

REVIEWS

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Recent advances in understanding migration systems of New World land birds

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Abstract. Our understanding of migratory birds' year-round ecology and evolution remains patchy despite recent fundamental advances. Periodic reviews focus future research and inform conservation and management; here, we take advantage of our combined experiences working on Western Hemisphere avian migration systems to highlight recent lessons and critical gaps in knowledge. Among topics discussed are: (1) The pipeline from pure to applied researchers leaves room for improvement. (2) Population limitation and regulation includes both seasonal and between-season interactions. (3) The study of movements of small-bodied species remains a major research frontier. (4) We must increase our understanding of population connectivity. (5) With few exceptions, population regulation has barely been investigated. (6) We have increasingly integrated landscape configuration of habitats, large-scale habitat disturbances, and habitat quality impacts into models of seasonal and overall demographic success. (7) The post-breeding season (late summer for latitudinal migrants) is increasingly appreciated for its impacts on demography. (8) We recognize the diverse ways that avian brood parasites, nest predators, and food availability affect demography. (9) Source-sink and meta-population models help us understand migratory avian distributions among fragmented habitats. (10) Advances in modeling have improved estimates of annual survival and fecundity, but for few species. (11) Populations can be limited by ecological conditions in winter, but habitat needs are poorly known for most species at this time. (12) Migration tends to occupy broad spatial fronts that may change seasonally or when migrants cross major barriers. (13)

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En route conditions can limit migrant populations; linking migration habitat quality indicators to fitness or population consequences presents a major challenge. (14) A variety of intra-tropical Neotropical migration patterns are recognizable, but almost nothing is known about these systems beyond descriptions of a few typical species' movements. (15) Global climate change scenarios predict range and phenology shifts of Neotropical migrant bird populations that must be considered in conservation plans. Future studies will depend on new technologies and the integration of modeling with sophisticated, large-spatial-scale measurement and parameter estimation; whether the pace of research and management involving migratory birds can match the growth of environmental threats remains to be seen.

Key words: austral migration; breeding season population limitation; carry-over effects; connectivity; en route ecology; intratropical migration; land birds; migration; source-sink demography; winter population limitation.

INTRODUCTION

With their ability to fly, relatively large size, highly developed nervous systems, and rapidly responding physiology, birds are clearly well adapted for taking advantage of seasonal variation in resource abundance through some form of migration. In North America alone, approximately six billion birds migrate annually, and in arctic regions nearly 100% of breeding birds move south to survive the winter. Whereas some of these species spend the nonbreeding period within temperate habitats in North America, most New World land birds move to tropical or even south temperate latitudes for at least part of the year. The majority of these spend the winter north of the equator in Mexico, the West Indies, or northern Central America, but several species travel further, well into southern South America.

Concurrent with north temperate breeders moving northward during the Nearctic spring, birds from the temperate zone of South America move northward toward the tropics to avoid the austral winter (Fig. 1), although the smaller size of the land mass in southern South America results in fewer species and smaller numbers of migrants there than in North America. In addition, as winter approaches across latitudes, birds that breed at high elevations migrate to lower elevations, a seasonal movement that closely parallels latitudinal migration but at a much smaller spatial scale. Likewise, some lowland tropical species migrate in response to annual wet and dry cycles. Thus, even within Amazonian rain forest bird communities, which are often viewed as largely stable in composition, the annual cycle involves movement of bird species from throughout two continents, such that each month has its own mixture of birds arriving, leaving, or just passing through, with breeding destinations ranging from the Arctic tundra to Tierra del Fuego.

With these diverse movement patterns, migrants are an exceedingly complex and difficult set of birds to understand, let alone conserve. Changes in abundance in many migrant species have raised concern about the future for these populations. The objective of this paper is to review and synthesize recent advances in understanding land-bird migratory systems, with emphasis on the ecology and conservation of those species that breed in North America and winter in tropical regions, i.e., Neotropical migrants. We then contrast this knowledge with what is known

about migration systems found primarily in Central and South America. In a separate paper (Faaborg et al. 2010), we discuss how these findings and the questions that remain should be incorporated into future research and conservation implementation plans.

DEFINITIONS

For a phenomenon as complex as migration, clear terminology is important. For most of the past two decades, the term "Neotropical migrant" has been used in the North American literature to denote those birds that breed in the temperate zone but winter in the neotropics, which for our purposes include much of Mexico and places further south. This term was used to distinguish long-distance migrants from those that wintered in the temperate zone in the United States and Canada, which were sometimes called "Nearctic migrants." Obviously, though, because migration occurs in South America, the center of the neotropics, all migrants there should also be considered "Neotropical migrants" (Levey 1994). Historically, this migration within South America has been defined as "austral migration" if it involved birds moving between south temperate breeding grounds and the tropics for the nonbreeding season, "altitudinal migration" if it involved movements up and down mountains within the neotropics, or "intratropical migration" for movements solely between the tropics of Cancer and Capricorn (Hayes 1995, Jahn et al. 2004). More recently, austral migration has been referred to as "South American austral migration" (Chesser 1998, 2005) or "Neotropical austral migration" (Cueto et al. 2008). Using these terms, however, fails to separate North temperate breeding species, some of which migrate to the tropics while others remain in the North temperate zone; for these, it has been suggested that hyphenated combinations ("Nearctic-Nearctic" vs. "Nearctic-Neotropical") be used when such precision is necessary (Levey 1994, Hayes 1995). In this paper, the focus is the North American land-bird migration system, specifically those species breeding in the north temperate regions and wintering in tropical areas, which, for simplicity, we refer to in this paper as Neotropical migrants.

HISTORICAL DEVELOPMENT OF STUDIES OF MIGRANT BIRDS

During much of the last century, Neotropical migrants were studied primarily during their breeding season in

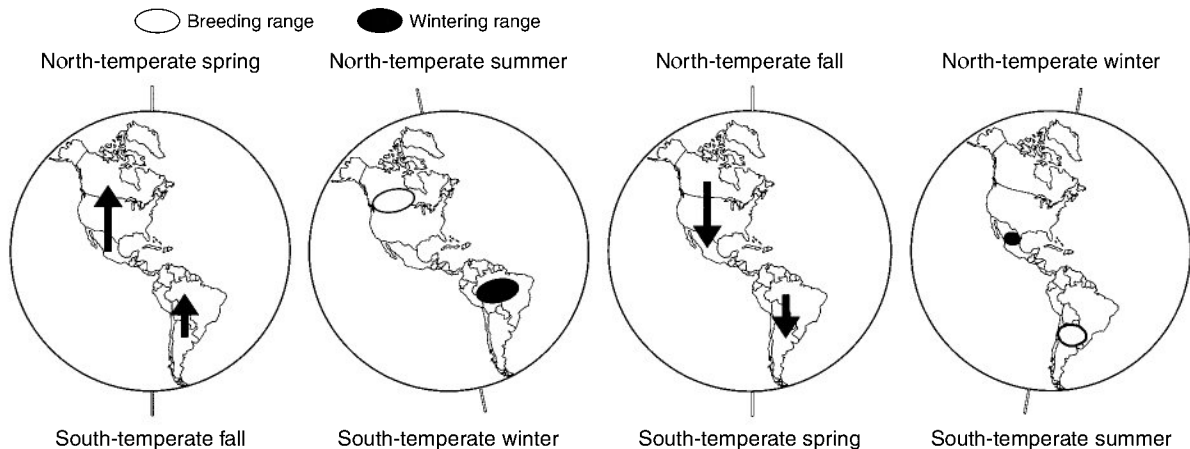


FIG. 1. Generalized seasonal movements and ranges of hypothetical populations of Nearctic–Neotropical and South American austral migrant species, showing the symmetry of movements through the annual cycle. The position of the sun is to the left of the diagram. The figure is from Jahn et al. (2004); reprinted by permission.

North America. Their winter ecology was largely ignored by ornithologists working in the tropics because exotic tropical species there were much more fascinating and even less well known. This changed in 1977 when the Smithsonian Institution sponsored a symposium on migrant bird ecology (Keast and Morton 1980). Until that time, the prevalent dogma was that species breeding in North America spent the winter in the tropics feeding on “excess” resources that were available to them, often in parks and gardens. Some of the main lessons learned from 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 to ant swarms, that many of these winter residents were territorial and very site faithful, and/or that some lived only in mature forest habitats (Schwartz 1980) that were already being extensively cut and degraded. After this symposium, the concept of migration from one of “North American” birds invading the tropics to avoid winter was expanded to include a model of tropical birds that employed a quick trip to the temperate zone as a reproductive strategy.

Few papers in Keast and Morton (1980) mentioned conservation; in particular, Terborgh (1980) asserted that migrant birds might face population declines from loss of wintering habitat. This became a visionary idea when numerous sources in the late 1980s suggested that populations of migratory songbirds were declining, with the strongest declines found among those species that wintered in the tropics. Terborgh (1989) himself fueled this conservation fire with his book *Where have all the birds gone?*, which advocated tropical causation for population declines. About the same time, Robbins et al. (1989) reported population declines among many forest birds in the eastern United States, with those species that migrated to the tropics showing the most pronounced declines. Also, Holmes et al. (1986) and Holmes and

Sherry (1988) reported long-term declines in breeding populations of Neotropical migrants in an undisturbed temperate forest, and Faaborg and Arendt (1989) showed long-term declines in the winter-resident warblers they had been monitoring in southwest Puerto Rico. Several long-term studies from temperate forest fragments showed similar trends, once again with long-distance migrants perceived to be the most vulnerable group.

Concern about these apparent declines led to a symposium at Woods Hole, Massachusetts, USA, sponsored by the Manomet Bird Observatory (now Manomet Center for Conservation Science) in 1989. Numerous scientists presented data on the population ecology of migratory birds in North America, much of it supporting major population declines in North America at least during the decade of the 1980s. The concern led to a meeting in December, 1990, sponsored by the National Fish and Wildlife Foundation, where individuals from state and federal government, nongovernmental agencies, universities, and elsewhere acted on their concern and started the Neotropical Migratory Bird Conservation Program, also known as Partners in Flight (PIF). PIF is a cooperative, proactive initiative that attempts not only to protect declining populations of migratory land birds, but also has expanded to “keep common birds common.”

The inception of PIF resulted in greatly increased interest in research on the demography of migratory birds throughout their annual cycle. In the last 20 years, there have been major advances in our understanding of the basic ecology of migratory birds and how this information can be converted into conservation action. The proceedings of a major symposium at Estes Park, Colorado, USA, was published both as a U.S. Forest Service technical report (Finch and Stangel 1993) and by Oxford University Press (Martin and Finch 1995); these did an excellent job of synthesizing both what we knew at that time and what was needed to conserve migrant

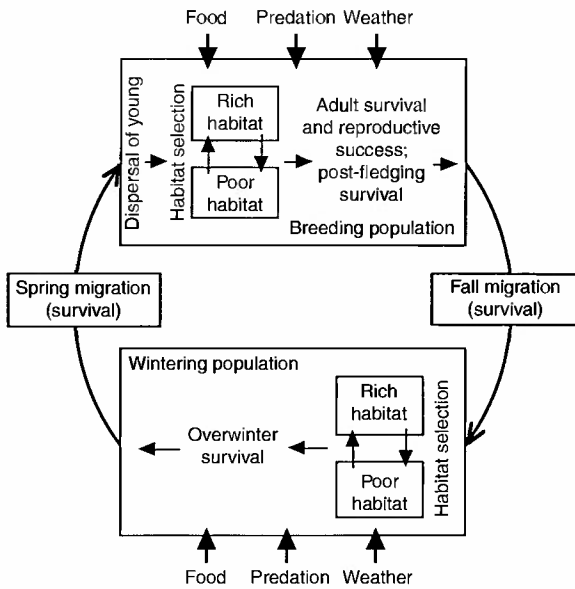


FIG. 2. The Sherry-Holmes model for understanding population limitation in migratory birds. Note that there are four major periods when populations may be studied (breeding, wintering, and two migration periods), but the factors most important to the evolution of migration vary by period. The figure is from Sherry and Holmes (1995); reprinted with permission.

birds in the future. Unlike the period before 1990, many studies were initiated to explicitly focus on migratory birds on their wintering grounds, often with conservation goals rather than elucidation of basic behavior and ecology.

The last two international meetings of PIF have shifted their emphasis to management implementation, while the focus on research, particularly during the nonbreeding season, seems to have lessened. Two migrant bird symposia were held in 2002, both published in 2005. One, a PIF symposium on conservation of New World migrant birds appeared as an enormous two-volume set (Ralph and Rich 2005); its title suggests its strong focus on implementation and integration of local management action plans. In contrast, the Smithsonian Institution hosted an international conference that returned the focus to the fundamental ecology and evolution of migratory birds, with less emphasis on conservation. The *Birds of Two Worlds* volume (Greenberg and Marra 2005) emphasized studying migrants in the context of the annual cycle. In addition, a national conservation plan was published by PIF (Rich et al. 2004) and nearly 100 regional conservation plans are either complete or in the works (information available online).²¹ The latest international PIF meeting, held in 2008, also continued the implementation focus, with the goal of “connecting birds, habitats, and people.” It is hard to argue with PIF’s contention that it is the largest bird conservation

program ever initiated, but it appears that PIF’s interest in basic research about migrant birds has languished in recent years. As researchers, we found the direct interaction with managers at early PIF meetings one of the most exciting components of this conservation effort, and we still feel that we are making scientific contributions that continue to be of importance to managers.

NORTH AMERICAN LAND-BIRD MIGRATION AS A MODEL SYSTEM

The Neotropical land-bird migration system can serve as a key model for New World bird migration systems for several reasons. Avian migration systems of the New World and Old World differ enough that few generalizations about these systems are apparent (Greenberg and Marra 2005). The North American migration system is the best studied of the New World migration systems, based on hundreds of papers (for a recent review see the volumes noted earlier). The breeding area of North American migrants comprises the only region that has had a systematic population monitoring survey (the North American Breeding Bird Survey) in place for 40 years, such that approximate distributions and changes of bird populations are known throughout the United States and southern Canada, and even total populations have been roughly estimated (Rich et al. 2004). Most of the basic research from this region has resulted in management guidelines that appear to apply broadly across habitats and species.

Any conservation plan must be grounded in basic demography, with emphasis on when and where population limitation may occur. A general model for understanding the demography of North American migrant birds has been presented by Sherry and Holmes (1995; Fig. 2). This density-dependent model suggests that migrant bird populations can be limited by conditions on either the breeding or wintering grounds, or by factors that occur while in transit between these areas. Breeding ground limitation can occur in the form of effects on survival rates of breeders or variations in nesting success that change population trajectories, with emphasis on the role of variation in habitat quality on the rates of survival and reproduction.

Nonbreeding-season demographic studies have tended to focus on survival rates, as this is the most obvious demographic factor at this time of year (but may be confounded by carry-over effects between seasons). Several studies have documented patterns of survival of long-distance migrants on their wintering grounds (Holmes et al. 1989, Sillert et al. 2000, Sillert and Holmes 2002, Dugger et al. 2004, Johnson et al. 2006), with emphasis on those species that are extremely site faithful; species that are less site faithful are generally harder to study. Although there has been only limited work on within-winter survival rates of marked populations, studies such as Sillert and Holmes (2002) on the Black-throated Blue Warbler (*Dendroica caerulescens*), Johnson et al. (2006) on the American Redstart

²¹ www.partnersinflight.org

(*Setophaga ruticilla*), and Latta (2003) on the Palm Warbler (*Dendroica palmarum*) document high winter survival. This suggests that, at least for sedentary species, most mortality actually occurs during migration. Unfortunately, because most migrants are too small to carry a transmitter large enough for tracking by satellites, migration is a period for which we have little direct survival information. Initiatives for the development of technology to remedy this problem are underway (Wikelski et al. 2007).

Although a model such as that of Sherry and Holmes (1995) is simplistic, it allows the insight that any one of at least four factors (breeding habitat, wintering habitat, and two migration seasons) could limit overall populations. When evidence shows that populations of a migratory species are declining, the goal is to determine which factor or factors limit these populations, information necessary for informed conservation. Moreover, we need to determine how and when density-dependent mechanisms regulate abundance (Rodenhouse et al. 1997, 2003, Sillett et al. 2004, Sillett and Holmes 2005). To date, studies that have documented detailed demographic conditions on either breeding or wintering grounds are independent points among a migratory bird's total distribution. Only when we can determine the strength of, and the geographic connectivity between breeding and nonbreeding populations will conservationists be able to focus efforts in specific problem areas; currently such connectivity remains mostly unknown (Webster et al. 2002, Webster and Marra 2005, Boulet and Norris 2006, Marra et al. 2006), but preliminary studies of connectivity in Black-throated Blue Warbler (Rubenstein et al. 2002), Yellow Warbler (*Dendroica petechia*; Boulet et al. 2006), American Redstart (Norris et al. 2006) and Wilson's Warbler (*Wilsonia pusilla*; Paxton et al. 2007) are available. It is clear, though, that our goal should be an understanding of how migratory bird populations are limited both within and between seasons, and in locations throughout the annual cycle.

In the remainder of this paper, we use the Sherry and Holmes (1995) model as an organizational framework, focusing on four major potential limiting periods: breeding season, wintering season, and spring and fall migration periods. The focus is on studies of North American land-bird migrants, particularly those that winter in Mexico and the Caribbean. We review advances in our knowledge that have occurred in the past decade, but we also identify areas that require further work before effective conservation plans can be designed. After summarizing our knowledge of North American migrants, we briefly examine the other Western Hemisphere and at least partially tropical migratory systems to explore the state of our knowledge.

BREEDING-SEASON ECOLOGY AND CONSERVATION

For a migratory bird, the breeding season typically involves choosing a habitat, finding a mate, raising young, and undergoing a complete molt, in addition to

simply staying alive. As noted in the Sherry and Holmes (1995) model, habitat for breeding often varies strongly in quality, with good habitats defined as those that lead to higher reproductive success and survival. Early studies primarily focused on describing the habitats selected; in the 1980s, fragmentation studies showed that the size and location of habitats could affect the extent that they actually were used by the study species. Development of the field of landscape ecology and spatial tools like GIS facilitated understanding of how larger scale distribution of habitats affected use of specific habitat types for breeding and surviving.

Habitat selection and suitability

Wildlife managers and conservationists have long known that individual species have habitat preferences and that effective management involves providing sufficient high-quality habitats. With the development of quantitative approaches to avian ecology in the 1970s (James and Shugart 1970, James 1971), a great deal of effort was focused on studying the effects of habitat structure on community composition as well as diversity and on developing models to predict habitat suitability (Kahl 1985). These studies usually involved comparing habitat structure at song perches, nest sites, or territories to "non-habitat," or relating relative abundance in habitats or stands to continuous measures of habitat structure, usually through multivariate statistics (Capen 1981). Although these models seemed to disappear as interest in habitat fragmentation increased, we recently have been exposed to what are termed multistate models that combine aspects of landscape ecology with the detailed habitat structure measures of earlier studies.

