intratropical or South American austral migrants are nearly unexplored, as these species are poorly studied and the distances involved are relatively small with few geographic barriers involved. Yet, if these species make their movements during the day by flying within the habitat present, they may be strongly affected by habitat gaps; as such, corridors along altitudinal or latitudinal migration routes may be necessary.

For researchers, the key questions involve when or where the journey can become dangerous enough to limit populations. Although use of stopover sites in the Caribbean and Latin America is relatively unknown (but see Latta and Brown 1999, Deppe and Rotenberry 2008), in eastern North America deciduous forest is widely available, and it is hard to believe that stop-over habitat is typically limiting in this region. In the American West, where much of the habitat is arid grasslands or alpine habitats, riparian vegetation is likely critical to the movements of many migrants and is potentially limiting; recent studies have identified adaptations associated with movements in this relatively harsh environment (Griffis-Kyle and Beier 2005, Skagen et al. 2005, van Riper III et al. 2008). Many species in this region make molt-migrations in midsummer, when they leave their breeding area and fly to parts of Arizona, New Mexico, and Mexico affected by monsoonal rains. There, they take advantage of resources stimulated by summer rains, restore body condition after breeding, and undergo molt (Carlisle et al. 2005). For most of these species, migratory distances are small relative to birds of the eastern United States, winds are less predictable due to the mountainous terrain, and habitats may be more limiting. In sum, further research on different migratory systems is needed to better understand the fitness components of migration ecology.

Ecosystem-Level Constraints and Migrant Bird Populations

All of the scenarios discussed above that have been used to account for widespread population declines among Nearctic–Neotropical migrant birds tend to be based on the accumulated effects of human activities on local scales. For example, widespread fragmentation through agriculture, urban development, and timber harvest has been linked to regional migrant population declines, with such human-induced habitat change potentially at work on breeding, wintering, and stopover habitat. Solutions for these problems are based on habitat management on both local and landscape scales (Rich et al. 2004). For most species, there are parts of their breeding and wintering ranges where populations seem to be more than adequately supported, and conservation actions may be needed only during parts of the annual cycle.

More disturbing explanations for migrant bird population declines are those based on broad geographic-scale ecosystem changes such as global warming, acid

rain, or other biogeochemical perturbations. In part, this is because such changes often are independent of patterns of species-specific habitat quality, and solutions require major changes in human behavior that are often either unlinked to perceived conservation problems, or are linked in ways that make effects difficult to track. The spread of exotic diseases such as West Nile Virus, or the avian influenza virus (Peterson et al. 2007) is another way to cause widespread population declines independent of regional patterns of habitat quality and other ecological factors. The spread of WNV across North America in the past decade caused local declines in populations of some species when it first appeared in a region, but these populations usually quickly recovered (Hochachka et al. 2004). However, the idea that population effects are locally short term was questioned by LaDeau et al. (2007), who showed correlations between BBS population declines and WNV in a variety of species across the continent over multiple years. If the movement of WNV into a region causes population declines, we would be mistaken to attempt to restore populations with conventional means involving habitats and landscapes.

In addition to exotic diseases, global climate change can affect populations of migrant birds (Root et al. 2003, Rodenhouse et al. 2008). There is evidence that climate change has advanced migration schedules from both Europe and North America (Jonzén et al. 2006, Zalakevicius et al. 2006, Hedenström et al. 2007). Demographic rates of Black-throated Blue Warblers in both breeding and wintering grounds have been shown to vary with fluctuations in the El Niño Southern Oscillation, leading to changes in local recruitment and population size (Sillett et al. 2000). If global climate change causes regional population declines, it may be futile to attempt to restore populations via standard habitat manipulations.

Analysis of long-term patterns across populations should allow us to detect those species responding in a fashion that best fits an ecosystem-level factor rather than a local factor. This may be easier for a disease such as WNV, which has moved rather quickly across the continent. In contrast, it is possible that the effects of climate change started to manifest themselves many years ago, but have only slowly affected abundances. One could even argue that the apparent initiation of migrant bird population declines in the 1980s correlates well with the initial occurrence of climate change effects in North America. If this scenario is true, then one must separate such widespread effects from declines due to local or regional habitat change across the annual cycle. Although convincing evidence exists that human-induced climate change is impacting ecological systems and the species that comprise them, there remains a need to be able to better quantify and separate change driven by global warming with other causative mechanisms, natural and anthropogenic (La Sorte and Thompson 2007). Once again, some of this may involve an element

