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Are Populations of Neotropical Migrant Birds Limited in Summer or Winter? Implications for Management

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Abstract—Understanding where in their annual cycle Neotropical-Nearctic migrant bird populations are limited is essential for developing effective management and conservation policies. A review of currently available information indicates that these long-distance migrant species may be limited by events and circumstances in both summer and winter, and possibly on migration as well. This has broad implications for management, which must take into account both the quantity and quality of habitat for these species at various times of year. Thus, the maintenance of viable populations of long-distance migrant species will require extraordinary communication, coordination, and effort involving resource managers, scientists, and the public across international boundaries.

INTRODUCTION

Recent evidence suggests that many songbird populations that migrate each year between temperate breeding areas and tropical winter quarters are declining and that these declines have accelerated in recent years (Robbins et al. 1989, Askins et al. 1990, Finch 1991). Potential causes for the declines are diverse, and may involve environmental changes and deterioration in breeding areas, in winter quarters, or even during migration. Understanding the relative importance of limiting or regulatory factors for these long-distance migrants, and when they operate during the annual cycle, is essential to the development of sound management plans, to avoid wasting limited financial and human resources in one area or season that may not safeguard a population. Thus, whether migrant species are more limited by events on their breeding grounds, on migration, in winter, or during a combination of seasons will determine where and what to manage. In this paper, we review briefly current knowledge about where and how migrant bird populations are limited, with emphasis on the implications for management. A more comprehensive treatment, with full literature review, is presented elsewhere (Sherry and Holmes MS).

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POPULATION LIMITATION IN SUMMER, WINTER, OR BOTH? AN OVERVIEW

During what phase of the annual cycle are populations of long-distance migratory passerine birds limited, and what are the ecological causes of these population dynamics? This topic is poorly understood because of the global scales over which these migrants travel annually, their long distance dispersal, their diverse responses to seasonal resources or habitats, and the many possible causes of population changes. As a result, we still do not know for any Neotropical migrant bird population how age-specific mortality is distributed across the annual cycle or what combination of factors limits a population in any one or more parts of its range. Nor do we know the relative importance of wintering, breeding, or migratory areas for any single migratory species. Nevertheless, enough information does exist to suggest that all three phases in the annual cycle are potentially important for many species.

Evidence for Limitation in Winter

Some biologists have proposed that long-distance migrant bird populations must be limited principally by events affecting overwintering survival (Fretwell 1972, 1986, Morse 1980, Alerstam and Hogstedt 1982, Baillie and Peach 1992, Rappole et al. 1992, Morton 1992). Evidence for this view, until recently, has been largely indirect. First, non-migratory species, mostly

resident in the temperate zone, tend to be limited mainly by winter mortality (e.g., Perrins 1980, Ekman et al. 1984, Arcese et al. 1992). Second, theoretical arguments (e.g., Fretwell and Lucas 1970, Fretwell 1972) and mostly circumstantial observations suggest that events where migratory birds winter in some cases influence the numbers breeding in subsequent summers (e.g., Winstanly et al. 1974, Morse 1980, Baillie and Peach 1992). And, third, studies in the temperate zone, where resource limitation either does not occur or does so infrequently (Wiens 1977, 1989, Pulliam and Dunning 1987), suggest that breeding habitats are unsaturated, breeding densities are below carrying capacity, and thus that populations must be limited by events occurring at other times, i.e., in winter. Finally, this view is supported by the observation that population declines have occurred in recent decades as tropical deforestation has been accelerating, suggesting that winter habitat loss is not just coincidental to, but is the major factor causing the declines (Terborgh 1989, Morton and Greenberg 1989, Morton 1992). Although these arguments for winter limitation are hard to refute, it is also difficult to test or provide supporting data. Robbins et al. (1989), however, noted that the migrant species showing the most significant population declines were those that depend on forest habitat in winter but breed in non-forested habitats, implying that forest loss in winter is a critical factor.