Whether using simple individual multivariate models or modern multistate models, our predictions have become quite good, particularly when it is recognized that most habitats are dynamic because of the effects of disturbance (e.g., fire, wind, flooding, logging) and succession, and because many species are dependent on some form of disturbance to create habitat (Brawn et al. 2001, Thompson and DeGraaf 2001). For example, grassland birds often respond to prairie dynamics that vary from year to year (Zimmerman 1988), whereas shrub-scrub species can change in abundance in as little as three to six years following cutting in eastern forests (Thompson and DeGraaf 2001, Fink et al. 2006). Moreover, the spatial scale of habitat selection and of disturbance is increasingly understood (Askins 2000, Shugart 2004). Lastly, while we tend to recognize that there are second-growth and mature-forest birds, this dichotomy is too simple. In reality, species show preferences for different ages of forest within the second-growth and the mature categories. For example, several studies have found that species such as the Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapilla*), and American Redstart may be most abundant in mid-successional forests (Holmes et al. 1986, Holmes and Sherry 1988, 2001, Thompson et al. 1992, Hunt

1996), at least in parts of their range, and are less common in the older, more mature stands. The Wood Thrush has received much attention for its widespread declines, including the possible effects of acid rain on eggshell thickness (Hames et al. 2002), but less has been said about the possibility that some portion of these declines may be from the maturation of forests in much of its former breeding habitat (Holmes and Sherry 2001, Ahlering and Faaborg 2006). Recently, there have been concerns because applications of these models often carried *Field of Dreams* ("if you build it, they will come") assumptions (Ahlering and Faaborg 2006), when recent behavioral work suggests that colonization of appropriate habitats may not occur without the proper behavioral cues. A final possible complication to our understanding of breeding habitat selection involves within-season shifts of territories, as birds fine-tune habitat use with the development of vegetation (Betts et al. 2008b).

New discoveries about habitat use after nesting but before migration require that we expand our look at habitat requirements at this season. For example, post-fledging juveniles and post-breeding adults may use different habitats than where they nested (Anders et al. 1998, Pagen et al. 2000). In the case of the Wood Thrush, the preferred late-season habitat involves lush second growth such as that found in clearcuts or riparian openings. In many cases, post-breeding adults also go to these habitats to molt late in the summer (Vega Rivera et al. 1999). Recent work clearly demonstrates higher survival and reduced daily movements by juveniles once they move into these habitats with denser cover, suggesting predation is one of the relevant selective pressures responsible for this behavior (Fink 2003). Juvenile Swainson's Thrush (*Catharus ustulatus*) move from riparian areas to mixed-hardwood forests and coastal scrub after fledging, searching for ripening fruit (White et al. 2005). Recent netting studies within clearcuts in eastern deciduous forest have expanded the list of forest-breeding species that appear to use second-growth vegetation in late summer, but these studies did not show if such habitats were required by these species (Marshall et al. 2003, King et al. 2006, Vitz and Rodewald 2006; J. Faaborg, P. A. Porneluzi, R. Brito-Aguilar, and R. L. Clawson, *unpublished manuscript*). These post-breeding habitats may be critical to both the juvenile and adult survival components of breeding-season fitness, but they have not been studied in depth (Ahlering and Faaborg 2006, Whittaker and Marzluff 2009).

It is interesting to note that, while most movements in eastern forest-breeding birds are in the range of 10 km or less, many western birds of the arid shrub-steppe apparently undergo a molt-migration, heading south to areas where monsoonal rains allow for higher quality habitats for the molting period, then finishing migration to the wintering site later (Young 1991, Voelker and Rohwer 1998, Voelker 2004). Although we have known about molt-migration in waterfowl for many years

(Allen and Rutter 1958), its occurrence in songbirds is significant for conservation efforts but poorly understood. This situation is made even more complex by the recent discovery that some of the birds that move to Mexico breed again in that region (Rohwer et al., *in press*).

It is possible that we have underestimated the importance of molting and molt-related mortality to the demography of birds. It has long been known that most temperate birds do not molt and breed at the same time due to energetic constraints (Murphy and King 1992, Hedenström 2006). In the tropics, molt and breeding may overlap, but only under specific demographic conditions (Foster 1975). Molt in small birds (such as most migrants) results in a complete turnover of body protein, while such costs are even greater in larger birds, which show less frequent replacement of feathers (Rohwer et al. 2009). If feather growth is rushed, the quality of the feathers has been shown to be poor (Dawson et al. 2000). Thus, heavy investment in breeding, perhaps through multiple failed attempts, may result in low-quality feathers, which may result in lowered subsequent survival and reproductive success (Nilsson and Svensson 1996). Is it possible that the movement of a forest-breeding bird in the eastern United States to a regenerating clearcut for molt is as critical as the molt-migration of a bird from Montana to Mexico? The importance of molt to migrant demography requires further investigation.

Habitat fragmentation and conservation

Much work focuses on how habitat fragmentation affects the distribution and abundance of birds (Villard et al. 1995). Much of this started by using an island biogeography approach centered on how birds responded to natural habitat "islands" that varied in size and isolation within the "sea" of human-disturbed habitats (MacArthur and Wilson 1967). Virtually all studies of avian distribution along a gradient of habitat sizes find that small fragments support fewer species than large, and that generally certain species or types of species disappear as fragment size declines. The result is that many species occur only on fragments of a sufficient size; this initially was considered the minimum area requirement (MAR) for a species. Obviously, managers needed to preserve habitat blocks of at least this minimal size to support the total regional species pool, but early attempts to define MARs for many species were simplistic. Subsequent work has shown a nested pattern of distribution and demography that occurs in many species with increasing habitat size. Often, the smallest fragments where a species occurs may have only a single or a few singing males, often without mates. With increasing habitat size, pairing success may increase, but only within a relatively large fragment does one find abundance, pairing success, and nesting success patterns that are typical of large, contiguous habitats (Van Horn et al. 1995, Burke and Nol 2000). Similarly, the kinds of

prospecting behaviors associated with locating the most propitious potential nesting site may necessitate larger areas of contiguous habitat than previously recognized (Sandercock et al. 2000, Martin et al. 2006; T. W. Sherry, J.-D. Lebreton, and R. T. Holmes, *unpublished manuscript*).

Attempts to understand the mechanisms leading to these spatially explicit patterns of demography quickly focused on what some viewed as the twin demons of nest predation and brood parasitism (Donovan et al. 1995, Robinson et al. 1995), the latter primarily involving the Brown-headed Cowbird (*Molothrus ater*). In many fragmented habitats, cowbird populations are artificially high, such that parasitism rates approach 100% for open-cup nesting birds. This parasitism reduces success of the host through a variety of means, mostly from a reduction of host fledging success through competition with the cowbird young, but also from a reduction of host clutch size through egg removal or breakage by the cowbird adult, and possibly increased predation on the nest through the noise made by the cowbird fledglings (Dearborn 1999). A single cowbird egg usually causes small hosts with relatively long incubation periods, such as some vireos and flycatchers, to lose their entire brood because of competition with the cowbird nestling (Rothstein 1975, Eckrich et al. 1999, Kus 1999, Whitfield and Sogge 1999). Some direct observations of cowbird depredation on eggs and young have been noted (Tate 1967, Sheppard 1996), and two studies have indicated that cowbirds may manage or “farm” host populations by destroying unparasitized nests that are too far along to be parasitized, thereby forcing the hosts to renest and make nests available that are in the early stage appropriate for parasitism (Arcese et al. 1996, Hoover and Robinson 2007). These predation behaviors do not appear to be widespread, as many other studies have not found these effects and other studies have documented a range of nonparasitic songbirds also depredate nests (Sealy 1994, Paradzick et al. 2000). Moreover, cowbirds committed only one of 25 videotaped nest predation events in a Missouri study site where they were abundant (Thompson et al. 1999).

Long-term, large-scale cowbird control programs have been instituted to protect several endangered species. Although these programs always result in large increases in host reproductive output, they have had a mixed record when it comes to the ultimate measure of success, namely increases in the size of the host's breeding population (Rothstein and Peer 2005). Least Bell's Vireos (*Vireo bellii pusillus*) and Black-capped Vireos (*Vireo atricapillus*) increased dramatically and quickly after the initiation of cowbird control on large military bases (Eckrich et al. 1999, Griffith and Griffith 2000), although increased habitat was probably also a significant factor. In contrast, Kirtland's Warblers (*Dendroica kirtlandii*) did not increase for 15 years after cowbird control eliminated nearly all parasitism, but increased dramatically after wildfire-created habitat of

appropriate age became extensively available (DeCapita 2000). Similarly, Southwestern Willow Flycatchers (*Empidonax traillii extimus*) have not increased after cowbird control programs in California and Arizona (Kus and Whitfield 2005), while populations without cowbird control have remained steady (Farmer et al. 2003a, b, Rothstein and Peer 2005).

It is possible that cowbird control programs were vital in keeping the Kirtland's Warbler (*Dendroica kirtlandii*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*) from going extinct. However, there is no hard evidence for this conclusion and good reason to attribute all cases of endangered species in which cowbirds are threats primarily to anthropogenic habitat loss having reduced these hosts to remnant populations that cannot withstand another pressure such as cowbird parasitism (Fig. 3; Rothstein and Peer 2005). Any host species unable to withstand cowbird parasitism under any conditions would have gone extinct long ago as fossils and DNA sequence data indicate that cowbirds have been in North America for at least 500 000 to a million years (Rothstein et al. 2002, Rothstein and Peer 2005). Nevertheless, it seems prudent to enact cowbird control when cowbirds appear to be a factor in an endangered species' plight. But there is considerable controversy surrounding all major cowbird control programs from ethical, financial, and practical perspectives (Ortega et al. 2005). The Kirtland's Warbler program alone has resulted in killing well over 100 000 cowbirds, which may no longer be necessary now that this species' population numbers at least 1300 pairs (data *available online*)²² and has expanded into Wisconsin, where the success has been attributed to cowbird control (U.S. Fish and Wildlife Service 2008) and Ontario, Canada, where there has been no such control (Richards 2008). Funds used for cowbird trapping might be put to better alternative uses. Furthermore, an undue emphasis on cowbird control means that it can sometimes be used as mitigation for habitat destruction even when the control is not needed and control deflects attention from the real problem, which is habitat loss (Rothstein and Peer 2005). Nevertheless, large-scale cowbird control programs assume considerable momentum and the managers involved frequently seem to be reluctant to change these programs.

Nest predation rates tend to be high in fragmented habitats, sometimes approaching 100%. Obviously, such high predation risk makes it difficult for a population to replace itself. Increased nest predation is often explained by the fact that fragmented habitats support higher populations of mid-sized nest predators such as raccoons (*Procyon lotor*) and crows and jays, although the role of specific predators on nest loss has been difficult to determine. Paradoxically, recent work in Canada has shown lower nest predation rates on a Neotropical migrant passerine occurring in small fragments compared to larger continuous habitat blocks (Hannon and

²² (www.michigan.gov/DNR)

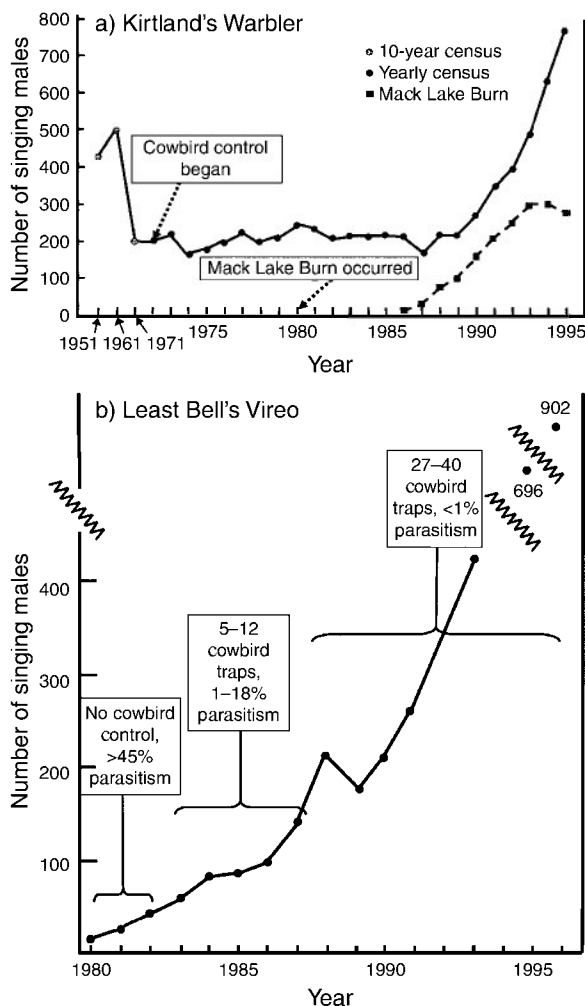


FIG. 3. Two examples of population response of endangered species to cowbird control. (a) In the case of the Kirtland's Warbler, cowbird control did not affect warbler numbers, but the increase in breeding habitat following the Mack Lake Burn did (DeCapita 2000). (b) In contrast, numbers of singing male Least Bell's Vireos at Camp Pendleton, California, USA, showed a drastic reduction in the rate of parasitism and a rapid increase in the number of vireos following cowbird control efforts (Griffith and Griffith 2000).

Cotterill 1998, Friesen et al. 1999), perhaps the result of fragmented habitats not being able to support certain predators such as accipiters and other raptors. Tewksbury et al. (1998) showed a similar situation, where the smallest fragments could not support the most common predator (rodents), such that birds in larger fragments had lower nesting success.

Much of the information about nest predation comes from the use of artificial nests, a method with important biases (Faaborg 2004, Moore and Robinson 2004). Recent studies using infrared video cameras to monitor actual nests day and night provide a very different picture of who the major nest predators are. For example, in Missouri, artificial nests were depredated primarily by

corvids and raccoons, real nests mainly by snakes (Thompson and Burhans 2004). Given that natural rates of nest predation in what we consider pristine habitats often approach 50%, most species have evolved rapid re-nesting behavior. Such re-nesting may be of little use when predation rates approach 100%, but in cases where predation is lower, individual pairs may be successful in most habitats following multiple attempts (Fink 2003, Morris 2005). However, the energetic and survival costs to females of repeated nesting remain unknown. In addition, when breeding continues late into the season and birds must molt before migration, they may arrive late on the wintering grounds, which constitutes a seasonal effect that may decrease fitness during the nonbreeding season (D. L. Morris, J. Faaborg, B. E. Washburn, and J. J. Millsbaugh, *unpublished manuscript*).

Whereas early studies of area sensitivity focused on habitat area, studies of parasitism and nest predation often tried to relate such patterns to habitat edge. Both fragment size and the amount of edge, however, are confounded because of the relationship between patch perimeter and area (Parker et al. 2005). The question then became "Do small fragments have low success because they are all effectively edge, or because they are small?" A great deal of effort was expended studying the importance of edge effects in fragmented systems and the threshold at which such edge effects end. Although 50 m has often been used as the relevant threshold for edge effects (Paton 1994a), other studies have shown species that respond to edge at 300 m or more (Van Horn et al. 1995). To some extent, these issues were resolved as ecologists developed more specific hypotheses for the mechanisms behind elevated brood parasitism and nest predation. Recent radiotelemetry work has shown that species previously considered "edge sensitive" readily use edges even if they are detected by point counts, walking transects, or spot mapping less frequently than in habitat interiors (Mazerolle and Hobson 2003). In part, this is because use of edges can vary tremendously with time of day (Mazerolle and Hobson 2004).

Landscape ecology and the source-sink scenario

As the number of studies of fragmentation increased, researchers found great regional variation in how species and communities responded to fragmentation. In highly fragmented Midwestern forests, for example, many Neotropical migrants required blocks of vegetation of at least 200 ha, whereas in other regions species-area relationships occurred but with smaller minimum area requirements for most species, and some studies in Canada found few fragmentation effects. Landscape ecology and GIS tools helped link biological factors such as nest predation, cowbird parasitism, and predator abundance to landscape measures such as percentage of landscape in forest or agricultural habitats, mean habitat patch size, and amount of edge (Robinson et al. 1995, Donovan et al. 1997, Howell et al. 2000, Thompson et al.

2000). Most of these studies showed how the landscape matrix affected fragmentation effects, with fragments in heavily forested landscapes showing smaller negative effects than those in highly agricultural or urban landscapes (Marzluff and Restani 1999, Hobson and Bayne 2000, Dunford et al. 2002). These patterns were explained by the extent that the matrix surrounding the fragments supported the relevant nest predators or brood parasites. For example, agricultural landscapes supported more cowbirds and raccoons, to the detriment of birds attempting to breed in the remaining forests, than forested landscapes, even if some of the forest was in early stages of succession (Gram et al. 2003).

In virtually all landscapes, low reproductive success characterized small habitat patches, despite relatively stable long-term population trends. Because most ecologists at that time were exposed to demographic models that assumed that emigration balanced immigration, we searched for mechanisms that could be maintaining these local, closed populations. For example, some effort was put into determining what the effective population sizes of these isolated populations might be (Wenny et al. 1993), while others tried to quantify the survival rates needed to balance low measures of fecundity (Robinson 1992). Simultaneously, modelers were resurrecting a variety of metapopulation models to explore their relevance to fragmented landscapes. With the publication of a source-sink model by Pulliam (1988) and the realization that migrants that traveled thousands of miles between breeding and wintering sites might also disperse hundreds of miles from one season to the next, open population models became more relevant.

Metapopulation models look at how levels of dispersal among relatively isolated patches affect patch occupancy (Levins 1968). A group of small populations may experience some local extinctions, or “wink out,” while others are successful enough to provide dispersers to recolonize patches. Metapopulations may be fairly stable if the extinction rate of patches is balanced by the rate of establishment or recolonization of patches. The subset of metapopulation models described as source-sink models is based on source populations that rarely go extinct and regularly produce surplus individuals that disperse to sink populations (Pulliam 1988). Sink populations do not produce enough young to be self-sustaining and depend on immigrants to persist through what some earlier had called the “rescue effect” (Brown and Kodric-Brown 1977). Source populations should generally occur in large patches or contiguous habitat, while the sink populations should generally occur in smaller and/or more isolated patches (Nol et al. 2005). The source-sink model was quickly adopted by conservationists, as it easily explained the situations they faced. The conservation message was that protection of source populations was the most critical step in maintaining regional populations or even entire species.

Quantifying sources and sinks

The quantification of source-sink dynamics requires use of a fairly simple model that estimates the population growth rate, usually referred to as lambda. In typical life table or population models, if lambda equals 1 the population is stable, if it is positive the population is increasing, and if it is negative the population is decreasing. More formally, the equation looks like this and typically focuses on the female component of the population (Pulliam 1988):

$$\begin{aligned} & \text{Finite rate of increase (lambda)} \\ & = \text{adult female survival} \\ & + (\text{number of female young/female/year}) \\ & \quad \times (\text{juvenile female survival}). \end{aligned}$$

Obviously, all one needs is to gather the appropriate data for adult survival, juvenile survival, and fecundity (measured as number of females produced per year per female) and solve the equation for the component populations in the metapopulation.

Unfortunately, none of the three components used in these source-sink models is easy to estimate. Rigorous measures of adult survivorship require use of capture-recapture models that call for relatively large marked populations studied for a minimum of three years but preferably longer. Simple measures of return rate within a study population can index survival (e.g., Loery and Nichols 1985, Martin et al. 1995), but these rates are usually negatively biased (Sandercock and Jaramillo 2002) because perfect detection of animals during any type of census or recapture effort is rare. Modern estimation approaches properly deal with the fact that not all birds return to the same breeding or wintering site and not all returning birds are detected (Pollock et al. 1990, Lebreton et al. 1992). There is evidence that some Neotropical migrants disperse such long distances after a year or more of breeding that they are unlikely to be detected again in most studies, which by necessity are at a local scale. For example, 13% of banded adult Southwestern Willow Flycatchers moved 0.4–190 km to new sites after one year, and over a four-year span 22–34% of adults moved 2–30 km with a maximum of 220 km (U.S. Fish and Wildlife Service 2002). Incorporating these dispersal rates can result in much more accurate estimates of adult survival rates.