of guesswork, but it also appears that the BBS may provide some important data for such analyses (Anders and Post 2006). While less rigorously designed than the BBS, the Christmas Bird Count has been used to demonstrate northward shifts in winter ranges of North American birds (La Sorte and Thompson 2007, Niven et al. 2009). The fact that climate change will affect arctic environments more substantially than temperate environments (IPCC 2001) means that we might expect more significant changes in population sizes due to climate change in arctic-breeding birds than in primarily temperate species. Few of these arctic-breeding species are monitored on their breeding grounds; arctic-breeding land-bird and boreal populations may be surveyed on their wintering grounds with Christmas Bird Counts, and arctic-breeding shorebirds can be monitored during migration (Skagen et al. 2003, Morrison et al. 2006), but the efficacy of these techniques needs to be explored for this subset of species.

Global climate change and the PIF conservation plan

How should the conservation and management community deal with global change in the future? Scientists first need to evaluate the extent to which the recent declines of Nearctic–Neotropical migrant birds could be the result of broad-scale processes such as global climate change as opposed to regional processes such as habitat loss and fragmentation. To do so, long-term population trends need to be analyzed with the appropriate environmental constraints as covariates. For example, most habitat fragmentation occurred long before the migrant declines of the 1980s, so it was difficult to say that fragmentation per se was causing those declines, because the two events did not coincide temporally (although perhaps cowbird and meso-predator population increases did [Faaborg 2002]). Because global constraints could act during breeding, nonbreeding, or migration seasons, and because patterns of regional and global change could be temporally correlated, trying to separate causation of population trends between global and regional factors will not be easy.

For example, if declining Ovenbird populations in the Missouri Ozarks are the result of poor reproductive success due to recent drought conditions that are the result of global warming, conservation efforts such as habitat manipulation directed at this species in this region may be misguided. Because Price (2003) suggests that by the year 2100 this region will not have the appropriate climatic conditions for the oak–hickory forest that this species uses, perhaps we will have to totally rethink long-term conservation plans within a global climate change framework. Alternatively, some Ovenbirds use other deciduous forest types elsewhere in their range; knowing if forest structure is more important than tree species composition might allow us new flexibility in managing this species. However, attempting to foster the forest that this species needs for

the next 100 years may be futile if the climatic conditions that provide the needed vegetative structure are unavailable. For this and other migratory species, smart conservation planning will have to take into account the development of alternative vegetation types, perhaps using management guidelines from states to the south, with the goal of saving all bird species, but with the recognition that doing so will require national or even international coordination to deal with problems related to movement of habitats. A first step may be to identify which species will be most habitat limited under predicted climate change scenarios, and focus on management plans for them (Sekercioglu et al. 2008).

Another aspect of global climate change that may be important to migratory birds is the expected increased numbers and strength of tropical cyclones, which tend to occur during fall migration. Late-summer hurricanes have been shown to affect movements of diurnal soaring species such as raptors, storks, pelicans, and anhingas, and has the potential to affect population trends (Bildstein 2006). J. Faaborg and S. A. Gauthreaux (*unpublished manuscript*) suggested that an unusual number of first-occurrence records for bird species in Hispaniola and Puerto Rico in 2005 may have been the result of numerous, intense hurricanes in the western Caribbean that fall, as wind records for October 2005 show that mean wind direction in the Caribbean was the opposite of its usual direction. These winds may have effectively forced trans-Gulf of Mexico migrants onto islands in the Caribbean where they had not been seen before. That these winds caused increased mortality seems likely given the direction of the winds after passing the Greater Antilles.

Partners in Flight was formed to save migratory birds and help conserve common birds. Yet, the Partners in Flight North American Land bird Conservation Plan (Rich et al. 2004) includes little reference to global climate change. On page 39 a short paragraph notes that climate change "has been identified as an issue for birds primarily in far northern latitudes and alpine areas." Rather than even consider the state of the climate/ vegetation nexus in the near future, the plan focuses on current biogeographic divisions in their existing locations, and sets population targets that are primarily based on returning to populations found in the 1960s (Rosenberg and Blancher 2005). A historic target was picked for consistency in approach to other bird conservation efforts (i.e., waterfowl, Northern Bobwhite [*Colinus virginianus*]), and the actual date corresponds to the start of the BBS. The methodology of Rosenberg and Blancher (2005) was reviewed by a "blue-ribbon" panel of experts (Thogmartin et al. 2006) and generally approved. Recently, Confer et al. (2008) field tested some of the assumptions of the Rosenberg-Blancher technique and found them to be quite deficient. Detection probabilities ranged from 3% to 49% among the most common species studied. Many of the authors of this paper were philosophically uncomfortable with

the use of population targets based on models using past estimates of abundance; all agree that we cannot base conservation on highly unreliable population estimation techniques.