More recently, demographic, experimental, and distributional studies have begun to show that migrants often compete for winter habitat, which implies potentially limiting conditions during winter. Evidence for such habitat limitation is based on (1) the pattern of even (rather than random or aggregated) local dispersion of individuals, presumably via territorial interactions (Elgood et al. 1966, Sliwa and Sherry 1992), (2) frequent winter site fidelity, i.e., a tendency to return to a territory held in a previous winter (Price 1981, Holmes et al. 1989, Holmes and Sherry 1992, Winker et al. 1990), (3) the occurrence of intraspecific aggressive interactions (e.g., Morton 1980, Schwartz 1980, Holmes et al. 1989, Kelsey 1989, Stacier 1992), or some combination of the above (see Greenberg 1986). Perhaps the best evidence that winter habitat may limit populations comes from experimental studies in which Neotropical migrants that were removed from winter habitat were replaced by other individuals almost immediately, suggesting competition for preferred sites and perhaps saturation of certain habitats (Rappole and Warner 1980, Morton et al. 1987, Marra et al. MS). The occurrence of apparently widespread sex- and age-segregation of migrants among winter habitats (Lopez Ornat and Greenberg 1990, Wunderle 1992, Sliwa and Sherry in prep.) also suggests behavioral dominance, and thus competition for highest quality habitats. The hypothesis that Neotropical migrants compete intraspecifically for limited winter habitat would be supported by variation in winter fitness associated with different habitats, and only Greenberg (1992) has provided suggestive evidence for such variation. Further research is needed to assess the degree to which differences in winter habitat quality influence survivorship.

Evidence for Limitation in Summer

An alternative view of population limitation in these migrant species is that events on the breeding grounds may be at least as important, if not more so, than those in winter (e.g., Probst 1986, Holmes et al. 1986, Martin 1987, Hutto 1988, Sherry and Holmes 1992). Fragmentation of forest habitats in eastern North America, for instance, has been strongly implicated as one cause of reduced breeding success and consequently lowered breeding densities of some songbird species (e.g. Whitcomb et al. 1981, Ambuel and Temple 1983, Lynch and Whigham 1984). Reduced breeding success has been attributed mostly to decreased area of undisturbed forest breeding habitat or to increased nest predation and nest parasitism along forest edges (see Askins et al. 1990, Finch 1991, Martin 1992, papers in this volume). Variable food abundance, however, even within unfragmented landscapes (Enemar et al. 1984, Holmes et al. 1986, 1991, Tomialojac and Wesolowski 1990, Rodenhouse and Holmes 1992) can also significantly affect bird reproductive success, survivorship, and ultimately recruitment of new individuals into these populations. Recruitment is particularly crucial, and four studies have now shown that recruitment into breeding populations of long-distance migrants is significantly and positively correlated with nesting success in the previous summers (Fig. 1, see Nolan 1978, Virolainen 1984, Sherry and Holmes 1992, Holmes et al. 1992). The importance of this relationship is that factors affecting reproductive output appear to have a major impact on subsequent population dynamics and abundance and, indeed, may override the impact of events on migration or in winter (Sherry and Holmes 1992). If this holds more broadly, breeding season events may emerge as the major driving force in determining the abundances of these species.

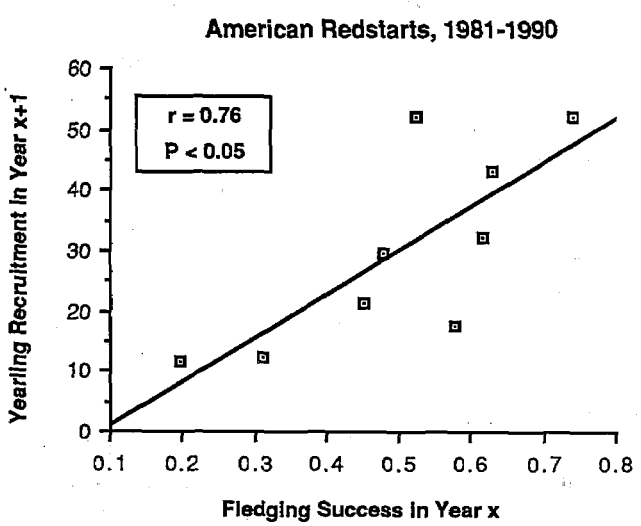

Figure 1. — Relationship between annual breeding productivity of American Redstarts in the Hubbard Brook Experimental Forest, N.H. in one year (year x, 1981-1989) and recruitment of yearling males into the population in subsequent seasons (year x+1,1982-1990). Adapted from Sherry and Holmes (1992).