These model-based estimation methods require data from marked populations that can be resighted or recaptured over multiple years. Until recently, very few rigorous empirical measures of annual survival rates were available for Neotropical migrant species, but now estimates are available for a range of migrants including small forest birds (Table 1) and larger, long-distance migrant shorebirds and waterfowl (Table 2). Interestingly, apparent survival rates currently available for Neotropical migrants tend to cluster around 0.50 annually, whether measured on the wintering or breeding grounds.

TABLE 1. Estimates of apparent survival ($\hat{\phi}$) and standard errors (SE) from mark-recapture studies for Neotropical migrants from the literature.

Species	Best model	$\hat{\phi}$ (SE)	<i>n</i>	Years
American Redstart	$\hat{\phi}_{\text{constant}}$	0.56 (0.07)	NA	1973–1990
American Redstart	$\hat{\phi}_{\text{constant}}$	$\delta = \text{♀}: 0.55 (0.09)$	212	1993–1996
American Redstart	$\hat{\phi}_{\text{age+habitat+interval}\dagger}$	natural overwinter: 0.70 (0.04)–0.82 (0.03) \ddagger agricultural overwinter: 0.83 (0.07)–0.97 (0.04) \ddagger natural, between winter: 0.43 (0.07)–0.66 (0.04) \ddagger agricultural, between winter: 0.43 (0.07)–0.52 (0.05) \ddagger	634	1987–2000
Bell's Vireo	$\hat{\phi}_{\text{sex}}$	$\delta: 0.68 (0.05); \text{♀}: 0.43 (0.07)$	$\delta: 71; \text{♀}: 31$	1996–1998
Black-and-White Warbler	$\hat{\phi}_{\text{constant}}$	0.59 (0.07)	NA	1973–1990
Black-and-White Warbler	$\hat{\phi}_{\text{rainfall}\S}$	$\text{♀}: 0.53 (0.06)–0.57 (0.05)\ddagger$	516	1989–2003
Black-throated Blue Warbler	$\hat{\phi}_{\text{constant}}$	$\delta = \text{♀}: 0.43 (0.04)\ddagger$	151	1986–1999
Black-throated Blue Warbler	$\hat{\phi}_{\text{sex}}$	$\delta: 0.51 (0.03)\ddagger; \text{♀}: 0.41 (0.04)\ddagger$	336	1986–2000
Cerulean Warbler	$\hat{\phi}_{\text{constant}}$	$\delta: 0.49 (0.05)$	74	1995–2001
Eastern Kingbird	$\hat{\phi}_{\text{sex+habitat}}$	$\delta: 0.63 (0.06)–0.78 (0.06)\P; \text{♀}: 0.56 (0.04)–0.71 (0.07)\P$	$\delta: 183; \text{♀}: 158$	1989–1998
Ovenbird	$\hat{\phi}_{\text{sex}}$	$\delta: 0.60 (0.05); \text{♀}: 0.21 (0.09)$	136	1993–1996; 1996–1999
Ovenbird	$\hat{\phi}_t$	$\delta: 0.57 (0.13)–0.74 (0.41)$	40	1992–1996
Ovenbird	$\hat{\phi}_{\text{rainfall}\#\}$	0.53 (0.07)–0.63 (0.08) \ddagger	364	1989–2003
Swainson's Thrush	$\hat{\phi}_{\text{age+transient}}$	0.56 (0.03)	365	1979–2000
Wilson's Warbler	$\hat{\phi}_{\text{transient}}$	$\delta = \text{♀}: 0.50 (0.04)$	978	1979–1996
Yellow Warbler	$\hat{\phi}_{\text{sex+}\dagger\dagger}$	$\delta: 0.41 (0.05)–0.59 (0.06); \text{♀}: 0.33 (0.05)–0.51 (0.07)$	$\delta: 287; \text{♀}: 149$	1995–1999
Yellow Warbler	$\hat{\phi}_{\text{SOI}\ddagger\dagger}$	$\delta: 0.48 (0.05)–0.60 (0.06)\ddagger; \text{♀}: 0.41 (0.07)–0.62 (0.08)\ddagger$	$\delta: 215; \text{♀}: 166$	1993–2001

Notes: For each study we report the best model, apparent survival estimates for resident adults by sex and time (if available and applicable), number of individuals (*n*), the years included in study, study location, and the source citation. Model notation for best survival models are as follows: t, time-dependent (i.e., yearly variation); sex, male survival different than female; age, age-dependent survival (number of age classes varies by studies, but we only report survival estimates for adults here); transient, survival of residents different than transients (only estimates for residents presented in table); rainfall, rainfall covariate (varies by species and study; see additional footnotes); constant, no variation over time, sex, etc. A plus sign (+) denotes an additive effect. The best structure for capture probabilities varied between studies and, although modeled in all cases, is not reported here (see original sources).

\dagger Separate analysis done for natural habitats (black mangrove, coastal scrub forest, coastal palm forest, and dry limestone) vs. agricultural habitats (coffee and citrus). In both cases, the best model includes survival differences by age (adult vs. yearling), among habitat types and time intervals (overwinter vs. between winter).

\ddagger Model averaged estimates.

\S Best rainfall covariate for Black-and-White Warblers was total rainfall during the first six months (January–July) on the wintering grounds (Guánica Forest, Puerto Rico).

\P Range presented represents the range in estimates associated with three habitat types (creek, floodplain, upland) investigated in this study.

$\#\$ Best rainfall covariate for Ovenbirds was summer rainfall totals from the breeding grounds (southeastern United States).

$\dagger\dagger$ These results represent estimates from “dispersal” analysis, which included resighting efforts for territory centers (where birds were banded) plus extensive resighting efforts in additional Yellow Warbler habitat in the vicinity.

$\ddagger\dagger$ Best model included positive effect of mean monthly Southern Oscillation Index (SOI) on survival; higher survival was associated with years of La Niña conditions.

Recent studies of at least three parulids have shown that mortality rates during the winter and summer stationary periods are low (Marra and Holmes 2001, Sillett and Holmes 2002, Jones et al. 2004). Additional rigorous estimates of annual and season-specific survival from more species across a greater range of locations are clearly needed. Understanding patterns of variation in survival within and between seasons and across long time periods in relation to climate change and habitat variation are also important areas for more research. Population models that incorporate long-term variation in demographic parameters will ultimately be the most useful for conservation.

All capture-recapture models require information on return rates of individuals to either breeding or wintering

grounds over a period of years. While this works for some species, many other species do not show enough inter-annual site fidelity for mark-recapture techniques to be feasible. As smaller radiotelemetry packages become available, we will be able to answer questions regarding dispersal and survival even for these less site faithful species. By combining color-banding and radio-tracking, Yackel Adams et al. (2006) estimated post-fledging survival of Lark Bunting (*Calamospiza melanocorys*) in Colorado, USA. In most cases, we do not have good data for comparing survival rates between different locations or habitat types, within or between species. Apparent survival of Ovenbirds is similar in contiguous and fragmented forests of Missouri (Porneluzi and Faaborg 1999), but not in central Saskatchewan, where apparent

TABLE I. Extended.

Location	Source
Puerto Rico	Faaborg and Arendt (1995)
Saskatchewan, Canada	Bayne and Hobson (2002)
Jamaica	Johnson et al. (2006)
Missouri, USA	Budnik et al. (2000)
Puerto Rico	Faaborg and Arendt (1995)
Puerto Rico	Dugger et al. (2004)
Jamaica	Sillett and Holmes (2002)
New Hampshire, USA	Sillett and Holmes (2002)
Ontario	Jones et al. (2004)
New York, USA	Murphy (2001)
Saskatchewan, Canada	Bayne and Hobson (2002)
Missouri, USA	Porneluzi and Faaborg (1999)
Puerto Rico	Dugger et al. (2004)
California, USA	Gardali et al. (2003)
California, USA	Chase et al. (1997)
Montana, USA	Cilimburg et al. (2002)
Manitoba, Canada	Mazerolle et al. (2005)

survival is much reduced in small fragments (Bayne and Hobson 2002). For reliable regional lambda estimates, empirical estimates of survival and reproductive success need to be available from the same region. Currently, researchers must resort to using a survival value from a Midwestern fragment or the wintering grounds to compute lambda in an eastern habitat fragment because that is all that is available for that or a similar species.

Another large gap in the demography of most Neotropical migrants involves age-related survival. Juvenile mortality is probably concentrated during the first several weeks after fledging (Dhondt 1979, Kremetz et al. 1989, Sullivan 1989, Anders et al. 1997, Thomson et al. 1999). There are few if any reliable estimates of survival from fledging until first breeding. This period incorporates the time after fledging and leaving the parents that is spent in the vicinity of the breeding grounds, the first fall migration, the act of finding and acquiring a wintering site, survival over the winter, and the first spring migration that takes the young bird to its first breeding location. Because the first breeding site is generally far removed from the natal site, standard methods of marking birds have not allowed for even reasonable estimates of juvenile survival or natal dispersal for any migratory species. In a few species, natal dispersal distances are short enough that some estimates of juvenile survival have been possible (Payne 1991, Gardali et al. 2003), but it is dangerous to generalize from these limited studies because natal dispersal may be even more condition-dependent than other demographic parameters (Studds et al. 2008).

Given the absence of actual measures of juvenile survival, population modelers resorted to estimating juvenile survival as one-half adult survival. This was justified by assuming a lower juvenile survival rate that would balance production of young and adult survival in a stable population. However, as far as we know, few good measures of juvenile survival exist for any Neotropical migrant songbird during the first year of life. Because of the interest in post-fledging habitat use in forest birds, we have some estimates of survival based on radio-tracking of juveniles up to migration in the fall. These measures include estimates of 0.19 for Hooded Warbler (*Wilsonia citrina*) four weeks post-fledging in northwestern Pennsylvania, 0.39 for eight weeks post-fledging in a population of Yellow-breasted Chat (*Icteria virens*) in Indiana (Maxted 2001), and 0.75 for 14 weeks post-fledging in a population of Wood Thrush in Georgia (Powell et al. 2000). Obviously, if most adults have a survival rate of around 0.60 and a juvenile survival rate of around 0.30 the first year is needed for a stable population, the lower survival rates observed during a bird's first summer (both nestling and post-fledging survival) must be resolved. Certainly, if survival from fledging through the first outbound migration is as low as 0.40, but apparent survival during the entire first year is around 0.30, survivorship during outbound migration, overwintering, and the return migration must be extremely high, which seems unlikely. This is an important component of population dynamics that needs to be addressed.

Confounding all of these estimates of annual survival are issues of dispersal, fidelity, immigration, and emigration. The Cormack-Jolly-Seber open population model, the model most frequently applied to Neotropical migrant mark-capture/resighting data, can separate detectability from survival, but a primary assumption of the model is that if birds are alive, they are present on the site available for detection (Lebreton et al. 1992). Permanent and temporary emigration, as well as natal dispersal for the younger age classes will violate this assumption and can negatively bias survival estimates from these models because mortality cannot be distinguished from emigration. Recent advances in mark-recapture model development allow the separate estimation of movement (multistate models; Hestbeck et al. 1991, Brownie et al. 1993) or site fidelity (Barker's live/dead models: Barker 1997, 1999) given appropriate data, but these models are data intensive and currently have almost exclusively been applied to non-passerine Neotropical migrants (Table 2; Kauffman et al. 2003, Craig et al. 2004, Cohen et al. 2006). One exception is T. W. Sherry, J.-D. Lebreton, and R. T. Holmes (*unpublished manuscript*), who used a multistate model to estimate American Redstart apparent survival as 0.65 by accounting for heterogeneity in individuals' site fidelity with seasonal reproduction estimates, and simultaneously estimates breeding dispersal probability with a core-periphery sampling design. In general, emigration and dispersal have not been given adequate consideration

TABLE 2. Estimates of apparent survival ($\hat{\phi}$; from live recapture models) or true survival (\hat{S} ; from dead recovery or joint live/dead models) and standard errors (SE) from mark-recapture studies for non-passerine migrants from the literature (except where noted).

Species	Best model	$\hat{\phi}$ (SE)	<i>n</i>	Years
Blue-winged Teal	$\hat{\phi}_{\text{age}}$	♀: 0.49 (0.13)	197	1982–1993
Dunlin	$\hat{\phi}_{\text{age} \times \text{grp} \times \text{t}}^{\dagger}$	♂ = ♀: 0.17 (0.04, 0.51)–1.0 (0.00, 1.00) \ddagger	1051	1979–1992
Pacific Brant	$\hat{\phi}_{\text{Late spring}}^{\S}$	♂ = ♀: 0.84 (0.03)	NA	1986–1993
Pacific Golden-Plover	$\hat{\phi}_{\text{age} + \text{grp}}^{\P}$	♂ = ♀: 0.80 (0.02)	163	1979–1991
Peregrine Falcon	$\hat{S}_{\text{age} + \text{hab}}^{\#}$	0.86 $\dagger\dagger$ (0.03)	718	1977–1999
Peregrine Falcon	\hat{S}_{age}	0.80 (0.05)	938	1974–2000
Piping Plover	$\hat{\phi}_{\text{t}}$	0.30 (0.23)–1.0 (0.35)	204	1984–1994
Piping Plover	\hat{S}_{t}	0.64 (0.09)–0.75 $\dagger\dagger$ (0.10)	71	2001–2005
Semipalmated Sandpiper	$\hat{\phi}_{\text{sex} \times \text{t}}^{\ddagger\dagger}$	♂: 0.53 (0.43, 0.63) \ddagger –0.73 (0.57, 0.85) \ddagger ; ♀: 0.43 (0.33, 0.54) \ddagger –0.71 (0.55, 0.83) \ddagger	486	1980–1987
Snowy Plover	$\hat{\phi}_{\text{t}}$	♂ = ♀: 0.58 (0.05)–0.88 (0.08)	261	1990–1993
Western Sandpiper	$\hat{\phi}_{\text{constant}}$	♂: 0.49 (0.04)	256	1994–1997

Notes: For each study we report the best model, survival estimates for resident adults by sex and over a range of years (if available and applicable), the number of individuals included in analysis (*n*), the years included in study, study location, and the source citation. Model notation for best survival models are as follows: t, time-dependence (i.e., yearly variation); sex, sex-specific survival differences; age, age-dependent survival (number of age classes varies by studies, but we only report survival estimates for adults here); grp, a group or treatment effect (varies by study and detailed in footnotes where applicable); and constant, no variation over time, sex, etc. A plus sign (+) denotes an additive effect and a multiplier symbol (×) denotes an interaction. The best structure for capture probabilities varied between studies and, although modeled in all cases, is not reported here (see original sources).

\dagger Group effect (grp) was age at banding, and only estimates for birds banded as adults are presented.

\ddagger Standard errors were not available for this study, so 95% confidence intervals are presented.

\S Annual estimates of survival generated from the product of mean seasonal survival rates for each year from the best model. The best model included variation in survival rates between years for the late spring period only (15 April–1 June), with no differences between other seasons or years.

\P Group effect (grp) represents winter foraging behavior, as some birds defend foraging territories (territorial) and others feed in large flocks of varying densities (non-territorial). Only estimates for territorial adults are presented here.

$\#$ Best model included survival differences by age classes plus the additive effect of habitat type (urban vs. nonurban) on survival of first-year birds.

$\dagger\dagger$ Model-averaged estimates for adults.

$\ddagger\dagger$ Best model included the additive effects of sex and time ($\hat{\phi}_{\text{sex} \times \text{t}}$), but only estimates from the model with an interaction between sex and time were available.

regarding how they affect estimates of survival or ultimately, population dynamics. Even species we believe exhibit high site fidelity can still experience high rates of emigration or dispersal in certain habitats or in response to specific environmental fluctuations. Female American Redstarts wintering in Puerto Rico exhibit enormous variation in recapture and apparent survival rates from year to year (Dugger et al. 2004; J. Faaborg, K. M. Dugger, and W. J. Arendt, unpublished data). These large fluctuations likely reflect large changes in population numbers within the forest each year, and high variability in winter site fidelity. This is an extreme example, but more subtle effects can become evident when enough long-term data are considered.

Much more effort has been expended on estimating the other component of the source-sink equation, fecundity, or at least components of fecundity such as nest success. Ideally, fecundity estimates would be based on observations of identifiable individuals and the total number of young produced in a season. Of course, this has been rarely done because of the perceived difficulty of marking and following a sufficient number of birds (but see Holmes et al. 1992, 1996, Sillett et al. 2000, Sillett and Holmes 2005). Alternatives to this include observing unmarked parents or territories (Porneluzi

and Faaborg 1999, Anders 2000) to get a credible measure of reproductive success, and Vickery et al. (1994) has developed a system of behavior mapping to aid in such approaches.

By far the most commonly measured component of fecundity is nest success, probably because nests are easier to monitor than marked birds. Typically, nests are located and visited daily or over multiple-day intervals to monitor their fate. Harold Mayfield recognized the potential bias of naïve or apparent nest survival estimates (the percentage of observed nests that fail or succeed) resulting from the fact the nests that fail before they were found are not included in the sample. He proposed a simple yet elegant solution that estimated daily survival based on a simple enumeration of the pooled number of observation days for a sample of nests and the number of failures, with one important assumption, that daily nest survival within the population of interest is the same for all days and all nests (Mayfield 1975). The “Mayfield method” was the method of choice for the last three decades for hundreds of studies covering thousands of nests. However, more recent methods (Dinsmore et al. 2002, Shaffer 2004) do not require the assumption of constant mortality and can include habitat and time-varying covariates (i.e., nest stage, date, year) and are

TABLE 2. Extended.

Location	Source
Saskatchewan, Canada	Arnold and Clark (1996)
California, USA	Warnock et al. (1997)
Alaska, USA	Ward et al. (1997)
Oahu, Hawaii, USA	Johnson et al. (2001)
California, USA	Kauffman et al. (2003)
Colorado, USA	Craig et al. (2004)
North Dakota, USA	Larson et al. (2000)
Long Island, New York, USA	Cohen et al. (2006)
Manitoba, Canada	Sandercock and Gratto-Trevor (1997)
Utah	Paton (1994b)
Mexico	Fernández et al. (2003)

now the methods of choice. A 2005 symposium at the Cooper Ornithological Society meeting focused on this topic and the resulting *Studies in Avian Biology* (Jones and Geupel 2007) provides a valuable review. A distinct advantage of these model-based methods is the user can select a covariate to derive a better estimate of nest survival for the population of interest than is typically generated by empirical estimates from a “sample of convenience” (Shaffer and Thompson 2007).

It is sometimes overlooked that success at single nesting attempts is only one component of fecundity and that nest survival does not necessarily correlate well with annual productivity (Anders and Marshall 2005, Jones et al. 2005). Nest survival, as an index of productivity, does not account either for nesting attempts following a failure (re-nesting) or for repeated nesting after raising a brood (double brooding; Grzybowski and Pease 2005). For waterfowl, Cowardin and Johnson (1979) and Johnson et al. (1992) illustrated the relationship between nest survival and the success of an entire breeding season. For songbirds, nest survival alone may not be an accurate index to fecundity in some situations. For example, nest survival in a population of Golden-cheeked Warblers (*Dendroica chrysoparia*) was estimated as 0.14 ($n = 27$ nests), while monitoring of breeding territories within the same population in the same year indicated that 87.8% of pairs successfully produced fledglings (Anders 2000). Based on data from a marked population of Wood Thrush studied from 1974 to 1995, nest survival explained only half the variation in annual productivity (Underwood and Roth 2002). Dececco et al. (2000) found a similarly weak relationship between Mayfield estimates of nest success and season-long productivity of Red-eyed Vireo (*Vireo olivaceus*), Blue-headed Vireo (*Vireo altilicola*), Wood Thrush, and Worm-eating Warbler (*Helmitheros vermivora*). Studies by Jones et al. (2005) with the Black-throated Blue Warbler, in which double brooding and multiple nesting attempts could be determined in a color-banded population, suggested that Mayfield method underestimated nest success by 33% and population growth by 20%. The message from these

analyses is that measures of nest success per se are not sufficient for estimating annual reproductive success or seasonal fecundity. Instead, all nesting attempts of color-marked individuals through the breeding season must be determined.

