

What Have I Learned about Broadleaf Forest Migrants from Long-term Attendance at Migrant Bird Symposia?¹

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Abstract

Our understanding of the ecology and conservation of migratory birds has changed dramatically in the past 25 years. In the Smithsonian symposium of 1977, scientists shifted from the idea of North American birds invading the tropics to that of tropical birds using the temperate zone, with little mention of conservation. By the Manomet meeting of 1989, declines on the breeding grounds led to our focus on conservation and answering, "Where have all the birds gone?" The first Partners in Flight meeting in 1992 had a strong management focus and provided much of the theory used in PIF bird conservation plans that are still being developed. Fewer meetings occurred in the past decade but research progress continued. Here, I synthesize what we have recently learned about the ecology of migrant birds during breeding, winter, and migration periods. I also note what I feel we have yet to learn to design effective conservation plans for the future.

Key words: broadleaf forest, management, migrants, symposia

Introduction

I think it is safe to say that studies of birds from the eastern broadleaf forests have been the dominant force in our understanding of the evolution and ecology of New World migration. This region also was pivotal in the establishment and development of Partners in Flight. For example, the analysis of trends in populations of Neotropical migrants from Breeding Bird Survey data focused on declines in migrant species from eastern forests and its early successional stages (Robbins et al. 1989a); populations of birds in the western United States did not show clear patterns of decline. Early studies of habitat fragmentation which documented the absence of many species on small fragments and which showed low rates of reproductive success on these fragments occurred almost solely in eastern forested habitats (see, for

example, Hayden et al. 1985, Robbins et al. 1989b, Whitcomb et al. 1981). Startling data suggesting declines in migrant populations focused on trans-Gulf migrants, most of which are birds of eastern broadleaf forests (Gauthreaux 1992). Finally, those early studies that dealt with wintering ecology and its possible limiting effects focused on such eastern species as the Hooded Warbler (*Wilsonia citrina*; Morton 1980), Wood Thrush (*Hylocichla mustelina*; Rappole et al. 1989), and Cerulean Warbler (*Dendroica cerulea*; Robbins et al. 1992) or documented community-wide declines in winter populations of common eastern forest birds (Faaborg and Arendt 1989).

Our understanding of Neotropical migrant birds has changed dramatically in the past three decades. My goal here is to summarize the state of our present knowledge about the ecology and conservation of migrant birds of broadleaf forests, including its early successional stages, note how we got where we are, and suggest those areas where further work is needed. Much of our current knowledge has been summarized expertly by speakers in this or other symposia at this conference, as will be noted. To provide an appreciation of where we are and how we got there with regard to the conservation of migrant birds, I begin with a review of major changes in our knowledge of migrants as shown from the various migrant symposia that preceded this one. Only then can I properly note the current state of the art and the future scientific information needed to make future Neotropical migrant conservation as science-based as possible.

Historical Changes in the Migrant Bird Paradigm

When I started graduate school in 1971, there certainly was no focus on studies of migrant birds as a group. Researchers might study the natural history of a migratory species on its breeding grounds or document its occurrence in winter, but little work had dealt with migrants as a group. Most tropical ornithologists focused their work on poorly studied tropical residents, often recording information on wintering birds only because these birds appeared in point count or capture rate samples taken of tropical birds. Migrants were known to be common in parks and gardens, so if there was a general dogma at the time, it was that these winter residents moved into sites

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that residents did not use or took advantage of seasonally superabundant food resources like fruit.

As far as I know, the first quantitative measures of migrant abundances in different Neotropical habitats occurred in work by Tramer (1974) from the Yucatan and Karr (1976) from Panama. These papers tended to promote the idea of winter residents using surplus resources, but Karr, in particular, did an excellent job of showing the variety of roles that winter residents filled in Panama. While doing his work at the Smithsonian Tropical Research Institute, Karr interacted with resident ornithologists Eugene Morton and Neal Smith, among others, who also were gathering data on migrant ecology.

At the same time, several graduate students, including Russell Greenberg, Richard Hutto, John Rappole, and Mario Ramos, were doing graduate projects whose focus was the ecology and distribution of migrant birds that winter in tropical habitats. These studies occurred because ecologists of that day were trying to delineate and understand patterns of diversity and abundance in the tropics, which included an understanding of seasonal movements in this region and how such movements might evolve. Migrants were a notable and sometimes major part of all these tropical bird communities.