These findings are not the only line of evidence that breeding habitat is of major importance in maintaining population levels. Competition for habitat occurs in summer, just as in winter, suggesting that suitable breeding habitat is also limited in its supply relative to demand. Evidence for summer habitat competition comes from the widespread occurrence of territoriality resulting in overdispersion of individuals, habitat saturation (e.g., Sherry and Holmes 1989), and despotic habitat selection, which is characteristic of many breeding populations of long-distance Neotropical migrants (see Sherry and Holmes MS).

Evidence for Limitation on Migratory Passage

Although less is known about habitat requirements and limitation of birds during migration, such times must also be critical. The facts that migrants need to refuel at frequent intervals, that they often become concentrated into particular flyways and stopover points, and that some at least are territorial in passage habitats indicate the potential importance of suitable stopover habitats (see Sherry and Holmes MS). Recently, it has been shown that migrants compete for food resources in passage habitats (Moore and Yong 1991). In addition, Moore and Simons (1992) suggest that high quality habitat during migration may be "limited in the absolute sense, or effectively so, because migrants cannot search for the 'best' stopover site." Thus, more research attention must be focused on the frequency and extent to which habitat for migrants during passage might be limiting, and the environmental features that determine habitat quality during these periods of the birds' annual cycle.

Summer-and-Winter Limitation

The evidence summarized above suggests that populations of Neotropical migrant birds are affected by events at all times of year. In one species, Kirtland's Warbler (Dendroica kirtlandii), evidence exists that the population is limited simultaneously by both amount of habitat in large stands of young jack pine (Pinus banksiana) and by rainfall effects on food abundance in the Bahamas where this species winters. But it is still not clear, even for Kirtland's Warbler, whether one season is more important than any other. A possible resolution to this question, suggested by both Morse (1980, 1989) and Svensson (1985), is that ecological conditions in both seasons might be limiting Neotropical migrant populations.

This idea was explicitly developed by Cox (1985) in his model for the evolution of avian migration systems. Cox proposed that migratory populations should be limited simultaneously in summer and winter by a dynamic equilibrium between fecundity and mortality in a changing array of habitats. Specifically, Cox argued that a population in which overwinter survival was temporarily increased would expand into a greater array of breeding habitats (because the greater winter survival would compensate for decreased fecundity in the newly added, but inherently less preferred breeding habitats). Conversely, improved breeding season fecundity would also, in a compensatory manner, increase the range of habitats in which individuals were found in winter. If this hypothesis is correct, we should expect to find density-dependent habitat selection in both summer and winter. This seems to be supported by current data, as reviewed above (see also Sherry and Holmes MS). Unfortunately no comprehensive studies have yet been conducted that consider populations of particular Neotropical migrant species in multiple habitats in both summer and winter. Such information on the ecology of individual species in both summer and winter habitats is needed to determine whether density-dependent habitat selection occurs, when mortality is greatest, and how the impact of varying levels of reproductive success affects recruitment and other population processes. Only in such a way can the relative importance of different habitats and environmental factors be rigorously evaluated.

The important point from the perspective of how to manage these migrant populations is that this summer-and-winter limitation hypothesis leads to the prediction that large-scale loss of habitat or decline in its quality can disproportionately influence a population in either season, and thus sufficient habitat in both seasons is unequivocally necessary for a sustainable population. It is tempting to focus attention on environmental changes in one season, for example when we have better data concerning that season or when our political institutions mandate concern for the landscapes at one end of the annual cycle. Dramatic loss of tropical rainforest habitats, for example, has focused much attention on the plight of migrants that winter within rainforest interior, but it is rarely possible even for such species to be certain that habitat change in one season affects a population more than that in another season. The demise of Bachman's Warbler (Vermivora bachmani) is often attributed to conversion of lowland forests to sugar cane plantations in Cuba, where the species wintered (Terborgh 1980, 1989; Rappole et al. 1983; Morse 1989), but Remsen (1986) argues just as plausibly for the importance of canebrake habitat loss in the southeastern United States where this species nested in summer. Evidence is accumulating that rainforest loss is contributing significantly to declining wood Thrush (Hylocichla mustelina) populations (Morton 1992), but changes in summer habitats are almost certainly important as well. The alarmingly sustained decline of Cerulean Warbler (Dendroica cerulea) populations may be the result of rapid habitat loss in both breeding and wintering areas (Robbins et al. 1992), but it is difficult to determine in which season habitat loss is most important.