The previous examples of weak relationships between nest survival and annual productivity are not surprising given that nest survival is only one component of annual productivity. Donovan and Thompson (2001) used a simple matrix model for a Neotropical migratory bird to demonstrate that, in addition to nest success, lambda was sensitive to the number of nest attempts, brood size, and occurrence of double brooding. In the absence of direct estimates of annual productivity, simple models that incorporate estimates of nest success, number of nest attempts, brood, size, and double brooding have been used to estimate annual productivity (Noon and Sauer 1992, Pease and Grzybowski 1995, Powell et al. 1999, Donovan and Thompson 2001), and the source-sink status of populations (Donovan et al. 1995, Burke and Nol 2000). Population projection models also need to incorporate density dependence. Sillett and Holmes (2005) show that although many factors limited a population of Black-throated Blue Warblers at Hubbard Brook, New Hampshire, over 20 years, density-dependent fecundity regulated abundance within the range observed on their study plots.

Even if birds in fragmented landscapes or low-quality habitats have similar annual productivity as those in higher quality habitats, juveniles may have lower survival if produced late in the season because of multiple re-nesting attempts. Some research suggests that young produced earlier in the year have higher survival rates than later produced young (McGillivray 1983), but none of this research is on Neotropical migrants. It seems reasonable to think that a Wood Thrush that fledges in September and makes it to the wintering grounds late will be less fit than a bird that fledges in June, has all summer to feed and learn how to avoid predators, and arrives on the wintering grounds early. But is this difference critical? For a Wood Thrush that needs to fit into a territory or home range on the winter grounds in competition with other Wood Thrushes, this may be a problem. The negative effects of such delays can be considered a seasonal effect. For an Indigo Bunting (*Passerina cyanea*) that joins a small flock in a cane field, it may be less of a problem. On the other hand, the bird that fledges early in the breeding season simply has to stay alive for a longer time before migration. Unfortunately, we know little about the factors that contribute to juvenile success in the nonbreeding season.

One might also wonder about the effects of repeated breeding and late productivity on female body condition, the female's ability to molt and gather enough energy reserves for migration, and ultimately her survival. Recent work by Morris (2005) has shown that Indigo Bunting that bred in fragmented habitat in central Missouri had to make repeated attempts and achieved

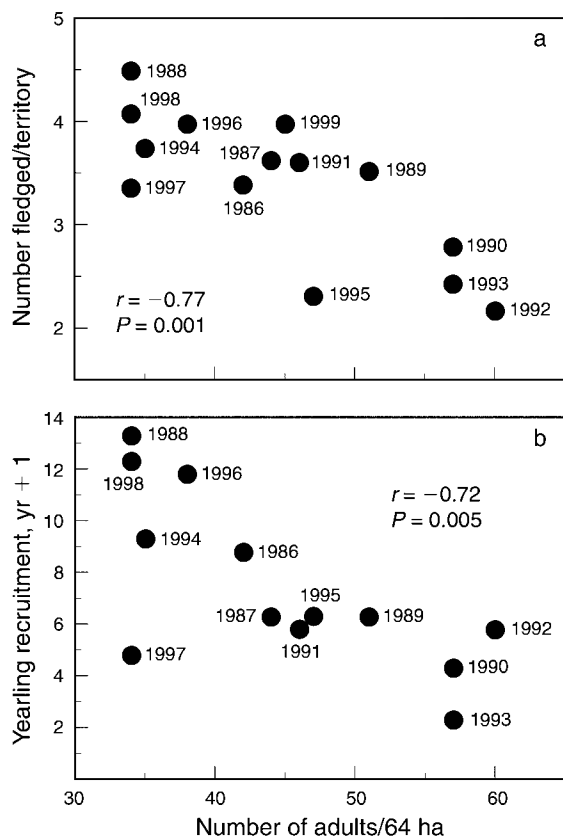


FIG. 4. Density-dependent relationships of Black-throated Blue Warblers at Hubbard Brook, New Hampshire, USA. (a) Annual fecundity is negatively correlated with adult warbler density in the same season, while (b) annual recruitment of yearling warblers is inversely related to warbler density in the preceding season. Numbers on the graphs are the years of study. The figure is modified from Sillett and Holmes (2005).

a lower body condition during the breeding season than females breeding within the Missouri Ozarks. The fragmented-site females, however, were able to recover this body condition quickly, while those in the Ozarks recovered more slowly, presumably because of differences in post-breeding habitat quality between these two sites.

Clearly better knowledge of fecundity of migrant species and the factors that affect it are needed to improve understanding of breeding ecology and conservation status and to model lambda or the source-sink dynamics of populations. Despite many studies of nest success more detailed knowledge is needed of season-long fecundity in a variety of landscapes. While there is general support for fragmentation and edge effects across many studies, most assessments of the population effects (estimates of lambda) are based on oversimplified models and many assumed parameter values. While this represents the state of our knowledge and is providing insight for conservation, a need remains for validation of the concepts through additional field study. The general failure of the only test of a management scheme based on

the principles of source-sink dynamics (Winter et al. 2006) reaffirms the need for additional fieldwork. This situation may be perfect for an active adaptive management program, where the results of management activities are followed in detail to test predictions related to the habitat changes made.

Making the case for breeding-season limitation

As noted earlier, most of the attention given to Neotropical migrant species prior to the 1970s focused on activities during their north temperate breeding season. During that time, numerous details accumulated on breeding life histories, nesting success, and habitat use of migratory species, but few if any investigators in those years even asked the question of when or where these populations might be limited. As a consequence, no research was designed to examine for limitation or regulation, although a number of studies provided quantitative data on local abundances and breeding biology (e.g., Nice [1937] on Song Sparrows (*Melospiza melodia*) and Nolan [1978] on Prairie Warblers (*Dendroica discolor*)). It was not until the Smithsonian symposium in 1977 and especially the Manomet-hosted meeting in 1989 that the questions about where and when limitation might occur came into focus.

The information summarized in the previous section on source-sink dynamics, patterns of reproductive success, and survival imply that events during the breeding period can have important impacts on the distribution and abundance of migrant birds, but do these conditions result in population limitation? Probably the only studies that have thus far been specifically designed to test, both observationally and experimentally, for population limitation in migrant birds in both summer and winter are those of Holmes, Sherry, Marra, Rodenhouse, and Sillett on Black-throated Blue Warblers and American Redstarts (see Holmes 2007 for a recent review). Long-term demographic data on Black-throated Blue Warblers, in particular, identify limiting factors during the breeding period and illustrate how abundance in this population is regulated (Fig. 4; Rodenhouse et al. 1997, 2003; Sillett et al. 2004; Sillett and Holmes 2005). Specifically, annual changes in abundance on a long-term study plot between 1969 and 2005 showed strong density dependence as indicated in a time series analysis (Rodenhouse et al. 2003), and most importantly, fecundity (number of young fledged per territory per breeding season) was found to be significantly negatively correlated with adult warbler density (Sillett and Holmes 2005). Experimental reductions in density of Black-throated Blue Warblers resulted in higher reproductive output (Sillett et al. 2004), illustrating the mechanism for this density dependence. Using a population model parameterized with field data, Sillett and Holmes (2005) demonstrated that this observed density-dependent fecundity was sufficient to regulate this warbler population within the abundances observed over the 30-year study. Further, the major factor limiting

fecundity in this system was found to be food (Lepidoptera larvae) abundance, and this was verified through both food reduction (Rodenhouse and Holmes 1992) and food supplementation (Nagy and Holmes 2005a, b) experiments. Nest depredation, although the major cause of nest loss, was shown not to be density dependent (Sillett and Holmes 2005), and its frequency related to an independent factor: annual differences in seed production by the dominant tree species affecting mammalian nest predator abundances (Holmes 2007).

Finally, recruitment of yearling Black-throated Blue Warblers into the breeding population was negatively correlated with adult warbler density in the previous breeding season (Sillett and Holmes 2005, Holmes 2007), and with fecundity in the previous season (Sillett et al. 2000). Moreover, recruitment of hatch-year birds into winter habitat in Jamaica was also negatively correlated with per capita fecundity on breeding grounds in New Hampshire. These relationships between breeding success and bird density in one year and the number of new recruits into both winter quarters and breeding grounds in the next season illustrate the importance of fecundity (i.e., a critical event of the breeding season) in maintaining local populations. These relationships between demographic events from one season to the next, which have also been reported for other migrant species (e.g., Nolan 1978 for American Redstarts), are all the more impressive when one realizes that two four-to-six week migratory periods and a six-month winter stay occur in the intervening time. A major implication of these findings from studies on Black-throated Blue Warblers is that habitat quality in the breeding grounds is of major importance to the maintenance of these populations through its effect on fecundity and the production of new individuals. More intensive demographic studies are needed of migrant populations in the breeding ground to identify high-quality habitats and then to determine how to maintain or increase these critical breeding habitats.

Ultimately, breeding-season events can impact a population in multiple ways, including fecundity, survival, and carry-over effects, and, as indicated above, can regulate migrant populations (Sillett and Holmes 2005). Carry-over effects are the ecological equivalent of delayed population limitation, or delayed density dependence in the special case of negative feedback on demographic parameters from population size (see Runge and Marra 2005, Ratikainen et al. 2008). For example, the Great Horned Owl (*Bubo virginianus*) is overwhelmingly the most important predator on breeding northern Swallow-tailed Kites (*Elanoides forficatus*) in Louisiana–Mississippi, causing extensive nesting failure as well as adult female mortality (Coulson et al. 2008), probably disproportionately in fragmented habitats because of the owl's preference for these landscapes. Such aspects of habitat quality need to be integrated into future research using modeling approaches that can

handle multiple, habitat-specific demographic measures (e.g., Morris and Doak 2002, Runge and Marra 2005).

NONBREEDING-SEASON ECOLOGY AND CONSERVATION

The fact that species showing the most consistent declines on the breeding grounds were those that winter in the tropics led many scientists to suggest that this was because of the loss and degradation of habitat on their tropical wintering grounds. Robbins et al. (1989), Terborgh (1989), and Rappole and McDonald (1994) supported this explanation, as did a variety of articles written for general audiences with such titles as *Silent Spring Revisited*, *Empty Skies*, and *Future Shock for Birdwatchers*. The logic underlying a cause-and-effect relationship is reasonable, given that extensive tropical deforestation was being documented at the same time as were Neotropical migrant declines, coupled with the fact that many of these species spend up to eight months on wintering grounds. Yet, the fact that so many scientists seemed to be willing to lump all Neotropical migrants into a single category and generalize about them is puzzling (Latta and Baltz 1997). Many knew that cutting down rain forest for pasture was devastating to many species, but they also knew that these pastures supported other species of Neotropical migrants, such that conversion of native habitats to agricultural habitats may just shift the amount of wintering habitat types available to migrants, creating both winners and losers: i.e., a “different” rather than a “silent” spring (Faaborg 2002). Although most of the discussion about declining migrants during the early 1990s focused on forest birds, subsequent analyses of Breeding Bird Survey (BBS) data showed that grassland birds had in fact suffered the longest, most widespread declines since the inception of BBS, even though they were not a major part of the initial focus (Peterjohn and Sauer 1999).

Survival is the key demographic factor during the non-breeding period. In winter, birds seek habitats in which to feed where they can avoid predators. In addition, some evidence suggests that winter habitat quality may impact the first steps in northward migration (Marra et al. 1998, Norris et al. 2004); because such cases involve just the final weeks before movement north, they are discussed separately.

Winter distributional strategies

Birds also display distinctive wintering strategies of habitat occupation. Some species move more or less perpetually in winter, as illustrated by the Northern Waterthrush (*Seiurus noveboracensis*) in northern Venezuela (Lefebvre et al. 1994). Among non-land birds, the Semipalmated Plover (*Charadrius semipalmataus*) and Black-bellied Plovers (*Pluvialis squatarola*) serve as other examples. Individuals of these species that go to northeastern Brazil in the fall stay only until December (Rodrigues 2000, Fedrizzi 2003), then move to unknown locations for the remaining two months of the non-breeding season, whereas those that spend the winter in

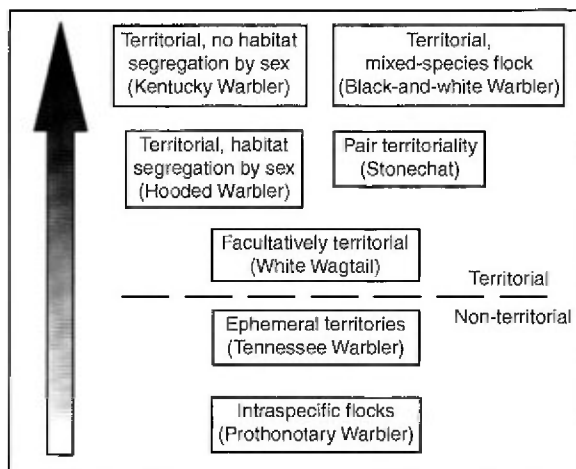


FIG. 5. Diversity of winter social systems in migrants to the tropics, arranged to show a hypothetical increase in male-female competition. Intraspecific variation may occur within this model; for example, the Black-and-white Warbler is common in dry forests in Puerto Rico despite the absence of mixed-species flocks there. The figure is from Stutchbury et al. (2005).

coastal Georgia stay there from November to early April (Rose 2006). Swainson's Hawk (*Buteo swainsoni*) is territorial on its breeding grounds, but adopts a largely nomadic, flocking lifestyle in the nonbreeding season (England et al. 1997). Other species may not have such a directed set of movements, but settle in a general area and more or less wander through the winter. This large home range could mean that most research techniques will list these birds as wanderers, even if this is not truly the case. Irruption species such as crossbills and nuthatches may move great distances in some winters and not at all in others (Bock and Lepthien 1976). Such vagile species present greater challenge in studying habitat use, survival, or other traits because of the difficulty of recapturing individuals through the winter, although radio-tracking is helpful for larger species (e.g., Wood Thrush; Rappole et al. 1989).

Many other winter residents exhibit behaviors where they remain in a relatively small area throughout the nonbreeding season as territorial birds to some degree, and many of these also show faithfulness to these sites from winter to winter (e.g., Holmes et al. 1989, Holmes and Sherry 1992, Marra et al. 1993, Wunderle 1995, Latta and Faaborg 2001, 2002, Faaborg et al. 2007). Both of these traits are conducive to studies that allow measures of habitat use and survival parameters. Many species show strong winter territoriality, such that individuals express nonoverlapping territories in winter much as pairs do during the breeding season (Holmes et al. 1989). In some cases, individual territories are occupied by a member of either sex with no obvious intersexual separation, often in sexually monomorphic species (Brown et al. 2000, Brown and Sherry 2008a, b, Smith et al. 2008), but in many species there is strong

dominance by age and/or sex, such that older males occupy the best territories, with females relegated to poorer sites (Holmes et al. 1989, Marra et al. 1993, Wunderle 1995, Marra 2000, Latta and Faaborg 2002). Species may also show strong site fidelity (Holmes et al. 1989, Marra et al. 1993, Latta and Faaborg 2001, Marra and Holmes 2001), with individuals returning to previously occupied sites for as long as 11 years (Black-and-white Warbler and American Redstart; J. Faaborg, *personal observation*; T. W. Sherry, *personal observation*). The wintering social system of the Ovenbird involves strong site fidelity, but broadly overlapping home ranges, possibly with strongly defended core feeding and roosting areas (Brown and Sherry 2006, 2008a). In some species, individuals have alternative wintering strategies, including both strongly site-faithful and floating individuals that are able to take advantage of differentially dispersed foods (Brown and Sherry 2008a). Other winter residents join mixed-species foraging flocks, with just one or two individuals of a species allowed within any flock (Hutto 1994, Latta and Wunderle 1996, Gram 1998). Because these flocks often have group territories, the winter residents may be overdispersed. Still others find their place as members of ant-following or other specialized foraging guilds, with social-dominance interactions limiting the number of individuals occurring at a site (Willis 1966). Other species commute from diurnal territories to nocturnal group roosting sites (Staicer 1992, Baltz 2000, Latta 2003, Smith et al. 2008).

Although we might learn much from a summary of where each Neotropical migrant fits into such a gradient of nonbreeding social behavior, we still suffer from limited data (Fig. 5; Froehlich et al. 2005, Greenberg and Salewski 2005). Most species have yet to be studied on the wintering grounds and for those that have, few have been studied at enough sites to understand regional variation. For example, Prairie Warblers in a large, native forest in southwestern Puerto Rico are sporadic in occurrence, rarely return to a site, and appear to wander widely. While more common in scrub and wooded pasture sites in southwestern Puerto Rico, this species is still non-territorial (Staicer 1992, Baltz 2000), contrasting with the territoriality observed in neighboring Hispaniola (Latta and Faaborg 2001). American Redstarts appear to be strongly territorial throughout most of their nonbreeding range, responding aggressively to playbacks in Florida, Trinidad, Puerto Rico, Jamaica, Cuba, Mexico, Belize, Honduras, and Panama (P. P. Marra, *unpublished data*). Redstarts also show strong site fidelity to most of these sites. However, females in the dry forests of Puerto Rico exhibit high annual variation in recapture and apparent survival rates, suggesting high annual variation in winter site fidelity at this site (Dugger et al. 2004, Faaborg et al. 2007). In addition, at the southern end of the redstart winter range females tend to be less territorial and even join mixed-species flocks (Lefebvre et al. 1994). Even for this well-studied species, patterns are variable

and more work is required to understand wintering ecology across its range.

Measuring nonbreeding habitat quality

Ideally, habitat quality in the nonbreeding season is measured using survival rates of the birds themselves (Johnson et al. 2006). Given the variation in strategies of spacing behavior among nonbreeding migrants, this measure is often hard to achieve. A variety of proxies for survival have been used. Site fidelity, as measured by overwinter site persistence and annual return rate, has been used as an indicator of habitat quality (Holmes et al. 1989, Wunderle 1995, Wunderle and Latta 2000, Latta and Faaborg 2001, 2002, Marra and Holmes 2001). However, using annual return rates to estimate site fidelity includes confounding factors of survival and detection probabilities. Annual return rates as measured in the winter quarters reflect winter survival, breeding-season survival, two long migrations, as well as site fidelity and detection probabilities. Therefore, site fidelity cannot be separated from annual return rates without separate estimates of survival and detection rates, which makes return rates of limited value unless resighting probabilities are extremely high. Overwinter (within-season) site persistence may be a better measure of habitat quality; those sites occupied longest or by the most dominant individuals can be considered higher in quality than those abandoned sooner or occupied by subordinates (Holmes et al. 1989, Marra and Holmes 2001). Detection probabilities should still be estimated to avoid bias, but presumably high site persistence within years is associated with increased amounts of resources, such as food and protection from predators, that are available to a wintering bird at a site.

For species with high levels of site faithfulness and that can be either recaptured or resighted easily, survival rates can be estimated and modeled in relation to habitat quality using mark-recapture models and computer programs such as MARK (White and Burnham 1999) and SURGE (Choquet et al. 2003). Modeling environmental effects on survival requires long-term data on marked individuals as well as measures of habitat quality and environmental variability. Relationships between survival rates and local or large-scale regional rainfall patterns as indices to habitat quality (Sillert et al. 2000, Dugger et al. 2004, Mazerole et al. 2005) and direct comparisons of survival among habitat types (Johnson et al. 2006) are among the few studies attempting to link apparent survival to habitat quality, but these kinds of models have great potential for the future.