This small burst of interest in migrants of the neotropics led Eugene Morton and Allen Keast to host a symposium on migrant birds at the Smithsonian facility at Front Royal, Virginia, in 1977. The results of this symposium, published as *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (Keast and Morton 1980), greatly expanded our knowledge about tropical migrants and totally changed the way we thought about them. Although the symposium was originally announced as one that would explore how "North American" birds fit into the tropics, one of the solid, take-home points of the symposium was that many of these migrants must be considered tropical birds. Most migratory species have specialized niches within the tropical communities, even in mature, undisturbed habitats. The observation that these species might be constrained through habitat selection, territorial behavior, distribution of foraging flocks, or other ecological factors in the tropics made the possibility of winter limitation worthy of consideration. Almost no mention of conservation was made at this symposium, but in a chapter added to the volume, Terborgh (1980) suggested that the fact that the winter range of most migrants that breed in North America was in Mexico and the West Indies, an area about 1/8th the size of the breeding range that was being dramatically modified by humans, meant that the future for these migrants did not look bright.

I am certain that the Keast and Morton (1980) volume stimulated new research on the role of migration in tropical bird communities, but for the decade following

the Front Royal meeting, this was in the guise of "pure" science. The situation changed dramatically in the late 1980s when a variety of studies suggested that Neotropical migrant birds might be in decline. This led the Manomet Bird Observatory to sponsor a symposium at Wood's Hole, Massachusetts, in 1989 to examine patterns in migrant bird populations and possible causes for population declines. Evidence of declines came from a variety of sources. In particular, the Breeding Bird Survey (BBS) had shown strong patterns of decline in birds of the eastern US during the 1980s, with the most pronounced declines among those birds that wintered in the tropics (Robbins et al. 1989b). Another extensive study suggested that the intensity of trans-Gulf migration had decreased dramatically by the late 1980s (Gauthreaux 1992). Wayne Arendt and I added to the frenzy by showing how captures of winter resident warblers in our Puerto Rican study site had declined precipitously during the period 1973 to 1989 (Faaborg and Arendt 1989).

A number of studies using Breeding Bird Census (BBC) or Christmas Bird Count (CBC) added other evidence of local declines. Possible mechanisms for declines were presented, with numerous fragmentation studies showing how predation and brood parasitism increased in fragmented habitats, leading to low rates of nesting success in these sites. Additionally, the loss of primary forest in the tropics was well documented, making it fairly easy to see how loss of rainforest or other habitats in the tropics could be causing declines in breeding numbers of Neotropical migratory birds.

Although the symposium volume *Ecology and Conservation of Neotropical Migrant Landbirds* (Hagan and Johnston 1992) did not appear until 1992, word of its results spread like wildfire. Numerous popular articles with titles like *Death of the Dawn* and *Silent Spring Returns* soon appeared, suggesting that loss of the tropics was causing the declines seen at home. Most importantly, John Terborgh published *Where have all the birds gone?* (1989), which documented evidence for declines of migrant birds and made a strong case that tropical habitat loss was at work. Although there were those who questioned this conclusion (Faaborg and Arendt 1992, James and McCulloch 1995), the general consensus seemed to be that Neotropical migratory birds were facing a crisis.

The response to this possible crisis was the development of the Neotropical Migratory Bird Conservation Program, which we know as Partners in Flight (PIF). PIF was formed at a meeting of managers, researchers, and other conservationists held in Atlanta in December 1990. This meeting was an exceptional mix of professionals from governmental agencies, NGOs, academic institutions, and other conservation groups. Participants agreed that there was a serious enough problem that a response was needed, and they designed the response with the complex (and

sometimes bewildering) array of committees that compose PIF. Among these committees was one for Research, which has had the involvement of most of the best migrant bird researchers throughout its history.

Among the first activities of the Research Committee of PIF was the scheduling of another symposium in the fall of 1992, which resulted in both *Status and Management of Neotropical Migratory Birds* (Finch and Stangel 1993) and *Ecology and Management of Neotropical Migratory Birds* (Martin and Finch 1995). Unlike the Manomet symposium that considered whether or not a problem existed, the goal of this symposium was to get researchers and managers together so that we could see what the patterns were, why they were occurring, and how things could be fixed. Conservation was the reason this symposium occurred.