Evidence from Migrants' Life Histories

As a final part of the review section of this paper, we note that life history characteristics of long-distance migrant birds are not only relevant to the question of population limitation and

habitat use, but also suggest important management goals. The very act of migration, taking advantage of seasonally changing environments, can be viewed as a kind of ecological opportunism, distributed over the range of habitats exploited in summer, winter, and while in passage in between. Thus, migrants necessarily evolved behaviorally opportunistic strategies to cope with constantly changing habitat abundances and variable ecological conditions annually (Morse 1989). This necessity for some degree of ecological flexibility to exploit several habitats during the annual cycle has led some to view migrants as weed-like opportunists that seasonally invade disturbed, fringe habitats of tropical and temperate communities because of an inability to compete with resident birds (Karr 1976; Morse 1980; Lack 1986; Leisler 1990, 1992; O'Connor 1990). A very different view has developed more recently, mostly because of rapidly increasing knowledge about how migrants use wintering habitats in the Neotropics. This alternative view is that migrants are tightly integrated into tropical communities because of competitive abilities evolved to facilitate efficient exploitation of specialized tropical habitats and resources (Morton and Greenberg 1989, Rappole 1991, Rappole et al. 1992, Morton 1992). The resolution of these different perspectives has important management implications, because ecologically resilient populations of behaviorally flexible opportunists would need far less management than habitat and resource specialists at a time when human populations are converting forests to pasture, croplands, second growth, and scrub habitats, particularly in tropical countries (Morton and Greenberg 1989, Rappole 1991, Powell et al. 1992, Rappole et al. 1992, Morton 1992). As Morton (1992, p. 582) put it, "There is little conservation value in the concept that migrants as a group are birds of successional habitats that chase after ephemeral, superabundant food, such that deforestation will not harm them." Although this extreme position may be based in part on political conviction, review of the literature provides some support for both points of view (Sherry and Holmes MS).

Neotropical-Nearctic migrants are sometimes characterized as "integral components" of tropical (or temperate) bird communities in recognition of the fact that these birds are not simply temporary visitors to tropical communities, relegated to disturbed ("fringe") habitats by superior competitive abilities of resident species, as was once widely believed. Instead, they are now widely considered to be not only well adapted to virtually every tropical habitat and community, but in fact evolved in the tropics. Levey and Stiles (1992) summarize the growing evidence for this conclusion, and argue that the precursors of long-distance migratory behavior are amply represented by diverse intratropical (e.g., elevational) movements exhibited by resident tropical species. Neotropical-Nearctic migrants are thus merely the endpoint of a series of tropical adaptations, involving behavioral plasticity and generalized diets, to exploit seasonal, and sometimes temporally and spatially unpredictable, tropical resources (e.g., fruit, nectar, and many kinds of small insects). Such resources are often found within relatively seasonal habitats such as forest canopy, dry forests, and second growth vegetation, but some migrants, such as wood thrushes and some Empidonax flycatchers readily winter within rainforest interior habitat. After spending over half the year in tropical habitats (Keast 1980), long-distance migrants then take advantage of seasonally abundant resources and safe nesting sites at higher latitudes (MacArthur 1972, Herrera 1978, O'Connor 1990). Migrants have relatively high annual survival (Greenberg 1980, Morse 1989, Ricklefs 1992), making them similar demographically to tropical resident species, which is probably facilitated by wintering in mild tropical habitats. Migrants maintain moderately high annual fecundity, higher than that of most tropical resident species, which offsets mortality costs of migration, but lower than that of most temperate residents (Greenberg 1980, Ricklefs 1992). Temperate residents may outcompete migrants for the best opportunities to produce large clutches and multiple broods by defending the best early season nesting and feeding sites (O'Connor 1981, Cox 1985). Thus migrants and residents in both seasons appear to compete for seasonal resources, reinforcing the view that migrants are well adapted, integral components of both breeding and wintering communities.