Another method for understanding habitat quality involves the determination of individual body or physical condition of birds that are resident in a given habitat. Various studies have attempted to correlate site fidelity with fitness measures such as pectoral muscle mass scores (Brown and Sherry 2006), body mass (Holmes et al. 1989, Wunderle 1995, Sherry and Holmes 1996), changes in body mass (Marra et al. 1998), and

adjusted body mass (Marra and Holberton 1998, Wunderle and Latta 2000); individuals with higher fitness indices are expected to show higher site fidelity. All of these approaches could also be combined with covariates to estimate the actual physical condition of individuals across habitats. If individuals in a given habitat maintain higher body mass over the nonbreeding period and also have higher within-season site fidelity or survival compared to individuals in a second habitat, a reasonable conclusion would be that the first habitat was of higher quality than the second.

Johnson et al. (2006) recently tested a variety of these condition measures to see which were most correlated with the survival rates that they measured concurrently. Not surprisingly, they found that the body condition of individuals just before spring migration was highly correlated with their annual survival. If other studies support this relationship, it might be possible to evaluate winter habitats efficiently by measuring body condition of birds during an annual visit to a site just before spring migration.

Any wintering habitat may support species showing a variety of occurrence or persistence patterns, such that one must evaluate each species' status individually. For example, Faaborg et al. (2007) captured 21 species of possible winter residents during multiple three-day mist net sessions in southwest Puerto Rico during January from 1972 to 2006. Of these, 14 species were considered sporadic, with four species captured only once, five species with 10 captures or less, and five species that were captured in about half of all annual samples. Four species were caught nearly every year, but with some gaps of a year or more; some of these had individuals that were regularly recaptured from one year to the next but others did not. Only three of the 21 species were captured every year, with enough recaptured individuals that the apparent survival rate models mentioned earlier could be used. Some species were quite unusual; the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) was captured during only five of 34 years, but as many as a dozen birds were captured during some of those years. As a caution against drawing conclusions from short-term studies, Faaborg et al. (2007) illustrated how single-year samples could give misleading results about the composition of winter resident bird communities relative to the patterns found over the total 34-year study. Five-year and 10-year studies using mark-recapture data provided more accurate estimates of species richness in this system (Faaborg et al. 2007).

For species that are not site faithful, cannot be marked, or cannot be recaptured or resighted, estimation of survivorship is even more difficult. Certainly, persistent, annual presence of a species is a sign that the habitat is of some acceptable quality, although the possibility of a "sink" habitat for a wintering bird exists. When a species occurs only sporadically in a site, that habitat should probably be considered of limited value, although it may provide an essential, albeit occasional,

safety net (Faaborg et al. 2007). In these cases, a researcher might be able to measure habitat quality in some more functional way, perhaps by examining foraging behavior, food habits, or other behaviors that provide some clue as to the quality of the site (Sherry et al. 2005). Exciting new developments in the estimation of species occupancy and occupancy dynamics have the potential to provide answers to questions regarding habitat use and quality by migrants (MacKenzie et al. 2002, 2003). The only application of these models to a Neotropical migrant so far is the study of Betts et al. (2008a) for a breeding population of Black-throated Blue Warblers.

Conservation of nonbreeding migratory birds in the tropics requires determining consequences of patterns of habitat use in these species. Understanding both within- and between-season consequences should be the ultimate objective. Once optimal habitat types are determined, the availability of these habitats and their protection status must be assessed. Obviously, protected winter habitat must fall within the known winter range of species of interest for effective conservation. To provide the critically needed information for management, research programs in the future must focus on determining the spacing behavior patterns and survivorship of migratory birds throughout their range, as well as developing measures of habitat quality. This will be a major challenge in the coming decade.

Determining winter range

Even fundamental information regarding the distribution and abundance of migratory birds is often lacking or misleading. For example, Remsen (2001) highlighted winter range estimates based on museum records of the Veery (*Cartharus fuscescens*) across what appeared to be a vast winter range in the Amazon basin. However, he found that all birds collected in the middle of the nonbreeding season were from a small part of the southern Amazon, suggesting that this relatively small area was the critical winter range of the Veery and that other specimens were birds that were en route between breeding and wintering areas. In this case, destruction of habitat in a small region of the Amazon could cause precipitous decline in this species, a decline unpredictable without some kind of weighting of winter observations. Directing conservation efforts for winter habitat for this species to any sites other than the true winter range would also be misguided, unless these sites were important to help migratory birds (stopover ecology).

While we may want to reevaluate the winter range of many species, for some species we know practically nothing about their nonbreeding range. For example, the eastern Arctic breeding population of the pelagic Red-necked Phalarope (*Phalaropus lobatus*) seems to disappear into the oceans, with a few sightings off the coast of Africa the only firm winter records. This species has shown a dramatic decline of over one million individuals at a migration stopover site in the Bay of

Fundy (Duncan 1996). Whether the decline reflects only decreased use of the Bay of Fundy or the decline of an entire species is unknown. Obviously, conservation action is impeded without knowledge of the nonbreeding range of a species.

Is habitat fragmentation a problem in winter?

Given that many Neotropical migratory birds are sensitive to habitat fragmentation on their breeding grounds (largely through reduced nesting success), it seems reasonable to expect similar sensitivities during the nonbreeding season. It is possible that habitat fragments may be very attractive to first-winter migrants, such that density and diversity measures are high over the short term (Greenberg 1980), but that turnover and mortality of these birds is high. Such a situation would be analogous to a "sink" or "habitat trap" on the breeding grounds. The mechanisms driving this response at this time of year would be higher predation on adults or through effects on food supply. To the best of our knowledge, only two studies have ever attempted to look at the distribution of winter resident land birds in the tropics with regard to patch size, shape, or proportion of edge. Robbins et al. (1987) found no effect of fragmentation on migrants in Jamaica; the densities and diversities of migrants were as high on little pieces of habitat as in contiguous forests. Robbins et al. (1987) used mist nets to measure abundance, which is perhaps problematic. Capture rates in nets reflect both densities of winter resident birds (as is often assumed in such studies and which can be confirmed by long-term measures of return rate or survival) and movement patterns; a single sample of a fragment may catch many birds because they are in poor condition and moving about more than usual. Longer term studies, such as that of Wunderle and Latta (2000) on individually marked birds, can more easily determine if fragmentation affects survival or return rates of Neotropical migrant birds and at what spatial scales. In their study, they used different sized shade coffee plantations isolated in an agricultural landscape as a model for fragmented forests. They found that overwinter site persistence and annual return rates in the plantations fell within the range of values reported for natural forests, and that site persistence and return rates did not decrease with plantation size for the Black-throated Blue Warbler or the Black-and-white Warbler, although it did for the American Redstart.

Even if habitat fragmentation in the tropics is not a problem for many migrants, numerous studies have shown it can be devastating to populations of resident tropical birds (e.g., Sodhi et al. 2004, Stratford and Robinson 2005, Ferraz et al. 2007). In fact, using the same coffee plantations mentioned in the previous paragraph, Wunderle (1999) showed that plantation size had a significant effect on numbers of a variety of permanent resident species on Hispaniola, including several endemics. In addition, ecological interactions

such as competition between residents and migrants, as suggested by Dugger et al. (2004), may make the avian dynamics associated with habitat fragmentation even more complex. More work is needed to affirm the findings that winter residents survive as well on fragments as in contiguous habitat before we assign any positive value of fragments for winter resident birds. For instance, fragmentation may lead to increased growth of young or shrubby vegetation and increased insect diversity (and perhaps local insect density).

Making the case for winter limitation

Winter limitation was a popular explanation for declines in Neotropical migrant bird populations where these were first appreciated. While the logic for such a general hypothesis was appropriate, little quantitative information was available for any species that would allow us to assess whether or not winter habitat limitation was causing population declines (Latta and Baltz 1997). Robbins et al. (1992) first argued that the Cerulean Warbler offered a valid example of winter habitat limitation because of having a small winter range and occurrence within a limited elevation that had been heavily modified by agriculture during the 1980s. Although this argument seems valid and has been expanded (Rappole et al. 2003), it remains unsupported by demographic data, fueling the continued debate about why this species continues to decline (Hamel et al. 2004). To assess the extent of winter limitation for a species, we need adequate data on the size of the winter range, the habitats used within that range, and the dynamics of habitat change within that area, and habitat-specific demographic data. Without these data for a species like the Cerulean Warbler, with such a restricted winter range, a general case for winter habitat limitation of other migrants is difficult to defend scientifically (Runge and Marra 2005).

There are several lines of evidence, however, that suggest the winter season is potentially limiting for at least some species of Neotropical migrants. Studies of migrants in Jamaica indicate that individuals are dispersed on territories that are defended through intraspecific aggression (Holmes et al. 1989, Sliwa and Sherry 1992, Marra et al. 1993, Marra and Holmes 2001), some habitats being of higher quality than others. Survival and body condition also vary among habitats, with the individuals occupying lower quality sites unable to maintain body mass over the winter period, which in turn leads to delays in their departure in spring migration (Marra 2000, Marra and Holmes 2001) and perhaps lower survivorship. Similarly, individuals in lower quality habitats had elevated baseline corticosterone levels and reduced acute corticosterone secretion compared with those in better quality habitats, indicating more stressful conditions (Marra and Holberton 1998) that could affect survival. Furthermore, the mean body mass of American Redstarts over the winter period varies among habitats and is a strong predictor of

apparent survival rates (Johnson et al. 2006). Similarly, food supply was shown to control body condition of the Ovenbird strongly over the winter in Jamaica (Strong and Sherry 2000, Brown and Sherry 2006). Sherry et al. (2005) review the evidence for food as a limiting factor for migrants in the winter grounds.

Population limitation through interactions between seasons

The scenario for winter population limitation described in the previous section invokes the hypothesis that birds that cannot find adequate winter habitat necessarily die. Marra and colleagues studying the American Redstart in Jamaica have suggested another, more subtle mechanism for population limitation in migrant birds, one involving crossover effects between seasons. Their detailed, long-term studies on individually marked redstarts have shown that males and females segregate by habitat in the winter grounds. Older males dominate younger males and females, forcing them into lower quality habitat, in this case second-growth scrub (Marra and Holmes 2001). Those individuals (largely females) that spend the winter in the poorer quality scrub are in poorer physical condition and take longer to depart on spring migration (Marra et al. 1998). Later departure causes later arrival to the breeding grounds, and later nesting birds generally produce fewer young (Norris et al. 2004). If fewer young are produced during breeding, one might conclude that it was a breeding-season problem, when it ultimately was an effect of nonbreeding-season habitat quality, i.e., seasonal effects or a combination of a seasonal effect and local density dependence in the breeding areas (Fig. 6). These seasonal effects were discovered through the use of stable isotopes (Marra et al. 1998), which allowed the researchers to identify the winter habitat of individuals upon their arrival in the breeding grounds. Such seasonal interactions may possibly be the norm, but only through the tracking of birds through the annual cycle and the use of new and innovative methods, such as stable isotopes, will we be able to detect such subtle but important phenomena (Fig. 6; Webster and Marra 2005, Marra et al. 2006, Ratikainen et al. 2008). There are interesting parallels between this territory-based age- and sex-related dominance and the age/sex dominance that occurs within single-species flocks of birds, flocks that normally form during the nonbreeding season (Keys and Rothstein 1991). In both cases, females may minimize the effects of male dominance by moving into different habitats (Marra 2000) or wintering ranges (Gauthreaux 1978, Cristol et al. 1999).

Another prediction from the sexual winter-habitat segregation model is the existence of skewed sex ratios among breeding birds (Marra et al. 1993, Marra 2000). Indeed, many migratory land-bird populations exhibit male-biased skews, at least within local areas or study sites (Holmes et al. 1989, Van Horn et al. 1995, Wunderle 1995, Latta and Faaborg 2002), as do many

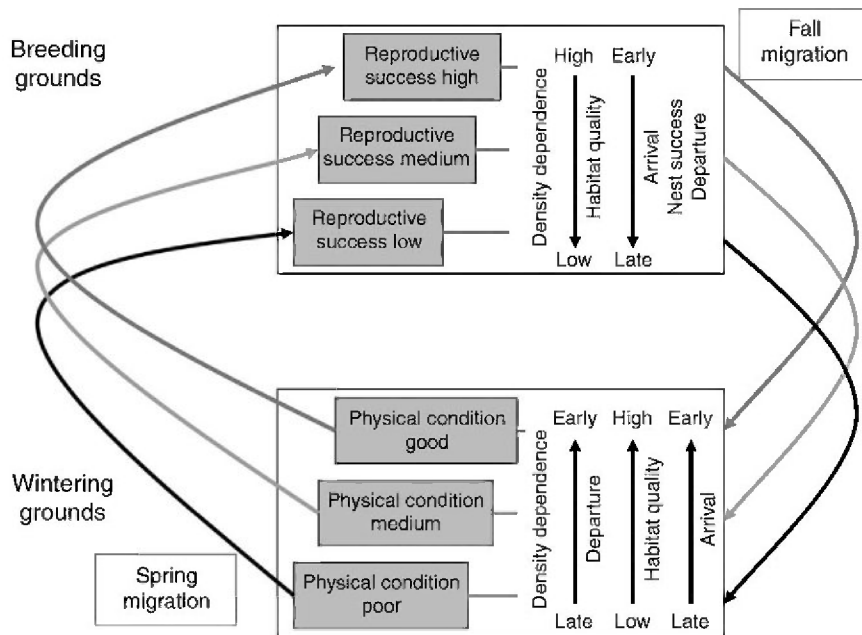


FIG. 6. A model showing seasonal effects (also called inter-seasonal or carry-over effects) from the wintering grounds on breeding success. Recent work by D. L. Morris, J. Faaborg, B. E. Washburn, and J. J. Millsbaugh (*unpublished manuscript*) on breeding success in fragmented forests suggests that, because many birds on fragments are not successful until late in the breeding season, similar effects may occur for them as they arrive late on the wintering grounds. The figure is modified from Runge and Marra (2005).

waterfowl (Johnson and Grier 1988). This difference has often been attributed to loss of females on the nest during incubation (a recent study found 10% of incubating Golden-cheeked Warblers (*Dendroica chrysoparia*) were lost to predators during nesting; Reidy et al. 2008). The winter-habitat limitation hypothesis, however, is a viable alternative (Marra and Holmes 2001). P. P. Marra (*unpublished data*) has shown that sexual habitat segregation occurs in at least 15 migrant land-bird species; if females are forced out of higher quality habitat by males, females may be disproportionately affected by habitat loss on the wintering grounds. Similarly, females forced to fly further from the breeding grounds to find a winter habitat may suffer higher mortality. Analysis of possible correlations between the existence of sex ratio skews and winter range and territorial behavior of migrant birds might be revealing (e.g., Brown and Sherry 2008a). For such tests, however, more study of winter behavior of migrants is needed to determine how rigid inter-sexual territorial behavior really is.

In one of the only tests of the Sherry and Holmes (1995) model of winter population limitation of migratory birds, Latta and Faaborg (2002) linked population responses and individual condition of the migratory Cape May Warbler (*Dendroica tigrina*) to prevailing ecological conditions across three habitats on Hispaniola to show how demography interacts with habitat quality, mediated by foraging ecology, to limit populations. Between-habitat differences in the types of resources available to Cape May Warblers (especially the availability of nectar)

determined foraging behavior, and a physiological effect of habitat differences on wintering Cape May Warblers was demonstrated through changes in adjusted body mass and body condition. A population response to differences in habitat quality was observed through sex- and age-class segregation and through between-habitat differences in the survival indices of overwinter site persistence and annual return rate. However, further work on the costs of late arrival on breeding grounds needs to be done across a range of species. Patterns supported by the American Redstart during the limited breeding season of such northerly areas as New Hampshire or Ontario, Canada (Marra et al. 1998, Norris et al. 2004), may not be as clear in more southerly breeding sites such as Missouri or Louisiana, where the breeding season is much longer.

EN ROUTE ECOLOGY AND CONSERVATION

A marvel of the Neotropical bird migration system is the fact that literally billions of birds fly hundreds to thousands of kilometers between breeding and non-breeding sites, many of them crossing such barriers as the Great Lakes, Gulf of Mexico, Caribbean Sea, and Atlantic Ocean. Even under the best of conditions, it is inevitable that many millions of birds may not make these journeys safely; with the intrusion of towers, buildings, and other human-made obstacles, migration certainly has not gotten easier in recent years. It is thus not surprising that Sillett and Holmes (2002) found that 85% of apparent annual mortality for the Black-throated Blue Warbler occurred during migration, a

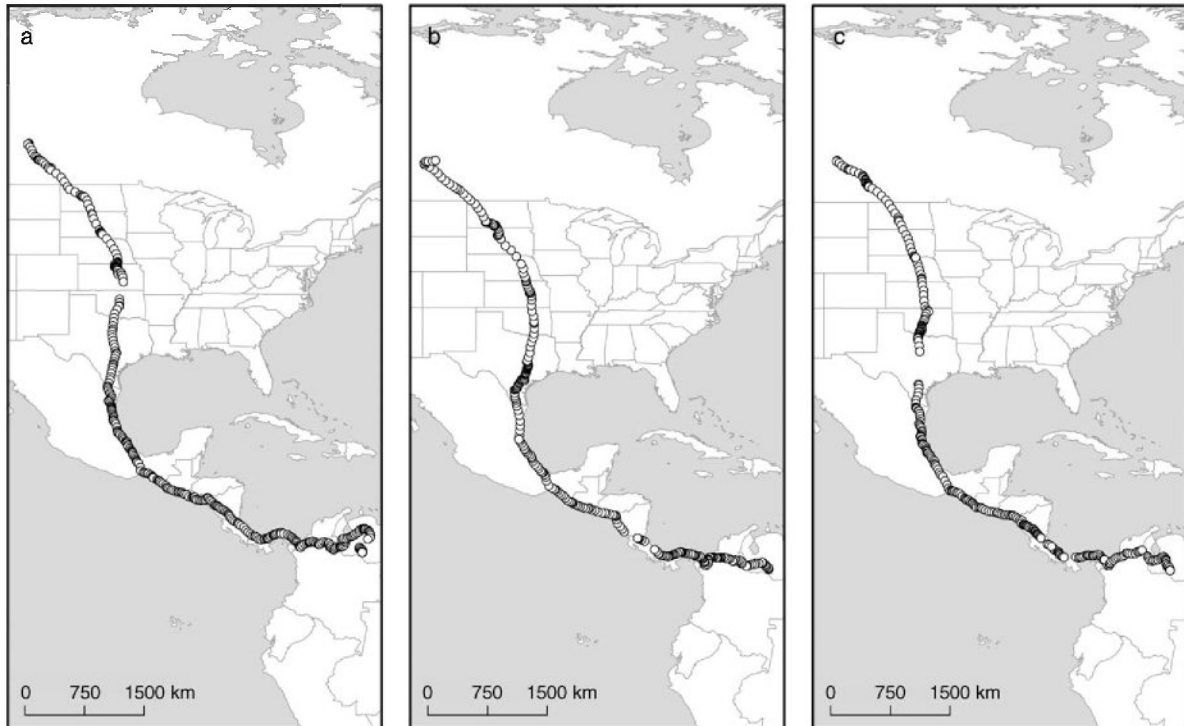


FIG. 7. Migratory tracks of a breeding adult Turkey Vulture (*Cathartes aura*), caught while nesting in a deserted farm house near Leoville, southern Saskatchewan, Canada, and fitted with a 70-g solar-assisted satellite platform terminal transmitter (PTT) and a dark-green wing tag with alphanumeric T-2. The bird was tracked for two outbound migrations and one return migration in 2007–2008. More than two million, and possibly as many as three million of these long-distance soaring migrants, travel from their western North American breeding grounds to wintering areas in southern Central America and northern South America each autumn (Bildstein 2006). The three maps represent (a) 1345 locations during outbound (autumn) migration on 60 days from 22 September through 20 November 2007; (b) 1036 locations during return (spring) migration on 45 days from 18 March to 1 May 2008; and (c) 1117 locations during outbound (autumn) migration on 52 days from 23 September to 13 November. Note the consistency of the flight paths across all three migratory journeys, as well as both breeding site and wintering area site fidelity. Darker areas indicate slower rates of travel; gaps reflect periods of missing data.

mortality rate more than 15 times higher than during the stationary periods of breeding and wintering. Despite the apparent importance of the migratory period as a cause of disproportionate mortality, we acknowledge again the potential importance of seasonal interactions, such as the importance of winter (or breeding) conditions that might influence the probability of which individuals actually die during migration. This possibility is strongly implicated by results such as those of Johnson et al. (2006), in which annual survival was well predicted by winter body condition.