We feel that a more realistic approach to the future must incorporate traditional approaches as well as the possible changes in habitat across time and space as global climate change affects bird distributions. Integrated or "all bird" conservation efforts being implemented through Joint Ventures (see the following section) have realized this, and some are working to develop more realistic population targets (Fitzgerald et al. 2009). With the combined effects of human-caused habitat conversion and global climate change, a plan for the future must at least acknowledge the possible dynamics of habitat change and movement and do as much as possible to provide suitable habitat for the bird species found across the continent. Existing natural areas may be critical during this time, as they may act as lifeboats while other habitats, natural or heavily managed, can be developed.

A symposium at the 2007 Cooper Ornithological Society meeting focused on climate change effects on national wildlife refuges, but provided a potential way to predict future effects on bird distributions. These approaches blended predictions about climates and associated shifts of vegetation with analysis of how birds might respond to these shifts. They provided insight into which species might be most susceptible to habitat changes related to climate change vs. those that seem tolerant of future change. Certainly, we must accept that the future involves climate change; going back to the climates of the 1960s is not possible, so using population levels from that period of time as a goal seems misguided. In addition to climate change, other global change factors are already known to interact with and exacerbate habitat fragmentation, leading to environmental deterioration from the perspective of diverse populations and communities of organisms, even to the point of ecosystem collapse in some cases (Laurance 2008). These complexities need to be incorporated into model forecasts to be credible.

Many management-related topics are associated with the effects of human behavior, socio-political activities, and global climate change on bird populations. For example, the increasing size of the human population as well as patterns of resource consumption will continue to challenge conservationists and politicians to devise practices and policies that mitigate or decrease human impact on environments. The critical need to shift from carbon-releasing energy to carbon-neutral forms of energy such as biofuels, solar, geothermal, and wind power, often involves trade-offs related to birds. Wind generation seems promising, but research on flight paths and migration behaviors needs to be advanced to help in locating wind farms so that they do not destroy thousands of birds on a regular basis. Ethanol production might keep energy dollars within the continent, but

it also may encourage farming on more land, including the conversion of conservation acreage to farming at the cost of bird populations. As ornithologists and conservationists, we must be aware of the various trade-offs involved in shifts in energy production.

Is Our Science Sufficient to Guide Conservation Efforts for Migratory Birds in the New World?

Whether science can guide conservation is a moot point; we are continually improving management decisions based on improved knowledge. However, we can ask this question in the context of identifying what areas of knowledge have both great uncertainty and great consequences for the species being conserved. Understanding the factors limiting populations for any wild animal is never easy; when the focal species spends three months on a breeding site, up to eight months on a wintering site, and one or two months in transit between these sites, which may be thousands of kilometers apart, the task is even more challenging. Because most New World migrants are too small to carry any sort of satellite transmitter or geolocator through the migration process, and our knowledge of linkages between breeding and wintering sites is currently limited, even the best data gathered to date still require a variety of assumptions to build models about which limiting factors occur where.

Given that it has been just over 30 years since the Smithsonian symposium in 1977, which stimulated a major paradigm shift in our understanding of migrant birds, and given the difficulty of the demographic task at hand, should we be comfortable with the state of the science regarding migratory birds as outlined above? How is this science being converted into on-the-ground management practices? Should we be concerned with the pace and the direction of research on migrant birds and its application across the New World?

There is a general model for population limitation in migratory birds that is applicable to all the systems described in this paper (Sherry and Holmes 1995), but do we have data for even a single species that tests this model rigorously enough so that we can derive management principles from the results? Among songbirds that migrate to the tropics, the species for which we have the most data are the American Redstart and Black-throated Blue Warbler, based on studies by Holmes, Sherry, Marra, Sillett, Rodenhouse and others in both New England and Jamaica. For these species, demographic data are available from both wintering and breeding grounds, evidence that these populations are at least generally linked geographically, and, for the redstart, even evidence for interseasonal effects on demography. These studies can serve as a model on how to study wintering migrants. At the same time, we must be careful about generalizing too much from two well-studied species. Part of the reason the winter studies of redstarts, in particular, have been so interesting and successful is that there is strong inter- as well as intrasexual competition for winter habitat, they are abundant on Caribbean islands, and they are extremely site-faithful between years. Some species lack such strong sexual variation in winter habitat use, particularly sexually monomorphic migrants (Brown and Sherry 2008), and it will be interesting to see how such sexual differentiation is distributed among different types of species. Some species seem to adopt a "vagrant" strategy when choosing wintering habitat, and are almost impossible to track from one year to the next with current technology; here the redstart model does not help (Faaborg et al. 2007). The West Indies is great for winter resident studies in part because these birds are often found at densities much higher than in mainland sites, perhaps because islands support depauperate resident bird communities and few predators. Thus, we must ask how well do West Indies studies generalize to mainland wintering areas?