Finally, despite opportunistic adaptations to seasonal resources on the part of many species, migrants appear to be no less specialized in their habitat and resource use than are many resident species. Most New World wood warblers (Parulinae), for example, are specialized for breeding in particular floristic associations (coniferous forest, or northern or southern hardwoods), in one or a few successional stages, in swamp or scrublands, in fire-maintained jackpine woodlands, and so on (Keast 1980, Morse 1989). The same is true of migrants breeding in Britain (O'Connor 1985, 1990), where specialized habitats are probably necessary for high enough fecundity to offset annual mortality losses. In winter, Neotropical-Nearctic migrants are ecologically segregated relative to each other and to resident species, and they exhibit as great a degree of specialization as seen in many tropical residents (Stiles 1980, Terborgh 1980, Morton and Greenberg 1989, Lynch 1989, 1992, Leisler 1990, 1992, Rappole 1991; but see Hutto 1992). Thus, habitat specialization is characteristic of many migrants in both summer and winter, and probably evolved to maintain both high breeding season fecundity (compared with tropical residents) and high winter survival (compared with temperate residents).

We therefore view migrants as a unique evolutionary response to seasonally changing environments. These migrants are both integral components of tropical and temperate communities, often competing effectively with residents for seasonal foods, and ecological opportunists at

a diverse range of spatial scales. Life-history adaptations of migrants to ecological conditions in both winter and summer habitats thus emphasize our proposition above that population limitation is likely to occur in both summer (breeding) and winter(survival)habitats.

MANAGEMENT IMPLICATIONS

The information available about populations of long-distance migratory bird species thus supports the hypothesis that habitats for Neotropical migrants may be limiting in both summer and winter, as well as during migration. These findings have important implications for conservation and management efforts, which we develop below in the form of seven recommendations.

1.The first recommendation, and we think the most important, is that management policy include habitat necessary to maintain populations of Neotropical-Nearctic migrants in summer breeding areas, in wintering quarters, and along migratory routes. Migrants compete for high quality habitat at essentially all times of year, and thus significant loss or deterioration of habitat at any major part of the annual cycle could lead to population declines. Existing examples of simultaneous summer and winter habitat changes that are correlated with population declines--in some cases in the same species populations--reinforces this management recommendation.

2.The second recommendation is that management should emphasize habitats as landscapes where migrants can maintain their own populations. Each species cannot be treated as an independent entity distinguishable from the habitat in which it evolved. Viewing a species outside the context of its habitat is particularly dangerous when it leads to arbitrary management targets (such as numbers of nest boxes or snags). Such targets too often address the symptoms of a population decline (e.g., loss of nest sites) rather than underlying ecological causes such as increased nest parasitism, increased nest predators due to habitat fragmentation, or insufficient time for regeneration of new habitat. Instead, management should focus on sustainable habitat quality and quantity necessary to support particular species. If a population has already reached threatened or endangered status, any action to increase the population should of course be considered, but actions such as putting out nest boxes or cowbird control programs should be viewed as temporary measures until sufficient amount of new habitat can be made available.

As mentioned above, an understanding of migrants' life-histories leads to a view of their habitats as entire landscapes characterized by inherent variability and continuous change--attributable to normal ecosystem processes. Habitats for migrant birds should not be viewed simply as assemblages of snags or plants with distinctive floristic and physiognomic characteristics, but as ecosystems capable of sustaining complex processes of disturbance, regeneration, and seral development in various ways. Many migrant species populations have evolved the ability to respond to variability in their habitats, including dramatic seasonal and year-to-year changes in food abundance (e.g., emergences of cicadas or aquatic insects, and irruptions of defoliating insects), nest predator populations, fires, and weather anomalies such as droughts, floods, and hurricanes. Birds in general, but migrants in particular, have extraordinary dispersal capabilities to find newly created habitats, or to move from deteriorating ones, depending on how great the distance is to the next suitable unit of habitat. Species such as Neotropical-Nearctic migrants can move over global scales to exploit completely different breeding versus winter survival niches (Alerstam and Hogstedt 1982). The ability to take advantage of seasonally and annually changing resources (i.e. opportunism), coupled with widescale movements literally define what migrants are, and help assure that they can effectively exploit changing environments. This opportunistic use of seasonal environments requires the availability of continually changing habitats within landscapes in order to provide safe and productive habitats for these species.