Distribution of migration routes

In both North and South America, migration pathways tend to flow in a general north–south direction (Fig. 1), although the distribution of habitat types can alter this generality. For long-distance migrants heading for the tropics, the geographical position of the West Indies and South America to the east of North America results in many migrants from the eastern United States actually heading to the southeast in the fall and to the northwest in spring.

Routes of migrating birds often follow major geographical features such as mountain ranges, large rivers, and coastlines. However, Neotropical migrants tend to move in broad bands across the landscape (Biebach 1990, Hutto 2000, Gauthreaux et al. 2003) rather than follow narrow corridors such as those defined by the North American flyway concept (Fig. 7; Lincoln 1952). For waterfowl species that are closely tied to available water and generally move in a north–south direction, flyways serve as administrative boundaries that have worked reasonably well for coordinated conservation and management actions. For most other types of birds, however, these boundaries do not work well at all; hence, the creation of joint ventures and interagency partnerships that allow the consideration of entire species' ranges or major portions thereof. For example, shorebirds tend to congregate for short periods of time at very specific locations often associated with wetland areas, and movements for many species can be tracked through the use of radio transmitters and color marking (Myers et al. 1987, Warnock and Bishop 1998) and, more recently, satellite transmitters (Butler et al. 2001, Gill et al. 2009).

For such species, specific locations may have high importance for conserving populations while en route.

Neotropical migrants are generally responsive to major weather conditions, yet there are vast differences in migration strategies among species (e.g., the distances they travel, their timing, their wintering and breeding grounds, and their mode of migration). It is unlikely that two species will follow exactly the same path of migration. Within a species, strong seasonal patterns may characterize migration routes, e.g., in western hummingbirds that migrate north along the Pacific coast and south down the Rocky Mountains (Phillips 1975, Calder and Calder 1992), or those that go south over the Atlantic in the autumn but cross the interior of North America in spring. For example, it is thought that most Blackpoll Warblers (*Dendroica striata*) fly from the east coast of North America nonstop to South America using favorable winds from fronts early in their journey and trade winds near the end of their trip (Hunt and Eliason 1999, but see Murray 1989, Latta and Brown 1999); these trade winds preclude a similar return trip, necessitating movement to North America and then north. Several studies to date have demonstrated the importance of riparian corridors to migrant birds, particularly in the xeric intermountain West (Rappole and Ramos 1994, Otahal 1995, Winker et al. 1997, Yong et al. 1998, Finch and Yong 2000). Other studies have shown that migrants concentrate in a variety of inland and upland forests (Petit 2000, Rodewald and Brittingham 2004) and in montane (Austin 1970, Greenberg et al. 1974, Blake 1984, Hutto 1985, Carlisle et al. 2004) and desert (Wolf et al. 1996) habitats, with great variation in abundances among habitats (Hutto 2000).

En route habitat quantity, quality, and distribution

Given that massive habitat change has occurred across North America, especially since the arrival of Europeans, the hypothesis that bird losses during migration have increased and have led to declining populations is not unreasonable. Bottlenecks in the amount and/or quality of stopover habitat at some point may reduce migrant populations to levels lower than could be supported by either breeding or nonbreeding habitat. A dramatic example of this in a Neotropical migrant, albeit a shorebird, the Red Knot (*Calidris canutus*) occurs at Delaware Bay where the overexploitation of Horseshoe Crab (*Limulus polyphemus*) eggs by various fisheries has resulted in population level declines in Red Knots that stage there in the spring to fatten up on Horseshoe Crab eggs (Baker et al. 2004). With birds that move such great distances and have such large mortality rates already embedded in the system, reaching the level of precision needed to justify and implement specific conservation activities with regard to stopover habitat is very difficult.

Understanding how migrants deal with major barriers is one way to understand the potential limiting factors associated with migration. For example, Moore (1999), Gauthreaux (1999), and their colleagues have focused on migration across the Gulf of Mexico, including the

importance of the appropriate habitat types on barrier islands when conditions force birds into those habitats. Numerous studies have demonstrated the value to migration of quality habitats adjacent to ecological barriers such as Chenier plains (Palmissano 1970) and pine forests along the shorelines of the Great Lakes (Ewert and Hamas 1995). A few studies have demonstrated that abundances and the variability in abundances at stopover sites in the southwestern United States are related to a species' breeding range (Hutto 1985, Skagen et al. 1998, Kelly et al. 1999). Whereas the geographic distribution of Neotropical migration routes is broad, areas of concentrated movement may change seasonally, and not all areas are equally important to particular species (Hutto 2000).

Hallmarks of migration include the deposition of large energy reserves prior to movement and the need to rest and replenish depleted energy reserves en route. Birds increase the size of flight muscles and accumulate fat and other nutrient stores in preparation for migration, and then refuel periodically along migration routes, presumably to protect much-needed muscle tissue (Piersma 1990, Butler and Bishop 2000, Bauchinger and Biebach 2001). Short-distance and long-distance migrants fatten to differing degrees. Short-distance migrants can refuel regularly and store small to medium fat reserves of 13% to 25% of body mass. Long-distance migrants that cross large barriers, e.g., the Blackpoll Warbler, are capable of almost doubling their mass (from an average of 11 g to 21 g) largely from deposited fat (Berthold 1975, 1996). With the exception of soaring migrants including many raptors (Bildstein 2006), adipose fat, or lipids, is the primary metabolic fuel for migration with protein from muscle and digestive organs supplementing the energy reserves (Piersma and Jukema 1990, Ramenofsky 1990, Lindström and Piersma 1993, Battley et al. 2000, 2001, Bauchinger and Biebach 2001, McWilliams and Karasov 2001, McWilliams et al. 2004). Recent work has shown that many shorebirds actually absorb much of the nutrient value from their intestines before long flights, such that stopover ecology involves rebuilding the intestinal tract before actually rebuilding fat loads (Piersma and Gill 1998, Karasov and Pinshow 2000, Guglielmo and Williams 2003). Despite the obvious importance of stopover sites along the migration route for recovery of stored energy and nutrients, the ecology and physiology of birds at stopover sites is poorly understood (Lindström 1995, Moore and Aborn 2000).

Until recently, few techniques existed to determine and compare the quality of different stopover habitats. Rates of mass gain in different local habitats can approximate the value of these habitats (Dunn 2000). Simple censuses of birds in different habitat during stopover events provide some data on habitat quality, and these suggest the importance of areas such as riparian vegetation in the western United States, but they do not show if use of suboptimal habitat increases mortality during migration

or just delays the migrant for some period of time. Given the importance of lipid stores for fueling migration, there has been recent interest in their fatty acid composition (Pierce and McWilliams 2004). How and why the fatty acid composition of adipose tissue in migrating birds appears to change seasonally is not understood, but technical advances are making this determination possible. In addition, recent applications of plasma metabolite analyses hold promise for evaluating avian refueling performance during en route stops. Plasma metabolite and stable-isotope analyses are currently being used as tools to assess and monitor habitat quality and to provide information on the relative importance of different stopover sites used by migratory birds (Pierce and McWilliams 2004, Guglielmo et al. 2005, Cerasale and Guglielmo 2006). Finally, for soaring migrants, including many raptors, which do not depend heavily upon lipids to fuel their migrations, understanding other potential limiting factors such as the availability of roosting sites for large numbers of individuals is needed to better understand how habitat loss en route may affect the conservation status of these species (Bildstein 2006).

These biochemical techniques may allow researchers to see variation in body condition associated with habitat types, which is a step in the right direction, yet the fitness cost of being in a poor habitat may be small in many cases. Birds en route are sampled without any knowledge of their condition at the start of migration. If overwintering habitat quality results in a bird in less than optimal condition at the start of migration, en route studies may still be measuring inter-seasonal effects. Despite their value in dealing with a large barrier for many Neotropical migrants, these trans-Gulf studies also do not tell us what may happen later in migration, when the barriers to migration are much smaller than the Gulf of Mexico. Most trans-Gulf migrants typically fly over isolated coastal woodlands after crossing the Gulf and land where extensive forests occur (Gauthreaux and Belser 1999), so we must keep a proper perspective on habitat required for this leg of the journey. In fact, high-quality sites on the margins of large barriers may be most important for the least fit individuals, while more fit (and often older) individuals travel to more inland sites (Gauthreaux 1999). Studies have used modern radar systems to discover the details of migratory movements (Bonter et al. 2009). Heglund et al. (2008) have developed a DVD which allows you to survey bird distributions in Wisconsin using NEXRAD radar over a six-year period to see if similar locations are used for stopover from one year to the next; if we can identify repeatedly used stopover locations, we may be able to focus conservation on the most important locations.

More research is needed on habitat selection and its net benefits along the migration route (Petit 2000), taking into account the current distribution of stopover habitat. Areas like the Great Plains are undoubtedly much easier for forest migrants to cross now, because they have thousands of small woodlots, most associated

with farms that were not there 100 years ago. The many forest fragments in the Midwest that are not attractive to breeding migrants may be great places for birds moving from place to place. In a unique study, McGrath et al. (2009) showed that insectivorous land birds migrating along the Lower Colorado River tracked flowering phenology of trees as a reliable indicator of overall arthropod abundance. Understanding cues used to assess food availability is key to understanding habitat selection, but more experimental work such as this needs to be done using protocols that are more sophisticated than counts or capture rates.

Are en route losses limiting populations?

The persistence of migrant populations depends on the ability of individual migrants to find favorable conditions for survival and successful reproduction throughout their annual cycle. Although the complex annual cycle of migrants has made it difficult to resolve “when” populations are limited, factors connected with migration and the stopover biology of migrants must figure prominently in any analysis of population limitation or regulation. Mortality associated with long-distance bird migration is thought to be substantial (Lack 1946, Ketterson and Nolan 1982, Sillett and Holmes 2002, Johnson et al. 2006), and yearling individuals undoubtedly suffer greater mortality than adults (Johnson 1973, Greenberg 1980, Ketterson and Nolan 1982, 1983, 1985). For example, a favorable trade-off between the greater mortality of longer migration and increased survivorship associated with Neotropical wintering is more attainable by adult migrants that are more experienced in satisfying energy demand and avoiding the risks of migration (Ketterson and Nolan 1983). Further, yearling migrants are probably socially subordinate to more experienced, adult migrants, which may restrict the former’s access to limiting resources en route and decrease the likelihood of their survival (Moore et al. 2003).

If mortality is concentrated in the migratory period, then we must assume that factors that increase the cost of migration could have a disproportionate influence on overall population levels. For example, whereas individual fragmented woodlots may represent local population sinks on the breeding grounds, birds that find themselves in these habitats can often select alternative or more productive habitats. In contrast, the rigors of migration often place birds close to their physiological limits in unfamiliar landscapes, where they simply do not have the luxury of selecting alternative habitats. Therefore, a lack of suitable stopover habitat could result in death and contribute substantially to future population declines.

En route context

Although many land-bird migrants are capable of making spectacular, nonstop flights over ecological barriers, including the Mediterranean Sea, Saharan Desert, eastern Atlantic Ocean, and Gulf of Mexico, few

actually engage in nonstop flights between points of origin and destination; rather, they stop periodically for a few hours or days before resuming migration. Generally, the amount of time birds spend not flying, at intermediate sites while in migration, far exceeds their time aloft. How well migrants “offset” the costs of migration depends on how well migrants solve the problems that arise during stopover (Moore et al. 1995). Visualize a Red-eyed Vireo (*Vireo olivaceus*) gleaning caterpillars from the edge of hackberry leaves after stopping in coastal woodland following a long flight across the Gulf of Mexico in spring. Consider the many “decisions” she must make in response to the problems encountered en route. Besides the energetic cost of transport, she almost invariably finds herself in unfamiliar surroundings at a time when energy demands are likely to be high, and often is faced with conflicting demands between predator avoidance and food acquisition, competition with other migrants and resident birds for limited resources, potentially unfavorable weather, and loss of sleep, not to mention the possible need to correct for orientation errors.

Although the problems encountered en route are not different from those occurring at other times and places, with the possible exception of orientation errors, their perplexity is exaggerated by virtue of the context. For example, conflict often arises between the need to satisfy nutritional demands and the need to avoid predation because foraging can increase an animal’s exposure to predators, as shown in a Swedish study of habitat use by migratory Brambling (*Fringilla montifringilla*; Lindström 1990). These trade-offs are particularly complex for birds during migratory stopover because: (1) predation risk is variable and unpredictable during migration, (2) migrants often carry relatively large fat stores increasing their inertia, (3) migrants experience elevated foraging demands, (4) there is pressure to travel quickly, and (5) migrants lack information concerning predation risks and foraging opportunities (Cimprich and Moore 1998). The combination of these factors creates a complex and shifting environment within which migrants must trade off safety and foraging. To date, the behavior of birds confronted by this dynamic situation has received limited attention (but see Cimprich et al. 2005, Cimprich and Moore 2006, Buler et al. 2007).

En route consequences

Successful migration depends on solving these often conflicting problems, and the solutions are measured in units of time and condition upon arrival as well as during passage (Alerstam and Lindström 1990). For example, if our hypothetical migrant stays longer than usual at a stopover site, a penalty may be attached to late arrival at the next stopover site if resource levels have been depressed by earlier migrants. If she does not make up lost time, arrival on the wintering or breeding grounds is necessarily delayed. Migrants that arrive late on the breeding grounds, for example, may jeopardize

opportunities to secure a territory or a mate, or may result in reduced clutch size. Just a few days delay in onset of breeding can have important fitness costs (Nilsson 1994, van Noordwijk et al. 1995). Early nesting individuals typically lay more and larger eggs, and produce heavier nestlings and fledglings than delayed nesters (Carey 1996). It is also well established that the pre-breeding nutritional condition of parents affects reproductive success (Drent and Daan 1980, Price et al. 1988, Rowe et al. 1994). Although it is unlikely that a small passerine migrant could accumulate energy stores sufficient to produce a clutch of eggs (*sensu* Perrins 1970), the availability of resources in the form of endogenous fat stores acquired prior to arrival on the breeding grounds should improve parental condition and influence reproductive success among land-bird migrants (Sandberg and Moore 1996). Moreover, if our hypothetical bird departs a stopover site with lower than usual fat stores, she will have a smaller “margin of safety” to buffer the effect of adverse weather on the availability of food supplies at the next stopover. If a bird expects to “catch-up” with the overall time schedule of migration and maintain a “margin of safety” vis-a-vis anticipated energetic demands, she must refuel faster than average during the next stopover, and a domino effect may ensue.

American Redstarts and Pied Flycatchers (*Ficedula hypoleuca*), both intercontinental songbird migrants that arrive earlier in the spring, commence breeding activity sooner, and those individuals that arrive on the breeding grounds with surplus fat stores experience enhanced reproductive performance (Smith and Moore 2005). Perhaps one of the most obvious benefits of arriving with extra fat stores is insurance against variable environmental conditions encountered upon early arrival. Land-bird migration often outpaces phenological development of vegetation and terrestrial invertebrates as birds move north during spring migration (Slagsvold 1976, Ewert and Hamas 1995). Consequently, birds may arrive at high-latitude breeding grounds when food abundance is low. Early arrival may increase the potential for exposure to poor weather conditions such as late-season snowstorms, low temperatures, or extended periods of rain. Food limitation and/or poor environmental conditions may lead to substantial mortality, reverse migration, or to shifts in foraging behavior as birds attempt to overcome food limitation and offset increased thermoregulatory requirements. If migrants encounter unfavorable circumstances during the transition from migration to breeding, fat stores accumulated during passage would serve to overcome unpredictable foraging situations (e.g., Møller 1994), sustaining an individual until the environment becomes more suitable.

Finally, time of arrival on the breeding grounds and reproductive performance have been shown to be linked to habitat quality on the wintering grounds (Marra et al. 1998). We should expect that the consequences of winter habitat quality will be evident when migrants stopover

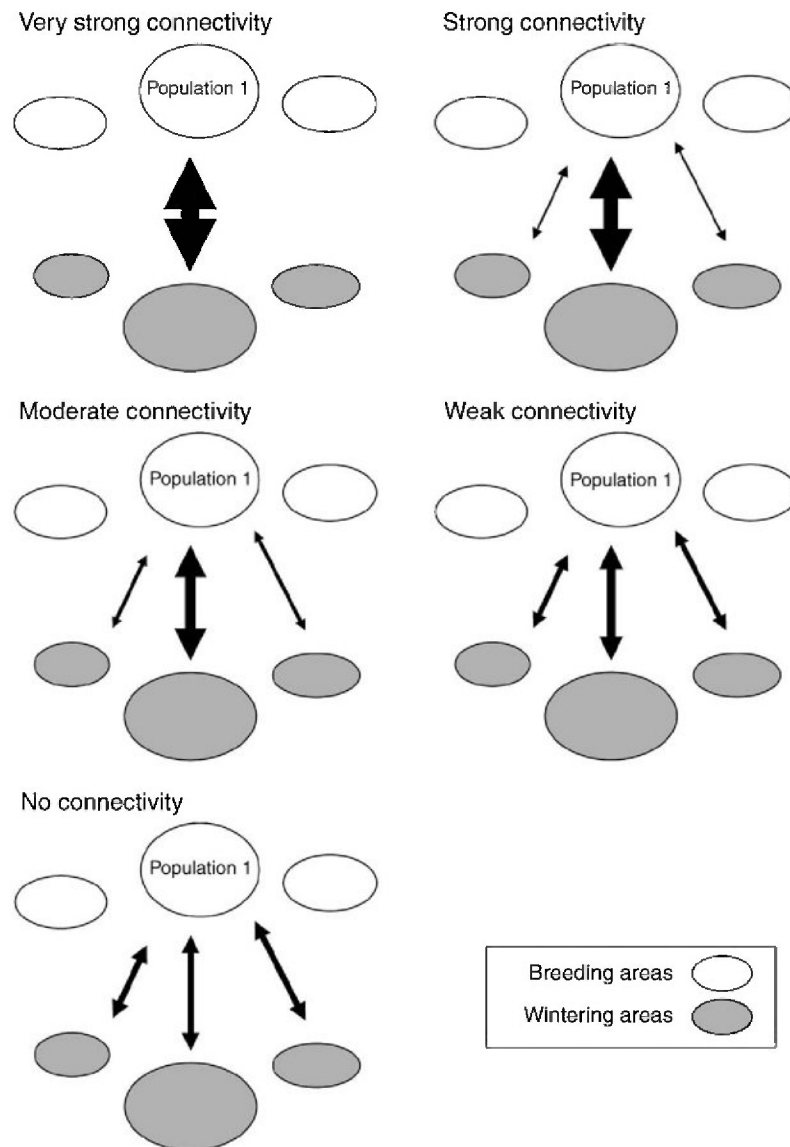


FIG. 8. Theoretical degrees of migratory connectivity in a fictional breeding population. Strong connectivity suggests that breeding and wintering grounds are tightly linked, while weak connectivity suggests that breeding birds mix widely on the wintering grounds. The figure is from Boulet and Norris (2006); reprinted with permission.

en route to their breeding grounds (i.e., linkage between winter ground events and stopover biology). Moreover, we should expect events during passage not only to influence the migrant's condition and schedule of passage established upon departure, but also to be responsible for differences in condition and schedule among migrants that departed at the same time and in the same condition.