Unfortunately, the number of intensive studies of winter resident birds has declined in recent years. Some of this decline may be because we were able to answer some of the questions about winter distributions and ecology with these studies, but much results from loss of funding sources. For example, the relatively large fund from the U.S. Fish and Wildlife Service for work on Nearctic–Neotropical migrants in Latin America and available to both U.S. and Canadian researchers has focused more on what the grant managers consider to be management and capacity building than on research or monitoring, despite the wealth of evidence (shown earlier) that we really do not understand wintering ecology well enough to make the most of such management for most species and in most regions. The Institute of Bird Populations MoSI stations may be filling some of the void with regard to winter studies with its numerous winter banding stations scattered through Mexico and Central America, but these stations are not enough to fill the need for more rigorous hypothesis-driven studies of the wintering ecology of migrant birds needed to improve management guidelines for tropical regions. For example, almost no work currently underway rigorously examines migration patterns within the Neotropics or austral migration in South America.

Knowledge of the importance of multiple spatial scales, and especially regional-landscape scales, has significantly impacted bird conservation on the breeding grounds. For example, the development of the "flight plan" for North American grassland birds suggested that a Bird Conservation Area (BCA) should possess a core area of grassland habitat of 800 ha (2000 acres), with a neighboring landscape matrix of 3200 ha that is at least 40% grassland, with at least half the grassland tracts at least 40 ha in size (Fitzgerald and Pashley 2000). This proposal was based on estimates of the minimum area required to preserve grassland birds as large as the Greater Prairie-Chicken (*Tympanuchus cupido*), with the assumption that smaller grassland

birds would probably do well under these conditions. The grassland BCA concept has been tested with intensive studies in the Northern Tallgrass Prairie (Winter et al. 2006), where prairie-chickens were too uncommon to study. This work suggested that for smaller grassland songbirds, the large core area of the BCA was not necessary, as reproductive success on the smaller grassland patches was not consistently different from that on larger patches (Winter et al. 2006). This is not surprising, as other studies of grassland birds had suggested that these species responded positively to small tracts of habitat, requiring smaller areas of acceptable habitat within their landscape than forest birds might (McCoy et al. 1999, Herkert et al. 2003). Unfortunately, the validity of the BCA concept for species as large as prairie-chickens or Northern Harrier (*Circus cyaneus*) has not been tested; we not only lack a good idea of how large a landscape is needed to support smaller migratory grassland birds, but we also do not know if the BCA concept would work to save prairie grouse populations, many of which are declining. As management agencies adopt concepts such as BCAs (e.g., Missouri prairie-chicken management plan [Missouri Department of Conservation 2006]) it would be good to remember that these are management hypotheses, and as such will be more effective if implemented in an adaptive management framework that includes monitoring, evaluation, and modification of practices over time (Williams et al. 2007).

The structural and functional complexities of ecological systems have long been recognized by conservation agencies, yet the issue of planning and implementing conservation across multiple scales is much more recent. This task is further complicated by the myriad federal, state, and nongovernment organizations involved in bird conservation. The recent emergence of Joint Ventures as the vehicle for delivering integrated bird conservation in North America is acknowledgment of how this knowledge has impacted bird conservation. Joint Ventures are regional-scale, self-directed partnerships involving federal, state, and local government agencies, corporations, tribes, individuals, and a wide range of nongovernmental organizations that integrate the objectives of national and international bird initiatives with other conservation efforts and local land-use priorities. Fundamental to this approach is a science-based process of conservation planning and evaluation that addresses the needs of all priority bird species for a given region, includes participation by a broad array of stakeholders, and provides efficient and effective strategies for action. This provides partners the benefits of regional-scale planning so that hopefully their local actions are planned and implemented within the context of regional goals.