3.The third recommendation is to manage for a normal range of migrant population sizes, rather than target any one level of abundance. Temporarily low populations might be acceptable as long as new habitats become available quickly enough to rebuild populations, and as long as genetic factors such as inbreeding depression do not inhibit successful reproduction. Thus management strategies must be sufficiently flexible to accommodate the continuous changes inherent in the habitats exploited by migrants, and the resulting, but normal, population fluctuations. Important in this regard is the need for management flexibility, especially in view of global climate change projected during coming decades. Global change scenarios suggest that habitats we recognize at present will not only move in location (potentially crossing present political boundaries and regional mandates), but will in some cases become completely unrecognizable due to independently shifting ranges of plant species comprising those habitats (e.g., Botkin 1990). Successful management will require the ability to anticipate such changes, to re-organize management guidelines and priorities, to transfer responsibilities for management among political entities, and possibly even to help mobilize the political support necessary to reorganize some landscapes (e.g., adding to current park boundaries to increase the range of elevations and habitats, or to establish wildlife corridors). For example, if global warming eliminates present jack pine stands in Michigan, and they cannot simply be shifted to the north due to lack of suitable sandy soils (Botkin 1990), then where else can sufficiently large burns be established to regenerate the necessary expanses of jack pine needed for Kirtland's Warblers to breed? More than anything else, managers must come to accept uncertainty and change as natural and acceptable aspects of the ecosystems in which most animals thrive (Botkin 1990). Variability in habitat characteristics, such as the frequency and

extent of environmental disturbances, may be the best argument yet for managing habitat-species complexes rather than managing any particular species per se.

Finally, given the large number of Neotropical migrant species, it will probably be far more difficult to manage for each species individually than to manage habitats containing several species (e.g., bottomlands hardwoods in the southeastern U.S., containing Swainson's Warbler, Parula Warbler, Prothonotary Warbler, and Cerulean Warbler). One can then use the success of single species as indicators of successful management of the habitat. Managing habitats has the additional benefit of conserving many other kinds of organisms.

4.The fourth recommendation, which is related to the previous one, is that migrant populations need to be managed for enough individuals to buffer against temporary, local habitat loss or disturbance. This point is derived from a knowledge of the demographic and life-history characteristics of migrants. Surprisingly for opportunistic species, many migrant populations may be less resilient than populations of temperate resident species to temporary declines, i.e. slower to recover from declines (O'Connor 1992). This is because migrants have relatively low fecundity compared with temperate residents, and possibly smaller population sizes, both of which decrease potential recolonization ability. Recent research on how migrants use habitats, particularly those in winter, has shown that migrants can no longer be viewed as behaviorally plastic ecological generalists, i.e. temporary invaders of disturbed tropical habitats (Rappole 1991, see Sherry and Holmes MS). Migrants are, in many cases, habitat specialists, and they often use very specific microhabitats (such as dead leaf clusters containing concealed arthropods) or specialized food resources (Morton and Greenberg 1990). Environmental disasters such as habitat loss, drought, or hurricanes may thus devastate migrant populations as much as, if not more than, resident bird populations. Managers must therefore manage habitats and landscapes such that migrant populations remain at a great enough total size and can spread across multiple landscape units, so that "normal" and natural, yet potentially catastrophic, local habitat disturbances do not eliminate an entire species.