CONNECTIVITY: CAN WE DELINEATE SUBPOPULATIONS OF MIGRATORY BIRDS?

We have reviewed the evidence that the effects on either the breeding or nonbreeding populations could have been caused by events in the preceding period, but

attempts to understand how these effects limit total populations are swamped by the size of the populations involved and our lack of knowledge about between-season movements within populations, i.e., migratory connectivity (Figs. 8 and 9; Webster et al. 2002). Until recently, though, we had very little information about any linkage between breeding and wintering populations, nor about whether birds from the same breeding region winter in the same area or disperse widely. Banding studies have been of little help, since far too few individuals are captured as adults on both breeding and nonbreeding grounds.

Fortunately, stable-isotope technologies, among others, have allowed us to address connectivity questions

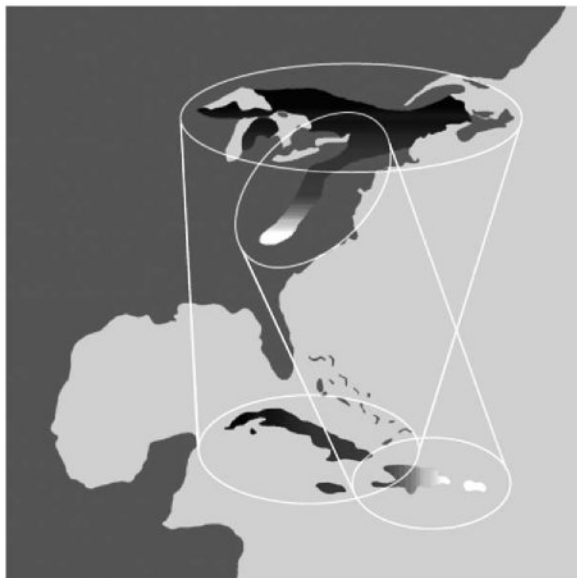


FIG. 9. Actual migratory connectivity in the Black-throated Blue Warbler. Birds from the northern part of the breeding range tend to winter to the west of those that breed in the Appalachian Mountains. The figure is from Holmes (2007), adapted from Rubenstein et al. (2002).

(Chamberlain et al. 1997, Hobson 1999, 2005, Rubenstein and Hobson 2004). Stable isotopes are forms of elements that behave identically chemically but differently kinetically due to slightly different masses of the nucleus. For example, the form of hydrogen known as deuterium (^2H) confers different behavior on water molecules because of a variety of processes that ultimately result in predictable isotopic gradients of this element in growing-season precipitation across North America (Hobson and Wassenaar 1997). Deuterium or other isotope levels in birds are acquired through diet and can remain fixed indefinitely in metabolically inert structures like feathers and claws. For metabolically active tissues such as blood, stable-isotope ratios represent a period of dietary integration that is ultimately related to the metabolic rate of that tissue, sometimes just weeks or months. One can collect a feather from a bird on its wintering grounds and get some idea of where that feather was formed (Rubenstein et al. 2002). Because it is thought that most birds in the eastern United States do not migrate large distances between where they breed and where they molt, we think that we get an excellent prediction of the general location of breeding of that bird. Thus, by combining knowledge of molt and the distributions of stable isotopes in food webs, researchers in North America have a reasonable chance of estimating at least the approximate latitude (in the eastern United States) or longitude (in northern Canada) of breeding or molt origin for a large number of migratory birds.

Although the use of stable isotopes in ornithology is relatively new, we have already learned a great deal

about the connectivity of migrant birds. Studies of the Black-throated Blue Warbler suggested that birds from the northern part of its breeding range (New England and Canada) wintered mostly in Cuba and Jamaica, whereas birds from the southern part of its range (mostly in the southern Appalachian Mountains) wintered further east in Hispaniola and Puerto Rico (Fig. 9; Rubenstein et al. 2002). Norris et al. (2006) surveyed the distribution of most populations of the American Redstart throughout the United States and found fairly strong linkages between wintering and breeding sites, with some populations showing leap-frog migration (northernmost breeding populations winter the farthest south and must pass over habitat with conspecifics) and others chain migration (latitudinal arrangement of populations is similar during both breeding and nonbreeding). Hobson et al. (2004) have linked wintering populations of Bicknell's Thrush (*Catharus bicknelli*) from the Dominican Republic with previously unknown breeding populations in southern Quebec and elsewhere (Hobson et al. 2001). Samples from Ovenbird, American Redstart, and Black-and-white Warbler from southwest Puerto Rico suggest that wintering birds mostly come from the eastern United States (Dugger et al. 2004), although the ranges of these birds cover much of North America. Furthermore, analyses of isotopic values in feathers of Black-throated Blue Warblers occupying local wintering sites in Jamaica showed that these individuals came from a wide range of breeding longitudes, e.g., from Nova Scotia to Michigan (Rubenstein et al. 2002). This finding indicates that there is considerable mixing of sympatric wintering individuals that arrive from different parts of the breeding range. The conservation implications of this finding are that loss of winter habitat will result in a broad and diffuse effect on migrant abundance in breeding populations, and vice versa (Rubenstein et al. 2002).

In perhaps the most thorough examination of linkages in a migratory species to date, Boulet et al. (2006) used stable isotopes, molecular markers, and banding records to understand the linkage between breeding and wintering sites in the Yellow Warbler. Individuals moved more or less north and south in this species, with eastern breeding populations also most common in the eastern portion of the winter range. The potential for linking breeding and wintering populations of birds with isotopes is impressive, and use of the methodology may provide other evidence about dispersal dynamics across regions. The use of stable isotopes is not without its problems (Hobson 2005, Wunder et al. 2005, Hobson and Wassenaar 2008), but many of these may be remedied by the proper understanding of the distribution of isotopes in the environment and better knowledge of how these isotopes are incorporated into different avian tissues. The latter requires carefully designed studies with captive birds (Pearson et al. 2003, Smith et al. 2008). The potential of this method is limited by knowledge of when and where molt occurs; depending upon which feather

was sampled on the wintering grounds, one might get variable answers about where breeding occurred (Gannes et al. 1997, Pearson et al. 2003). In many cases, the use of more than one feather type can overcome these problems at the species and population level, and the stable-isotope approach can be used to elucidate molt patterns of individuals (Pérez and Hobson 2006). Ultimately, integrating multiple isotopes with additional markers (including genetic and banding data with information on subspecific variation) and possibly trace metal signatures (Ruelas-Inzunza and Páez-Osuna 2004) could provide our best opportunity to probe migratory connectivity in a variety of species.

Alternatively, technological advances in remote-tracking devices such as radio-transmitters and data loggers (i.e., geolocators) have the potential to improve knowledge of migratory connectivity in land birds considerably, as it has already for raptors and seabirds. Stutchbury et al. (2009) recently used geolocators on Purple Martin (*Progne subis*) and Wood Thrush. Cochran's pioneering radiotelemetry work on migrating thrushes, already begun in the 1970s, has clearly shown the potential of this method by tracking individual birds over 1000 km stretches of their migration pathway (Cochran et al. 1967, Cochran and Kjos 1985). Various other studies have begun elucidating detailed long-distance movements of land birds using telemetry (e.g., Aborn and Moore 1997, Wikelski et al. 2003, 2007, Cochran et al. 2004).

MIGRATION WITHIN THE NEOTROPICS

The Neotropical Biogeographic Realm is generally described as including all of South America, including the vast Amazonian rain forests, plus Central America, the West Indies, and much of Mexico. Understanding migratory behavior is critical to understanding avian communities across this region, because the neotropics encompass the region where most temperate-breeding birds spend their nonbreeding season. We have already noted that most North American long-distance migrants winter in Mexico and the West Indies, although many populations occur in Central and South America, and locations as far south as the Pampas of Argentina support a number of North American breeding birds. Many tropical habitats in South America support a mix of migrant types, depending on the time of year. For example, a checklist of the birds from the Cocha Cashu Biological Station in Manu National Park in the upper Amazon Basin, Peru, includes 30 species of migrants from North America and 11 species of South American migrants, but half of the North American species are either shorebirds or raptors, and about half of that group simply pass through the region. In addition, while 41 species may seem like a lot, this constitutes less than 10% of the 526 species of birds recorded at the site (Terborgh et al. 1984).

Migration within the Neotropical Realm is less studied, and consequently less well understood, than the Nearctic–Neotropical migration we have discussed

earlier. The varying distance, direction, and periodicity of movements in migratory species in the neotropics leads to a bewildering array of migratory patterns. Intraspecific variation in migratory behavior adds another layer of complexity, with migratory status varying between populations in a given species, between individuals in a given population, and over time in a given individual. In part, this intraspecific variation results in a high incidence of overlap in breeding and nonbreeding ranges (Jahn et al. 2006), a relatively rare pattern in Neotropical migrants.

Here we attempt a broad overview of the migratory patterns observed within the Neotropical Realm. A wide array of terminology has already been brought to bear on the subject (Joseph 1997, Jahn et al. 2004, Mueller and Fagan 2008). We attempt to classify migration within the neotropics into four categories, not necessarily mutually exclusive, but broad enough to create a useful conceptual framework, and simple enough to avoid coining new terminology. The categories are austral migration, intratropical latitudinal migration, altitudinal migration, and (for lack of a better term) complex intratropical migration (Fig. 10).

Austral migration

Austral migration is the annual movement of birds from breeding ranges in temperate South America to nonbreeding ranges in the tropics, the mirror image of Neotropical migration. Approximately 50% of birds in Tierra del Fuego are austral migrants (Humphrey et al. 1970) and all Tyrant flycatchers (see Plate 1) are migratory at that latitude (Chesser 1998), placing the predominance of avian migration in temperate South America on par with comparable latitudes in North America. Yet, despite the enormous diversity of birds in subtropical and temperate regions of South America, woefully little is known about the migratory habits of the vast majority of its species. Thus, the entire indexed literature on South American austral migration can be reasonably summarized in several paragraphs (Jahn et al. 2004), an obviously impossible task for North American migrants!

This is an unfortunate situation, considering the benefits resulting from a basic knowledge of the biology of these species. Aside from better knowledge of how to conserve many of these species, a deeper understanding of this migratory system could provide a novel approach toward studying the evolution of bird migration across the New World in general. In effect, a different evolutionary “draw” from the New World migrant pool (i.e., South American austral migrants) could yield an independent set of species with characteristics predicted from those among Nearctic–Neotropical migrants, such as for the Tyrannidae (Chesser and Levey 1998). Two general groups of austral migrants can be distinguished biogeographically: those that breed and overwinter within the south-temperate latitudes (South American Cold–Temperate migrants) and those that breed in the



FIG. 10. General patterns of migratory movements within the neotropics. Altitudinal migrants presumably make short-distance movements within shaded regions or to adjacent unshaded regions.

south-temperate latitudes and overwinter within the South American tropics (South American Temperate–Tropical migrants; Joseph 1997). These parallel the short-distance and long-distance migrant categories often used when discussing North American systems. Recent work in Argentina by Cueto et al. (2008) shows that these groups clearly differ in taxonomic composition, behavior, and population dynamics.

From a conservation standpoint, because there are no long-term data bases comparable to North America's Breeding Bird Surveys or Christmas Bird Counts, population trends at the continental level are unknown. The few studies of population declines in South American birds have largely focused on forest fragmentation and, in telling contrast to similar studies in North America, do not tend to distinguish between migratory and nonmigratory species (e.g., compare Robinson et al. 1995, Stouffer and Bierregaard 1995a, b). The state of knowledge is so primitive that it is often unclear whether seasonal population fluctuations in a given species represent migration or nomadism (e.g., Stouffer and Bierregaard 1993). In cases where migration can be confirmed, it remains a challenge to determine both

breeding and wintering ranges. To add to the confusion, most species of austral migrants have overlapping populations of migratory and resident individuals (i.e., partial migrants; Jahn et al. 2004) such that much research is needed on migratory behavior at the population level (Jahn et al. 2006). For example, Trejo et al. (2007) have recently attempted to determine whether all populations of White-throated Hawk (*Buteo albigula*) migrate or if some populations at tropical latitudes are sedentary.

There are fundamental similarities and differences between the austral and Nearctic–Neotropical migration systems, many of which have conservation relevance and affect research priorities. The most fundamental similarity between South American austral and Neotropical migrants is that both groups fly northward as the earth's axis of rotation tilts toward the sun (north-temperate spring) and southward as it tilts away from the sun (north-temperate winter). The northward journey for one group of migrants is to the breeding grounds and for the other is to the nonbreeding grounds, with the breeding status of the two groups switching after their southward journey. Despite the higher avian diversity in South America than North America, there are ~50% more species of



PLATE 1. A Fork-tailed Flycatcher (*Tyrannus savana*), a common South American austral migrant, photographed in Bolivia, South America. Photo credit: Vanesa Bejarano.

Neotropical than South American austral migrants (~340 vs. 230, respectively; Chesser 1994, Rappole 1995, Stotz et al. 1996). This discrepancy arguably results from the much larger landmass within South America north of the Tropic of Capricorn (most of Brazil, Bolivia, and countries to the north) compared to that south of the Tropic of Capricorn (Argentina and Chile); austral migrants are drawn from a relatively small breeding area (Hayes et al. 1994). Because temperate South America has a larger proportion of its landmass situated nearer to the equator than does North America, austral migrants do not generally need to travel as far (Chesser 1994) and are not as concentrated on their nonbreeding grounds as is the case with Neotropical migrants. Stated differently, destruction of one hectare of tropical nonbreeding habitat is likely to have a much smaller impact on austral migrants than on Neotropical migrants. A final geographical difference between South American austral and Neotropical migrants is that the former have very few topographic barriers to migration (Chesser 1994); many must deal with arid areas of central South America, but they do not need to cross large bodies of water and are presumably less susceptible to destruction of stopover habitat.

From a perspective of conserving the largest number of species possible, a focus on the Tyrannidae (New World flycatchers) would be easily justified in a research program on austral migration. Tyrannids account for roughly 33% of all species of austral migrants (Chesser 1994) compared to the major families of Neotropical migrants: Parulidae (15% of totally Neotropical migrant species) and Tyrannidae (9%).

As mentioned previously, migration in South America is not as clear cut as in North America. Most species of South American austral migrants include nonmigratory

subspecies, populations, or individuals (e.g., Fork-tailed Flycatcher, *Tyrannus savanna*; Chesser 1995, Stiles 2004). The most urgent need for research is to document which species migrate and, more specifically, which subspecies or populations of those species are migratory, especially in those species thought to be threatened. Such information will provide a better understanding of how bird migration evolved in South America. For example, because the migratory status of different subspecies of Swainson's Flycatcher (*Myiarchus swainsoni*) is known in different regions Joseph et al. (2003) were able to document phylogenetic relationships between known migratory and sedentary subspecies and therefore piece together the evolution of migration in this species.

From an applied perspective, conservation planning for potentially threatened migratory species would greatly benefit from information on population level migratory patterns. For example, several Emberizid migrant species of the genus *Sporophila* are dependent on lowland tropical grasslands (e.g., Remsen and Hunn 1979, Silva 1999), which are a highly threatened ecosystem in South America (Dinerstein et al. 1995, Stotz et al. 1996).

Distinguishing migratory from nonmigratory populations will require extensive sampling across the continent, which can best be accomplished by an international team of collaborators. Simple records of seasonal population fluctuations would represent a good start. Two general approaches can be taken in this regard: (1) Species- or family-level research such as that of Marantz and Remsen (1991), who attempted to determine the seasonal distribution of Slaty Elaenia (*Elaenia strepera*), or that of Chesser (1995), who documented the seasonal ranges in the Tyrannidae; and (2) A site-specific approach documenting seasonal changes in

abundance and species composition of birds at single study sites (Brooks 1997, Jahn et al. 2002, Stiles 2004, Cueto et al. 2008). This second approach would obviously require research at a number of localities distributed throughout South America in order to determine migratory habits of species across their ranges.

Furthermore, stable-isotope analysis of feathers and genetic sampling might reveal population-specific breeding and/or nonbreeding ranges (see isoscape depictions in Bowen et al. 2005), which represents a second issue of high priority. An international, multiagency consortium in South America similar to Partners in Flight could ignite such efforts. A first step is to increase communication and strategic planning among South American biologists with interests in bird migration. A symposium at the VII Neotropical Ornithological Congress resulted in a website for this purpose (*available online*).²³

Intratropical latitudinal migration

Many species breed in the northern or southern neotropics and migrate toward the equator during the nonbreeding season. This migratory pattern is essentially the same as the migrations described earlier in the North American and South American austral migration sections, except that the breeding range of the species involved does not extend beyond the tropics. Using the Tropics of Capricorn and Cancer to demarcate the boundaries of this category is, of course, arbitrary. In eastern North America, this strategy works well because the Gulf of Mexico, which straddles the Tropic of Cancer, provides a real barrier to migration, such that birds crossing the gulf are easily labeled as temperate-tropical migrants, while those wintering in the southern United States are strictly temperate migrants. The distinction becomes less useful in western North America and South America, where either the breeding or wintering range of a species may cover both temperate and tropical latitudes. Although intratropical latitudinal migration is a category of convenience, its members have one thing in common: They are considerably less well studied than their temperate-tropical migrant counterparts. The lack of research on these migrants has led many authors to argue for a broader view of New World migration (e.g., Levey 1994).

In some intratropical latitudinal migrants, all populations of a species vacate northern or southern breeding areas for wintering areas in the central tropics, most often in the Amazon basin. This pattern of migration has been observed in the Yellow-green Vireo (*Vireo flavoviridis*; Morton 1977) and the White-throated Kingbird (*Tyrannus albogularis*; Chesser 1995). If the breeding range of a species also includes the central tropics, populations in the central regions may be non-migratory, while those from the periphery are migratory. Patterns like this have been observed in a number of

raptors (Bildstein 2004) and flycatchers (Morton 1977, Chesser 1997).

Other more unusual forms of intratropical latitudinal migration exist as well. One population of the Lined Seedeater (*Sporophila lineola*) migrates northwest from its breeding range in the caatinga of northeastern Brazil to its nonbreeding range in Venezuela (Silva 1995), while the closely related Lesson's Seedeater (*Sporophila bouvronides*) migrates south from Venezuela, presumably into western Amazonia (Schwartz 1975). Other species display variation in migratory tendency within a single population (e.g., *Pipra mentalis*; Levey 1988, Blake and Loiselle 2002).

Intratropical altitudinal migration

The general idea that tropical resident species are sedentary was challenged by work showing altitudinal migration in a number of montane birds in Costa Rica (Stiles 1988, Blake et al. 1990, Levey 1994). In particular, Levey (1988) and Loiselle and Blake (1991) found a strong correlation between bird abundance and fruit abundance along an altitudinal gradient, leading them to speculate that frugivores may track seasonal changes in resource abundance, a hypothesis that has since been supported by other studies in Costa Rica (Chaves-Campos 2003, Chaves-Campos et al. 2003, Boyle 2006). An alternative hypothesis is that altitudinal migration is driven by birds seeking areas in which nest predation is low compared to where they spend the nonbreeding season (Boyle 2008). Although altitudinal migration has been studied best in southern Central America, it appears to occur throughout the rest of Central America (Navarro-Sigüenza 1992, Escalona et al. 1995, Ornelas and Arizmendi 1995, Renner 2005), right up to the northern edge of the tropics (Howell and Webb 1995).