Many Joint Ventures are using spatial models to evaluate current distributions of birds and predicted distributions under various management scenarios (Fitzgerald et al. 2009). These models often incorporate many of the concepts we reviewed in this paper;

however, as in any modeling exercise, they also highlight our knowledge gaps and often require strong assumptions and expert opinion. Nevertheless, the development of these models by scientists and their application by the conservation community is valuable because they highlight what we need to know and provide a mechanism for implementing science-based knowledge (Thompson and Millspaugh 2009).

As far as we know, none of the other PIF conservation plans has incorporated quite as rigid a plan for landscape-level distribution of habitat as grassland BCAs, but most accept that some sort of source–sink dynamic is present in most regions, so the focus should be on preservation of source habitats. It is possible that early work may have overestimated the production of young in source habitats and underestimated production in sink habitats, and no study in recent years has done a good job of establishing some sort of minimum area requirement for a species within a region, with this minimum area including some measure of replacement-level reproductive success (Ribic et al. 2009, Faaborg et al. 2010). In some cases the reanalysis of existing data may allow a measure of how much habitat is needed to support a species in a landscape, but in other cases we will need on-the-ground studies of local annual production. The application of multi-state models may be valuable (Betts et al. 2008*b*), but these must also include parameters such as reproductive success and behavioral traits such as conspecific attraction (Ahlering and Faaborg 2006, Betts et al. 2008*a*).

Traditionally, agencies have approached habitat conservation, restoration, and enhancement with an emphasis on "more"—more protection, more restoration, and more management. Managers and planners are now recognizing that they need to reframe the goal of "more" to "how much more," and "where" those actions should take place to increase the effectiveness of their management actions. In response to this need, the U.S. Fish and Wildlife Service in collaboration with the U.S. Geological Survey is making a fundamental change in how they address the conservation of birds and other trust resources. The U.S. Fish and Wildlife Service has made Strategic Habitat Conservation a science-driven framework for defining and implementing landscape conservation priorities (U.S. Fish and Wildlife Service 2009; Fig. 6), and a key element is the development of population-based objectives instead of indirect measures such as hectares of habitat (Johnson et al. 2009). PIF and Joint Ventures have similarly responded with the development of population targets. While there is debate about the targets and methods used to establish them (Confer et al. 2008), one advantage to a focus on population objectives is that it encourages the evaluation of factors affecting birds throughout the annual cycle. Population targets focus on species viability. However, a population approach requires that managers acquire more sophisticated tools
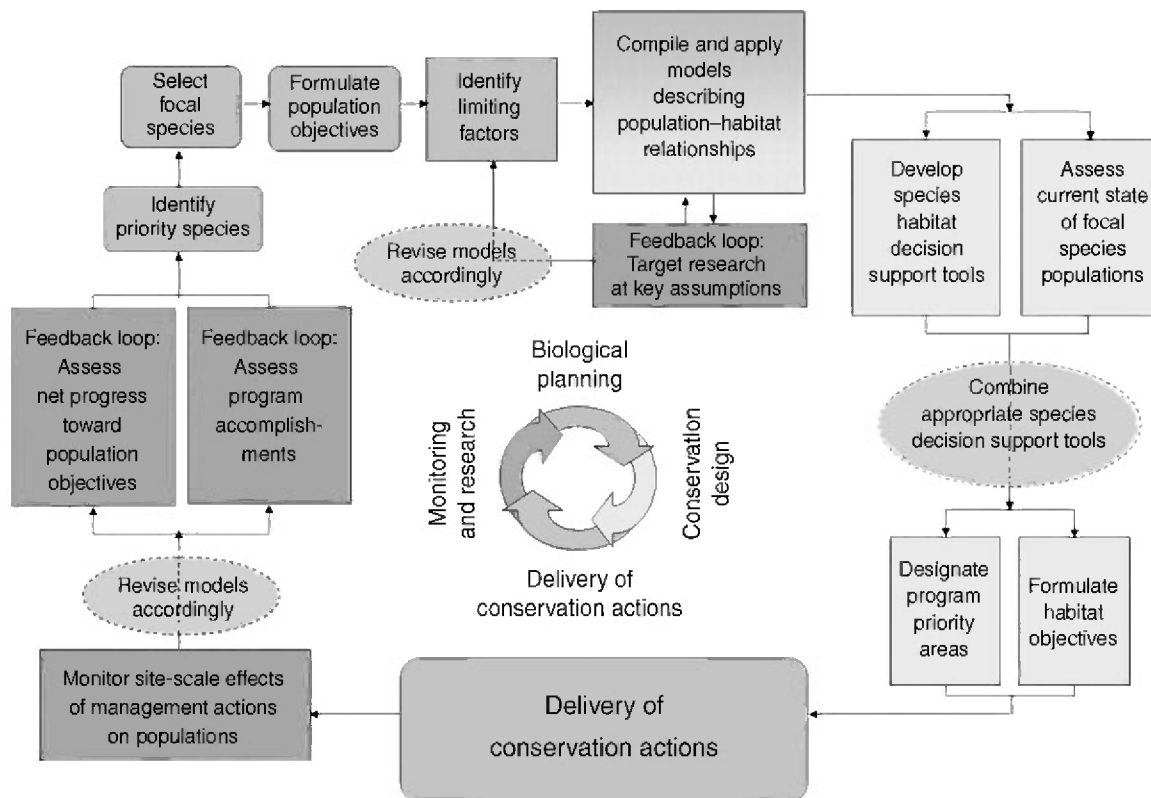
FIG. 6. The strategic habitat conservation diagram developed by the U.S. Fish and Wildlife Service and U.S. Geological Survey to guide conservation delivery efforts and monitor their success in the future (from U.S. Fish and Wildlife Service 2009).