5.The fifth recommendation is that management at times must be tailored to the needs of individual species. Although seemingly contrary to the points above, there are times where some species are so rare that we must take every effort to boost their populations, even if this means targeting those particular habitats or even breeding birds in captivity. Migrants include a diverse set of species, each with its own particular habitat requirements, demography, and life-history. Thus, some species may behave very differently from others in response to habitat changes, and may require fundamentally different management considerations. Some migrant species are extraordinarily flexible in terms of habitats and diet (e.g., Yellow-rumped Warblers and American Redstarts) and these probably require little concern from managers at present. Other species are presently endangered in part because of stereotypical dependence on particular safe nesting sites, nesting materials, foods, or other resources (Morse 1989). A good example may be Bachman's Warbler, as we mentioned above, even though we cannot presently resolve whether summer or winter habitats were more important.

6.The sixth recommendation is the need to manage for, and distinguish between, the quantity and quality of habitat available for Neotropical-Nearctic migrants. Assessment of habitat availability or quantity is of primary importance. On a first approximation, the total abundance of a migrant species is roughly proportional to the total area of suitable habitat available. Thus, for example, managers responsible for Kirtland's Warblers must provide an adequate area of early successional, recently burned jack pine stands in Michigan to maintain enough individuals to avoid genetic or demographic bottlenecks, and the same may be said of the "cedar brakes" in Central Texas, to which the Golden-cheeked Warbler is restricted (Morse 1989). Habitat quantity will probably be monitored most efficiently in the future using a variety of increasingly sophisticated methods developed recently, such as that involving remote sensing and Geographic Information Systems (GIS), coupled with accurate census data from the ground (e.g. Powell et al. 1992).

Identifying habitat quantity, however, is not sufficient--quality is also important. In the breeding season, some habitats are more suitable than others, as indicated by bird densities, mating success and, particularly, breeding productivities (Sherry and Holmes MS). Likewise, variation in quality of winter habitat for migrants occurs frequently, as evidenced by differences in density, sex- and age-distribution patterns, and competition for "good" sites (Sherry and Holmes MS). Information about habitat quality is crucial for management purposes because it helps in prioritizing habitats, and in developing models of how changing habitats in a landscape will alter total population size. Differences in population abundances among habitats tell us how populations change, but demographic information will tell why populations are changing and is crucial for evaluating why densities are changing, i.e., the effect of food abundance, predator or brood parasites on nest success, to mention a few. Thus, management policies must also be based on demographic parameters, the most important of which are listed in Table 1.

Habitat quality raises the issue of "source" and "sink" populations (see Pulliam 1988, Pulliam and Danielson 1991). A source population reproduces sufficient individuals to maintain local abundance and produce colonists of newly available habitat, whereas a sink population is maintained by continual immigration of individuals from other, more productive habitats. Many populations of Neotropical migrants occupying fragmented woodland habitats, at least in parts of the midwestern U.S., are presently sink populations (Gibbs and Faaborg 1990, Robinson 1992). Migrant species breeding in the White Mountains of New Hampshire, on the other hand, benefit from extensive, non-fragmented stands of northern hardwoods forest, and these probably represent source populations (Holmes et al. 1992, Sherry and Holmes 1992). Using Black-throated Blue

Table 1. — Some important demographic parameters of bird populations useful in assessing habitat quality.

Fecundity
Clutch size
Number of annual broods (many migrants single brooded, but some double-brooded)
Nesting(fledging) success
Mass at fledging, or other index to post-fledging survival
Age of first breeding (by sex)
Mating success
Survival
Annual survival (summer-to-summer, or winter-to-winter, see Holmes and Sherry 1992)
Over-summer survival
Over-winter survival
Other parameters
Age-structure (proportion of yearlings:adults)
Sex ratio
Dispersal distances (by age, or sex)

Warblers as an example, and assuming annual survival is between 50% and 70% and that fledglings survive to the start of the next breeding season about half as well as adults, then it is easy to show that 1.7-4 fledglings are needed to replace adults lost (Sherry and Holmes manuscript). Holmes et al. (1992) found that Black-throated Blue Warblers fledged an average of 4.3 young per female per season (range = 3.5-4.9) over a period of four years, indicating that this population was producing more than enough fledglings to maintain the population. Similarly, American Redstarts at Hubbard Brook produced enough fledglings to offset typical mortality rates most years, although the population declined when nest predator populations decreased nesting success in the mid-1980's (Sherry and Holmes 1991, 1992). We should certainly become concerned when populations exist in sinks, where production of offspring is insufficient to balance losses occurring because of mortality or emigration. Source populations need be of less management concern. Management policy should attempt to increase population source areas in a landscape, but secondary habitats can also help stabilize population dynamics (Bernstein et al. 1991).