Altitudinal migration in the Andes is relatively poorly understood relative to Central America, but the spatial dynamics are possibly more complex. There are a number of puna-breeding birds that migrate to the coast during the nonbreeding season (Pearson and Plenge 1974, Roe and Rees 1979, Ferrari et al. 2008), and there may be some that migrate periodically to the Amazonian lowlands (e.g., raptors; Bildstein 2004). Work in humid montane forests on the Pacific and Caribbean slopes of Colombia suggests that some species make regular altitudinal movements (Hilty 1997, Strewe and Navarro 2003). Work on the moister eastern slope of the Andes is virtually nonexistent, although Tinoco et al. (2009) have documented apparent altitudinal migration in the endangered Violet-throated Metaltail (*Metallura baroni*) in Ecuador. Hobson et al. (2003) found further evidence for altitudinal migration in hummingbirds in Ecuador using stable isotopes.

Details on possible altitudinal migration in the mountains of southeastern Brazil are sketchy at best, but there are some hints that migration may be more common than previously thought (Sick 1985). Presumably, species there migrate to lower elevations during the

²³ (<http://www.zoology.ufl.edu/CENTERS/migration/index.html>)

austral winter. Records from the Amazonian rain forests of Pará, Brazil, suggest the presence of an altitudinal migration system there as well (Silva 1993).

Short-term facultative altitudinal migration occurs when usually sedentary species make short-term movements downslope to avoid periods of harsh weather. This phenomenon has been recorded in the cloud forests of Mexico (Winker et al. 1997), the puna of Peru (O'Neill and Parker 1978), and the cloud forests of Peru (C. L. Merckord, unpublished data). Such movements probably occur in most mountainous regions of the world (e.g., Hahn et al. 2004).

Complex intratropical migration

A few species in the neotropics show complex regional movements within the tropics that are neither latitudinal or altitudinal. We place them in this catch-all category of poorly understood species. Possibly the best studied of any of these complex migrants is the Three-wattled Bellbird (*Procnias tricarunculata*), whose loop migration incorporates both short-distance altitudinal and latitudinal shifts and has major relevance for conserving this species (Powell and Bjork 2004).

Seasonal variation in the abundance of birds in high-Andean *Polylepis* forests (Herzog et al. 2003) may be indicative of seasonal migrations or simply local movements. In neighboring Amazonia, seasonal flooding of riverside sandbars and marshes induces movements in a diverse group of species (Remsen and Parker 1990, Petermann 1997). Tracking of food resources may be the proximate cause of movements in many frugivores (e.g., Ramphastidae; Sick 1985) and some raptors (Bildstein 2004). Many marine birds make regular migrations along the coasts and throughout the West Indies. During the wet season, the Brazilian Pantanal receives an enormous influx of waterbirds that disperse to other regions during the dry season (Antas 1994). In most of the aforementioned cases, the extent to which movements are local movements, directed migration, seasonal wandering during the nonbreeding season, or nomadism are unclear and require much more study.

Also unclear are the underlying proximate and ultimate mechanisms driving intratropical migration (Jahn et al. 2006, Mueller and Fagan 2008). One of the few examples of such research in the neotropics is that of Styrsky et al. (2004), who documented development and migratory restlessness of Yellow-green Vireo fledglings under controlled conditions (i.e., photoperiod length).

Obviously, migration within the tropics is poorly understood. Even if it occurs in only a small percentage of species, knowledge of its occurrence may be critical for conservation purposes (Powell and Bjork 1994, 2004, Chaves-Campos et al. 2003). It has been suggested that many of the short-distance migrants within the tropics make their movements during the day and within vegetation. For intratropical migrants it is important to identify and protect areas used at each stage of the annual cycle, and especially in the case of altitudinal

migrants, corridors connecting those areas. Habitat loss could quickly stop these migrations, perhaps leading to rapid extirpation or even extinction of these intratropical migratory birds.

ECOSYSTEM-LEVEL CONSTRAINTS AND MIGRANT BIRD POPULATIONS

Many of the scenarios discussed in this paper to understand population variation among Neotropical migrant birds involve human effects on birds, but these tend to be the accumulated effects of human activities on local scales. For example, widespread fragmentation through agriculture, development, or timber harvest has been linked to regional 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 adjustments on local scales, although recent work has shown that landscape-level patterns of habitat distribution are important components of management plans. For most reasonably abundant species, we assume that there are parts of their breeding and wintering ranges where populations are more than adequately supported, whereas only in other parts of the distribution are populations declining and conservation actions needed (James et al. 1992).

Much more alarming 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, because these are often independent of patterns of species-specific habitat quality; moreover, solutions require major changes in human behaviors that are often either uncoupled from perceived conservation problems or that have a link that is complex and difficult to track. For example, Hames et al. (2002) suggested that the widespread decline of the Wood Thrush in the eastern United States is related to eggshell thinning. Their eggshells are thin because of reduced numbers of snails in these forests; snails are rare because of calcium limitations due to acid rain, with populations of Wood Thrush downwind from major industrial regions suffering the most. Certainly, those of us old enough to have witnessed the decline of such top predators as Bald Eagle (*Haliaeetus leucocephalus*), Peregrine Falcon (*Falco peregrinus*) and Osprey (*Pandion haliaetus*) due to the effects of DDT recognize that such ecosystem-wide effects can occur. Fortunately, we also have seen how these effects can be remedied by the proper control of chemical use. The question, of course, is whether any of the ecosystem changes that we know are occurring can explain migrant bird declines to date or will lead to migrant (or other) bird population changes in the future in such a way that the key solution to bird conservation is found at a macrogeographic level rather than directly with regional and/or local habitat management.

Global climate change, particularly in the form of global warming, is the ecosystem trait that has received

the most attention in recent years, with support from numerous multinational panels. It is abundantly clear that the world is warming, and nearly all the scientific experts agree that it is due to human-caused additions of greenhouse gases including carbon dioxide and methane (Root et al. 2005). In addition to changes in temperature and rainfall regimes across the globe, such warming is shown in rapidly melting glaciers on mountains, loss of ice in both the Arctic and Antarctic, sea level rise, increased frequencies of unusually strong tropical storms, and intensification of El Niño and La Niña and other climate oscillations. Until recently, scientists had a difficult time distinguishing the effects of human-caused warming from long-term temperature cycles. Of course, the ultimate natural periodicity involved the occurrence of "ice ages" in which glacial advances greatly increased the ice caps, lowered ocean levels, and reduced rainfall in many regions (Overpeck et al. 1991).

The difference between anthropogenic global warming and natural cycles of hot and cold is timing. It appears that current warming is occurring at a much faster rate than ever recorded, which means that it will be more difficult for natural systems to adapt, behaviorally or genetically, to whatever environmental changes occur. For example, it has been suggested that during the end of the most recent ice age, temperature increased at a rate of about 0.5°–1.5°C per thousand years, while current projections show the earth warming at 1°–5°C per century (Root and Schneider 2006).

The basis of virtually all conservation and management is the strong relationship between climate and vegetation types, with birds being adapted to various types of vegetation. The worst-case global climate change scenarios suggest that vegetation types will have to move rapidly across the continent to keep up with the climatic conditions to which they are adapted, much more rapidly than occurred in the past. Of course, individual species move at varying rates, with some species of eastern forests lagging greatly behind others following the last glaciation. Whether any of the species can keep up with climate change remains to be seen, particularly given that movement of vegetation across fragmented agricultural landscapes will be much more difficult than under the conditions existing with the last glacial retreat. With restricted movement of plants between natural areas, it is hard to predict what sort of changes may occur with regard to habitat quality locally. Rodenhouse (1992) used a simulation model to evaluate the impact of climate change on annual productivity of Black-throated Blue Warblers, and found that increases in summer rainfall would lead to lower nest success, while increasing temperatures would enhance food abundance and lengthen the avian breeding season. The overall result would be to increase breeding productivity, but this will depend on the balance between changes in rainfall and temperature. A more recent review of the potential effects of climate change on birds of the

northeastern United States indicates that bird species breeding at high elevations may already be at the threshold of critical change, with as little as 1°C of further warming reducing suitable habitat by more than half (Rodenhouse et al. 2008).

The future scenario suggests that birds will face the choice of staying in the locations where they have lived for the past few thousand years, even as these habitats may change from altered local climatic conditions, or will track the movements of their most favored vegetation types as this vegetation moves to the climatic conditions where it is most favored (if the vegetation is able to move). Global modelers are able to make fairly precise predictions about how climatic conditions will change under scenarios of differing levels of atmospheric greenhouse gases, and they can match these climatic predictions with what we know about current relationships between climatic conditions and vegetation types/bird communities (Sekercioglu et al. 2008). However, little can be predicted yet about how vegetation types and their associated faunal communities will be able to move in the totally unnatural situation existing across most of the world today (but see Tape et al. 2006).

Scientists can already see pronounced changes in bird distributions, behavior, and abundance that seem related to global warming. European ornithologists seem to be ahead of their North American counterparts in detailed studies of the apparent effects of global climate change on avian demography, perhaps because of the European history of long-term and detailed demographic studies. A book edited by Møller et al. (2004) combined detailed studies of effects of climate change with looks into the possible future. Some patterns have appeared with regard to arrival and departure dates of migratory birds (Lehikoinen et al. 2004), breeding dates and success (Dunn 2004, Visser et al. 2004), and effects on population dynamics (Sæther et al. 2003); whereas possible effects on migrant fueling rates (Bairlein and Hüppop 2004), banding rates (Fiedler et al. 2004), and other factors were less clear.

North American studies also seem to be documenting earlier arrival of migratory birds and earlier breeding. La Sorte and Thompson (2007) analyzed Christmas Bird Count data to suggest that many nonmigratory North American species have moved their breeding ranges northward, but for most species this movement has been fairly small and, in many cases, regional processes also appear to be contributing to the range extension. A broader study by Niven et al. (2009) used Christmas Bird Count data to show how a variety of species have moved the center of their winter range to the north and west. Although range extension to the north because of warmer conditions may enlarge some populations, negative responses to associated climatic factors such as rainfall may counter these benefits. Anders and Post (2006) suggested that Yellow-billed Cuckoo (*Coccyzus americanus*) populations declined in regions where

rainfall was low, presumably because of the negative effects of drought on caterpillar populations, the cuckoo's main food. Some scientists are concerned that migrant birds may not evolve quickly enough to deal with advanced vegetative phenology on the breeding grounds, such that migrants may miss peak periods of food that are important during migration or may arrive too late on the breeding grounds to track resource peaks that are critical to their reproductive success. For example, the migration of the Ruby-throated Hummingbird (*Archilochus colubris*) is timed with the flowering of a number of species of plants as the hummingbird moves northward. If the timing of hummingbird migration cannot adjust to the rapid advancement of flowering in these plants, migrant hummingbirds will be less successful and populations will likely decline. Finally, Strode (2003) identified an uncoupling of migration dates for several species of North American wood warblers (Parulidae) with their associated food resources.

Migrants may also suffer from climate change on the wintering grounds, although the general consensus is that tropical regions will not be affected by global temperature change as much as temperate regions (but see Deutsch et al. 2008). Neelin et al. (2006) modeled the effects of plausible global warming scenarios on rainfall and noted many tropical and subtropical locations where rainfall would decline. All models agreed that the Caribbean–Central American region would become more arid in the future, perhaps reverting to the very arid conditions found during the Pleistocene. This region is very important for migrant birds, with several species confined to this region during the winter. While we assume these species adapted to these arid conditions during the Pleistocene, we cannot assume that they will be able to make the adjustment quickly if such is required, or maintain current population levels. Moreover, the intensification of El Niño events, which exacerbate Caribbean droughts, could be problematic for wintering Neotropical migrants (Sillert et al. 2000).

Price (2003) has modeled where vegetation types and bird species might move under various scenarios of global warming. Of course, given scenarios of warming, most forest communities will be moving northward, with subtropical habitats (or at least climates) moving into the southern United States. Under a model using a doubling of global carbon dioxide by the year 2100, Price suggests that dozens of species that are common and widespread in the United States will be forced to move to breeding ranges outside of the lower 48 states and southern Canada. For most regions, 30–50% of resident species will be lost as birds move north. While it is possible that some southern-breeding species can move northward with more subtropical vegetation types, the predictions are that there will be fewer of these arid habitat species doing so, such that net losses of species in the United States will range from 5% to 30% by region (Price and Root 2001).

Although it is clear that global climate change may cause incredible upheavals in the distribution and abundance of birds during the next century, it is possible that global climate change may be affecting avian demography now, and may, in fact, have started to reduce bird numbers in the recent past. As noted, several studies have shown changes in seasonal phenology or winter range, but few if any have made a clear case that climatic shifts associated with global change have caused regional bird population declines. Even the Anders and Post (2006) paper showing declines in the Yellow-billed Cuckoo, which were associated with ENSO-related drought conditions, did not relate these conditions to global change directly. It is not surprising that scientists conducting long-term local studies are hesitant to assign causation to something as broad as global climate change when shorter-term, more measurable and parsimonious explanations such as rainfall exist (Dugger et al. 2000, 2004). Yet, recent papers have explained some recent natural events by invoking climatic patterns over the past 25 years as part of the global warming process. Westerling et al. (2006) analyzed the ties between climatic patterns and the frequency and intensity of forest fires in the western United States for the period 1970–2003. While attempting to control for forest management and history, they found that wildfires got much worse beginning in the mid-1980s, with the average fire since 1987 larger and longer lasting. Fire frequency seemed to be linked to snowmelt, with early snowmelt meaning drier conditions and more frequent fires; snowmelt is linked to “recent changes in climate over a relatively large area.” These wildfires compound their effects by adding tremendous amounts of material to the atmosphere, further increasing future global warming. Long-term monitoring of bird populations in southwestern Puerto Rico using mist nets has shown a continuous decline of winter resident captures on a netline operated annually since 1973 and a severe decline in captures during the past seven years among a set of nine netlines operated annually for the past 20 years (J. Faaborg, W. J. Arendt, K. M. Dugger, J. D. Toms, and M. Canals Mora, *unpublished manuscript*). Several endemic Puerto Rican resident species have also shown declines in captures over the past 20 years, a period of time characterized by atypical rainfall patterns, particularly during the residents' breeding season.

Research that can show the effect of these widespread climatic or atmospheric factors on bird populations is critical to our conservation response. If acid rain or global climate change is the cause of regional population declines, one certainly must put the role of local habitat restoration into the proper regional context, or waste great effort making or restoring habitat that will fail to maintain populations. Obviously, though, the sorts of studies required to understand macrogeographic factors are quite different from the more classic studies detailing local or regional demographic patterns, although both types of studies are essential.

CONCLUSION: PAST SUCCESSES AND FUTURE NEEDS

As this review of research has shown, we have made great strides in understanding the ecology and evolution of migrant birds since the late 1970s. The science and management of migratory birds are now robust, interconnected endeavors; alternative plausible hypotheses are being tested actively for just about every aspect of migratory bird ecology, from the geographical and thus seasonal loci of population limitation to the mechanisms of population regulation and even the evolutionary history and origins of migratory behavior in birds. On the North American breeding grounds, the role of landscape-level distribution of habitats has become a widely understood and accepted part of the knowledge necessary to manage bird populations. Within this landscape framework we can also understand variation in the roles of predators, brood parasites, and food availability on migrant demography. Habitat selection models that once were based on tiny plots can now incorporate multiple spatial scales and broadly based census data in such a way that the most recent Partners in Flight goals involve abundance targets for each species. Recent insight into post-fledging behavior has forced us to examine seasonal variation in habitat use across these same spatial scales. Studies on en route migration have expanded well beyond those landmark studies that occurred along the Gulf of Mexico or other major barriers to incorporate the day-to-day (and night-to-night) decisions facing a migrant during its journey, with insights gained from recent advances in physiology, Doppler radar, and stable isotopes. At least two Neotropical migrant passerines are exceptionally well studied, namely the American Redstart and the Black-throated Blue Warbler, with extensive data and highly developed models of how these species respond to conditions during winter, the breeding season, and to some extent while en route between those two range extremes. Other studies have added important insights into winter ecology through shorter term studies or long-term monitoring. The use of stable isotopes is providing a way of linking regional populations, and thus identifying and quantifying inter-seasonal carry-over effects. The accumulation of such information on North American migrants provides an excellent example for those attempting to understand migration in the Southern Hemisphere, where initial efforts at documenting migration make clear that very little is known.

These many advances in our knowledge of migrant birds are tantalizing because they show that it is possible to develop the detailed knowledge of migrant bird ecology that will be necessary to conserve these highly mobile, widely ranging species. However, there are still many gaps in our knowledge. For example, the theoretical framework and many of the findings on which we base our understanding of the ecology of migrant birds often depend on relatively few studies of one or a few species, in one or a few geographical locations. For example, fragmentation studies tended to

be focused in the Midwest, precipitating argument about generality of the Midwest models. It is clear that there are generalities associated with fragmentation and landscape ecology, but management may require calibration of the conditions for those sites targeted for conservation. Likewise, the most detailed studies of breeding productivity have been limited to species in the eastern or northeastern United States, potentially unrepresentative of species elsewhere. Studies of en route ecology and dispersal still suffer from our inability to track small birds over long distances, although the use of satellite transmitters for larger birds gives us hope. Most studies of winter ecology have been conducted in the West Indies, where wintering migrants are abundant due at least in part to the low diversity of resident bird species, but again may not generalize beyond this region. Studies of equal intensity need to be replicated on mainland wintering sites in Central and South America. Concern is increasing about the precision of stable isotope applications to some of the bird studies reviewed, which may limit conclusions about complex phenomena such as breeding-season dispersal, connectivity, and seasonal effects. There certainly is the need for more studies of migrants during breeding, wintering, and the migration period in between in new locations and with new approaches. Moreover, ecosystem changes such as acid rain and global warming are forcing us to predict how migratory birds can survive in a rapidly changing planet, which leads to new questions and requires new approaches to be developed. Perhaps our most daunting challenge is how to integrate the results of detailed population studies with the rapidly advancing field of bioclimatic envelope modeling (Oberhauser and Peterson 2003, Pearson and Dawson 2003, Guisan and Thuiller 2005, Keith et al. 2008). Such an effort would facilitate the prediction of shifts in species distributions and source populations, as well as proactive reserve design in a changing world.

Just as many of the breakthroughs in ecological knowledge of the past decades have involved new technologies (GIS, stable isotopes, corticosterone measures), technology will likely lead future research. Recent physiological advances provide new measures of body condition during migration, which allows insight into both the bird's physiological condition and, perhaps, habitat quality. We have seen surprising results about movements and destinations when large birds have been fitted with satellite transmitters; what can we learn when transmitters are small enough to fit most of the smaller species of Neotropical migrants? Furthermore, study sites can be examined in detail by nearly any computer that has Google, either before or after that same computer has performed landscape ecology or population modeling. Computers are also not just for computations anymore; scientists can communicate almost instantly in today's world, a level of communication that can promote the scientific process from start (selection of study sites, hiring of field assistants) to

finish (electronic publication). Further collaboration between North and South American ornithologists will greatly assist in developing the kinds of studies needed to understand the factors affecting populations of such wide-ranging species as well as basic underlying ecological and evolutionary processes.

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