Unfortunately, because the Estes Park symposium was only 3 years after the Manomet symposium, there were not a lot of new research findings to present. Some fragmentation studies presented new gloom-and-doom scenarios, with predation and parasitism rates that were nearly unbelievable. Further documentation of declines from BBS data were presented, along with more information on tropical habitat conversion rates. Breeding season managers could see that they needed larger tracts of habitat and might have to control cowbirds, while those from the wintering grounds were not told much that could be converted to effective management other than the preservation of native habitats. There were few positive notes from this symposium, but it was one of the first places where the idea was presented that landscape management and regional source/sink dynamics might be important to our understanding of the demographic situation on the breeding grounds. In addition, it was suggested that analytical methods for BBS results had been giving us some misleading trends, or at least impressions (James et al. 1996).

Although our knowledge of how migrant bird populations were limited was still very primitive at the Estes Park meeting, the leaders of PIF seemed to feel that we knew enough to start managing. Thus began what I call the “no-meeting decade,” although that is not completely true. A major PIF conference was held in Cape May, New Jersey, in 1995. Research constituted a small part of this meeting, and my research colleagues who attended told me that they felt that they were not very welcome. The results from this conference did not appear until 2000, and then the distribution of the results was much less than that of the Estes Park meeting. A cowbird meeting in 1993 produced some great new information; this publication (Smith et al. 2000) also did not appear until 2000, although it was then readily available. An international meeting on the role of mist netting in monitoring populations also occurred in 1993, but it still has not been published.

Although symposia volumes were not published during this period, many important research findings did occur. Fortunately, the interaction between researchers and managers that was a result of the PIF structure meant that most of the people developing the regional Bird Conservation Plans of PIF continued to consult researchers. For this reason, most of the regional plans do seem to be as timely as possible. Three major areas of research during the late 1990s were critical to our current understanding of migrant bird populations: First, researchers expanded their demographic studies to include large tracts of habitat, where they often found that reproductive success was high, even high enough for these areas to serve as regional sources (Robinson et al. 1995). Second, landscape level studies of breeding birds helped to explain some of the regional variance of fragmentation studies, including variance in edge effects in different locations, cowbird populations, and predators (Donovan et al. 1995, Donovan et al. 1997). Finally, studies of winter social behavior in the American Redstart (*Setophaga ruticilla*) showed strong social interactions that could lead to population limitation and sex ratio skews on the breeding grounds (Marra et al. 1998). All of these breakthroughs are critical to our current understanding of Neotropical migrant bird ecology.

The “no-meeting decade” ended in February 2002, with the “Birds of Two Worlds” symposium sponsored by the Smithsonian Institution. This symposium was very international in nature, including numerous Old World researchers talking about Asian and African birds. Most of the papers could be called “pure” science, and the word “conservation” was rarely spoken, although, as we shall see, some of the findings may be useful to future work on migrant conservation. A month later we had contributions such as this in the third international Partners in Flight conference.

A Modern Paradigm for Migrant Bird Conservation in Broadleaf Forests

So what do we know about migrant bird conservation as we start this new millennium? First of all, we must remember that a Neotropical migrant bird population can be limited by conditions on the breeding grounds, by conditions on the wintering grounds, or by conditions that occur during migration itself. In any given year, one or more of these locations/situations could be limiting. Of course, the effects of limitation from one season may be expressed at another season, so even a clear understanding of mechanisms at one time of the year requires an understanding of how these effects may extrapolate to other periods (Marra et al. 1998).

Breeding season management: Modern breeding season management for Neotropical migrant birds must

focus on the maximization of reproductive success rates, either through local manipulations that control artificially high predation or parasitism rates or through the protection of large areas which serve as regional source pools for migrant populations. Fragmentation studies have shown that many species have minimum area requirements that must be recognized in management schemes. Unfortunately, such minimum area requirements may vary depending upon whether one is measuring presence/absence, density, pairing success, or reproductive success (Winter and Faaborg 1999); scientists have discriminated these different minimum area requirements for few forest species. Rather, we have fallen back on pointing out the importance of large regional forests that may serve as the source population of even larger regions with fragmented habitats.

Thompson (this volume) does an excellent job of pointing out the logic used to develop our current ideas about forest bird management. He shows clearly how landscape factors may ameliorate fragmentation or edge effects, with the accompanying lessons for managers. He also points out how management for early successional species (especially those of regenerating forest) can be balanced with the negative effects of timber harvest on mature forest birds, with the observation that some second-growth species may require clearcuts of some minimal size. Villard (2002) expands some of these ideas to show the effects of natural disturbance and silviculture on bird distributions and management. Friesen et al. (this volume) also show how these rules fit into urbanizing landscapes.