The effects of diverse ecological factors on the quality of a habitat are thus best assessed by monitoring a population's demography, but this procedure requires a substantial commitment of time, effort, and trained personnel. Ralph et al. (1992) provide an up-to-date manual on standardized methods and information necessary to study bird populations in the field, such as methods to quantify seasonal productivity of offspring using nest-monitoring studies. It may be possible for managers to involve scientists and amateur bird enthusiasts in the process of monitoring migrants demographically, and not just numerically.

It should also be noted that the quality and quantity of habitat may be independent. For example, a cowbird-elimination program begun in Kirtland's Warbler habitat in 1971 resulted in dramatic increases in nestling productivity (see Morse 1989: Fig. 11-2), but did not dramatically increase the population. Several factors probably contributed to this result, including the difficulty of many birds finding mates (Probst 1986), but the biggest factor was almost certainly the limited quantity of habitat, as evidenced by the effect of newly burned jack pine stands (Mayfield 1992).

Finally, it is becoming increasingly clear that many migrants compete for quality (source) habitats (e.g. Sherry and Holmes 1989, Marra et al. MS), suggesting that they are limited in supply relative to demand year-round. In such habitats, individuals behaviorally limit the density of birds sustainable per unit of habitat (Newton 1992). In such cases, management plans that focus on expanding the availability of habitat will be far more effective than trying to push densities above these habitat-specific carrying capacities.

7.Our final recommendation is that safeguarding of the annual range of habitats necessary to maintain viable migrant populations will require extraordinary communication and coordination among managers, scientists, and the public across international borders. Migrants illustrate particularly well the adage that a chain is only as strong as its weakest link. We thus cannot overemphasize the importance of habitat preservation and management year-round, i.e. throughout the entire breeding and wintering (and migratory passage) ranges of particular species, since any migrant population is sensitive to loss of habitat at any part of its annual cycle. No matter how much money goes into preserving habitat in the breeding range, a population could still go extinct due to deterioration of its wintering habitat, and vice versa. What we know presently about the biology of these birds clearly emphasizes the importance of simultaneous breeding and wintering season population limitation for these species.

We thus urge that those vested with managing these populations increase communication and collaboration with scientists and land managers in all countries where these species spend part of the year. Partnerships organized to span the geographical range of particularly threatened or endangered migrant species, involving North American and Latin American/Caribbean governments, resource-management agencies, private conservation organizations, or scientists in tropical countries must be encouraged. Such formal partnerships, including "sister forests," would be particularly productive if they paired up groups working on the same threatened or endangered species at different times of the year, such as the Kirtland Warbler Recovery Team with agencies in the Bahamas.

We have stressed repeatedly the importance of conserving large tracts of quality habitat throughout the year to safeguard healthy populations of Neotropical-Nearctic migrants. This is,

of course, a far more complicated task than it sounds for a variety of reasons besides just the global extent of the habitats under consideration. This task will require maintaining not only large quantities of habitat, but also quality habitat in terms of the potential fecundity and survival probabilities of the birds. Thus, monitoring of abundances and demographic characteristics of populations must be extensive and accurate. Considerable political will may be required to act on the information so gathered, because much habitat is already occupied or under pressure to be used by humans in ways that are not necessarily compatible with the birds' requirements. Conservation of habitats in the wintering ranges of migrant birds will be particularly important, because loss of habitat in the tropics continues unabated. Thus it is difficult to escape the conclusion that tropical wintering habitat will become limiting to at least some species in the near future, if such is not already occurring (Terborgh 1980, 1989; Morton 1992; Rappole et al. 1992; Robbins et al. 1992). Declines in habitat quality in North America have also severely affected Neotropical migrant populations. Preliminary efforts are underway to assess the potential vulnerability of species and habitats most threatened in winter (Morton 1992) and year-round (Terborgh 1989, Reed 1992), and such efforts need to be refined and expanded.

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