that integrate habitat and landscape dynamics with species viability modeling (Bekessy et al. 2009, Thompson and Millspaugh 2009). These models require the demographic estimates we have called for in this review, but in the interim generic demographic values for Neotropical migrants can be used along with sensitivity analyses.

Once again, little is known about how intratropical or austral migrants respond to habitat perturbations during their breeding period, although the work from North America should serve as a good model to begin these studies. As we discover which tropical-breeding species are migratory, the list of New World migrants will grow. Obviously, we cannot determine all of the details of the migratory behavior of all of these species well enough to have conservation plans based on detailed science for each. Rather, it seems that we must fall back on the general principles discussed earlier, concepts like protecting source populations, providing corridors for tropical migrants, dispersing adequate amounts of stopover habitat along migratory pathways, and so forth. These should be founded in good ecological theory and supported as well as possible by the available demographic data for species involved. In many cases, it appears that the large tropical parks that are needed to preserve low-density tropical residents may serve as an umbrella for many of the temperate and

tropical migrants. To the extent that such habitats as pasture or shade coffee plantations can be manipulated to further support migrant and resident birds, management can expand its effects in more human-dominated environments.

Recent shifts in the timing of migration and breeding in many bird species are one of the strongest signals that climate change is affecting avian life histories (Cotton 2003, Both et al. 2006) and, thus, potentially altering existing trade-offs between fecundity and survival for species and populations. We need to understand the nature of these life history trade-offs to predict the population consequences of climate change and other habitat shifts for migratory birds. A fundamental challenge to this goal is unraveling how much of the observed diversity of life history strategies is due to phenotypic plasticity (Ghalambor et al. 2007) vs. how much is due to genetically based factors (Ricklefs and Wikelski 2002, Roff 2002). Unfortunately, we know little about the natural history of most passerines, let alone how the behavior and demography of a species varies throughout its range (Ardia 2005, Salgado-Ortiz et al. 2008). We would therefore benefit greatly from comparative studies of single species in different parts of their range or along environmental gradients.

As human populations and resource consumption increase across the New World, it will be increasingly

difficult to maintain most bird populations as we have known them in recent decades. Even an optimal system of parks and reserves across the New World may not protect all species. To attempt to save species that respond negatively to land-use change, we need to develop systems of monitoring population abundance and demography throughout the New World so that species with declining trends can be identified early enough in the process that focused research can determine the causes of these declines and management responses can be developed and implemented. Harder yet will be making decisions about which species we can no longer sustain in future landscapes due to a species' inability to cope with climate and concomitant environmental change.

The question remains: Do we know enough? The answer is almost certainly no, but we do know enough to get started with conservation efforts. Much of what we know has only been discovered in the past 30 years of research; a comparison of where we were with regard to knowledge of migrant birds at the 1977 Smithsonian symposium and where we are now suggests tremendous progress in applying our scientific knowledge to conservation theory and management. But before we feel too good about our progress, we must realize that the increasing human population, resource consumption patterns, and threats from global climate change by themselves are enough to necessitate a greater increase in knowledge over the next 30 years. Most likely, these birds will depend on our research findings to guide conservation in much more trying times than we face today.

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