An attempt to convert the modern theory to regional conservation practice was made with the development of grassland Bird Conservation Areas (BCAs; Fitzgerald et al. 1998). Here, a BCA was suggested to be effective if it had an 800 ha core area of high quality habitat plus a regional landscape with a large percentage of smaller habitat fragments. It appears that the Greater Prairie-chicken (*Tympanuchus cupido*) was used to develop the details of this model, with the idea that a management area large enough for chickens would be more than large enough for smaller passerines. Unfortunately, a recent test of the suitability of these grassland BCA constraints has provided less than satisfying results (Johnson and Winter, this volume).

Even without the details, we know that larger protected areas have a better chance of supporting healthy bird populations, although one must take into account the dynamics of the habitats within these protected areas. As we better understand the limitations of such regional management, we can better fit migrant management into other management schemes. We already have mentioned the trade-off between managing for mature forest vs. second-growth species within the

broadleaf forest region, with the realization that one cannot manage for both in a single location. Yet, in forested landscapes, second-growth birds often have high nesting success because the landscape is free of predators and parasites. Regional management schemes also may be flexible enough to allow specialized management for sensitive species with restricted habitat requirements, such as the Golden-winged (*Vermivora chrysoptera*) and Cerulean warblers discussed by Hamel et al. (this volume). These landscape-level guidelines also often can fit within broader conservation schemes, as discussed by Uihlein (2002).

Winter management: Individual survival is the key factor with which a migrant bird must deal during the 6 to 8 months that it is not on the breeding grounds or in transit.

Although we have learned much about the winter behavior of migrants in the last decade, we have not made nearly as much progress with regard to management suggestions for this time period when compared to the breeding season. The work of Richard Holmes, Tom Sherry, and Peter Marra on American Redstart has shown how rigidly structured winter distributions might be for this species and how behavioral constraints might have breeding season repercussions for species with similar constraints of habitat and behavior. But Morton and Stutchbury (this volume), Baltz, (2000), Latta and Faaborg (2001, 2002), and Wallace (1998) have shown that a great variety of wintering strategies seems to exist among migratory birds. For some species we are still not sure what constitutes the winter range (Remsen 2001), let alone what habitats are truly required. While we must accept that some species may act like American Redstarts on the wintering grounds, we also know that others show markedly different behavior and must accept the fact that too few species have been examined in detail.

Stopover ecology and management: As birds are migrating between what are often fixed wintering and breeding sites, they require access to sites with high food availability and protection from predators. In some cases, particularly when large barriers such as the Gulf of Mexico or Great Plains must be crossed, these sites may be limiting. This has been discussed in two recent books (Able 1999, Moore 2000) and in a symposium at this conference. Although this period may be critical to annual demography, the evidence that stopover habitat is limiting is weak for most eastern broadleaf forest birds. In particular, the development of forest fragments throughout the Midwest has probably made migration easier for most migrants in this region. Yet, those cases where stopover limitations occur may be very important, so further work in this area is needed.

What Else do We Need to Know: Breeding Season?

Although I think we have made tremendous progress in the past decade with regard to our understanding of how migrant bird populations are regulated, we mostly have hypotheses that need further testing. Our “Midwest model” of landscapes and source/sink dynamics has a lot of demographic support, but we have no evidence that dispersal rates are actually driving this system (Faaborg et al. 1998). We need to better understand the demographic characteristics of all the component regional populations and determine where dispersal does and does not occur before we get very comfortable with, for example, a “protect the Ozarks and Missouri is OK” attitude.

On the contiguous forest end of the landscape scale, we need to be careful with determining what spatial constraints a landscape really has before we push for too much forest cutting because of its favorable effects on second-growth birds. In fragmented sites, we need better demographic studies to determine how one can optimize what are generally sink conditions. These also might allow us to initiate special cases of predator or parasite control when necessary, but we must have good demographic data before we initiate expensive conservation practices. For example, we know that parasitism is high in many midwestern forest fragments, but cowbird eradication in most of these cases would be useless, because nest predation rates are the ultimate factor controlling populations. We need more information, but our success of the last decade means we now can ask much better questions than we could before.

What Else do We Need to Know: Winter?

We need sound data on the habitat requirements of winter resident birds throughout their winter ranges. We must recognize that migrant birds use nearly all habitat types, such that converting primary vegetation types to secondary types affects some species negatively but may affect others positively. We must determine which habitats a wintering species truly needs to maximize survival over the winter. This research is not always easy to do, as there is a lot of noise in determining winter habitat selection in these migrants. Our long-term study in dry forest in Puerto Rico has captured 16 species of warblers in the winter, but we only consider this habitat to be a major wintering habitat for 4 of these. We need to determine which species have strong social dominance systems, like the American Redstart, such that subordinate age or sex groups are forced into what may be limiting

habitat; these may show winter limitation sooner than those species with more egalitarian distribution systems in winter. Can we develop monitoring systems that allow us to detect those species whose post-breeding populations seem larger than their available winter range? As we attempt to understand the potential for winter limitation, we need to keep in mind that habitat modification affects wintering birds differently. For example, converting rainforest to sugar cane is disastrous to Wood Thrush but good for Indigo Bunting. The future is most likely one of a different spring, rather than a silent spring.

We will need to fit the needs of winter resident conservation into broader plans that deal with the conservation of tropical resident birds. As shown by a whole symposium at this conference, winter residents are only a small component of the forces driving avian conservation in many tropical countries. Along this line, some studies have suggested that winter residents do not respond negatively to habitat fragmentation on their wintering range. First of all, we need to verify that this is true. Just because winter residents may use fragments in high abundance does not mean that they survive there as well as in contiguous forest. Once again, solid demographic data are needed to see if this hypothesis is true. More importantly, even if it is true that migrants survive as well on fragments as contiguous forest, we must remember that habitat fragmentation is generally devastating to resident tropical bird species diversity. Any statement that suggests that fragmentation is acceptable because of its value to winter residents must be presented within the context of the severe loss of resident diversity that nearly always accompanies habitat fragmentation in the tropics.

Our Ultimate Goal: Understanding How Populations of Migrants are Regulated on Large Spatial and Temporal Scales

We must always remember that populations of Neotropical migrant birds are regulated over large spatial scales on annual or longer time scales (Sherry and Holmes 1995). Even excellent studies of local limitation have reduced value when extrapolated range-wide, whether this study is on the breeding or wintering range. Until we can actually link breeding and wintering sites, we are constrained in our population and demographic inferences. Ideally, we need broad scale studies of the evolutionary fitness of individual migrants throughout the annual cycle to make the most scientifically sound management plan. This will never be easy to do, in part because the migrant strategy involves so much mobility that is difficult to track. Although new technology using DNA traits (see Mila et al. this volume) or isotope patterns

(Hobson and Wassenaar 2001) suggests that we may be on the verge of making the appropriate linkages between breeding and wintering grounds, we will still be limited to comparing regions rather than actually tracking individuals.

In addition, we must remember that we have 200 or more species that we might consider Neotropical migrants. Each of these is susceptible to the above limiting conditions, but because each species has its own habitat requirements, social system, food habits, and such, the probabilities that each species will be limited by any given season will vary by species. We *must* avoid thinking of Neotropical migrants as a group that will simplistically go up or down as the amount of rainforest or other single ecological factor goes up or down. We might be able to group some species together into functional units, but we should be sure that we are not making some bad assumptions when we do so, and we must accept the fact that at some point we may have to consider each migrant species individually.

Finally, although the migrant strategy is successful enough to have evolved in so many species, it still involves a great deal of individual failure. A healthy population may have over half of its nest attempts fail in a given breeding season and nearly half of the adult birds die each year. This involves billions of deaths annually. As avian ecologists and conservationists, our goal is to sort through all of this noise to eventually understand the details of population regulation for species which may breed across half of North America and winter across all of Mexico and the West Indies. And we must do this well enough to tell the managers what they can do to help these species thrive.

While I am certain we are on the right track, we still have much to learn and, hopefully, many more PIF conferences in the future. I also hope that it is clear from this presentation that research which at one time seemed very "basic" and of little applied value turned out to be critical to the development of the conservation principles on which our current management practices rest; without continued support of migrant bird research that does not seem to have immediate conservation value, we will undoubtedly be limited in the quality of the management schemes we can design in the future.

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Lessons from Migrant Symposia - Faaborg

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