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CONSERVING STOPOVER SITES FOR FOREST-DWELLING MIGRATORY LANDBIRDS

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OVER THE PAST two decades, reported declines in populations of migratory landbirds have inspired high levels of activity and commitment from conservationists and scientists. Together, these groups have sought to overcome the particular political and ecological challenges of protecting migratory species by developing innovative conservation plans at multiple scales (Pashley et al. 2000, Andrew and Andres 2002, Faaborg 2002, Rich et al. 2004). However, after more than two decades of concern and attention, conservation strategies for Nearctic–Neotropical migrants remain incomplete. Challenges to the goal of protecting migratory birds arise from incomplete information on population

sizes, interseasonal connectivity and demography (Webster et al. 2002, Lovette et al. 2004); difficulties in assessing population viability (Cooper and Nur 2000, Donovan et al. 2002); and a poor understanding of how vulnerability varies across the stages of the annual cycle (Sherry and Holmes 2000, Sillett and Holmes 2002, Rodenhouse et al. 2003, Newton 2004). Furthermore, although conservationists take action on breeding and wintering priorities, unanswered questions about how to identify, prioritize, and protect those places used by migrants *en route* undermine the creation of realistic and comprehensive conservation strategies for Nearctic–Neotropical migrants (Moore et al. 1995, Moore 2000, Petit 2000, Donovan et

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al. 2002, Tankersley and Orvis 2003). Given that migration may constitute the most vulnerable and unpredictable period of the annual cycle (Moore 2000, Sillett and Holmes 2002, Berthold et al. 2003), we suggest that if the conservation of migratory stopover habitat is not addressed, it is likely that "conservation measures which focus on temperate breeding grounds and/or Neotropical wintering areas will be compromised" (Moore and Simons 1992:353).

Nearctic–Neotropical migrants spend up to one-third of each year migrating. Most individuals stop frequently during their migratory journey to rest and refuel, occupying almost any conceivable shelter, from city parks to vast forests. These stopovers vary in duration and frequency on the basis of some combination of at least four factors: (1) prevailing weather; (2) physiological condition of the individual migrant; (3) risk of mortality associated with predation, exposure, or other threats; and (4) resource availability at current, past, and possibly future stopover sites (Alerstam and Lindström 1990, Moore 2000, Schaub and Jenni 2001, Berthold et al. 2003). Weather, condition, risk, and resources vary spatially and temporally, cumulatively affecting a migrant's ability to successfully negotiate migration (Alerstam and Lindström 1990, Simons et al. 2000, Mabey 2002). Furthermore, successful migration translates not only into survival but also timely arrival on breeding or wintering grounds (Sandberg and Moore 1996, Smith and Moore 2003).

We suggest that conservation of migratory landbirds requires a network of sites along migration routes. Specific attention to stopover habitat is critical, because important segments of stopover habitat do not fall under the umbrella of breeding or wintering habitat (Moore et al. 1995, Simons et al. 2000). We define "stopover habitat" as the set of habitats that migratory landbirds use during the spring and autumn migration seasons. Many conservation groups, most notably Partners in Flight, a cooperative effort involving partnerships among many groups and agencies, have struggled with how best to incorporate stopover habitat into their prioritization schemes and conservation plans (Rich et al. 2004). Most of these conservation strategies have begun by identifying species of high conservation priority (Carter et al. 2000, Donovan et al. 2002). However, when

considering the needs of *en route* migratory landbirds, we believe that it is generally more appropriate to identify high-priority places and habitat types than to focus on individual species. The large number of species involved, their common use of the same critical areas during the migratory period (Moore 2000), and the lack of information on most species-specific stopover requirements combine to make a habitat and site approach more efficient.

A major obstacle for successful conservation of stopover habitat has been the perception that conservationists must choose among broadly different types of sites to ensure that the most critically important areas are protected. Another conceptual barrier has been the difficulty of defining significant levels of migrant use and habitat quality at stopover sites, because both factors can vary dramatically at a given site both within and between seasons. For example, enormous numbers of individual birds have long been observed "falling out" and using astonishingly small areas of habitat when certain weather conditions prevail near geographic barriers (Lowery 1945, Gauthreaux 1971). Yet, in other migration seasons, these same sites are virtually unused. This variability has made it difficult to determine whether protecting these fall-out sites is a good conservation investment. By contrast, advances in radar ornithology and similar techniques for measuring bird migration have suggested that certain large blocks of forested habitat consistently contain numerous individuals of migratory birds (Gauthreaux and Belser 1998, 2003). Additionally, the observation that migratory birds use a variety of places that are not normally considered potential conservation areas, including small woodlots, parks, and cemeteries, is gaining additional support from radar ornithology (Diehl et al. 2003). Presumably, individual birds derive some value from each of these types of sites, but the extent to which conservation resources should be invested among them remains unclear. To advance the conservation of migratory birds, efficient allocation of conservation resources with explicit consideration of these issues must be addressed systematically—an effort that, we believe, has not been previously addressed.

Here, we present a framework for describing migratory stopover sites so that their conservation can be more efficiently and

comprehensively accomplished. It represents a synthesis and summary of a workshop held in early 2001 to discuss stopover site protection for forest-inhabiting migratory birds along the Gulf of Mexico coast and Great Lakes (Duncan et al. 2002). The framework developed at that workshop provides a new perspective on how to approach the conservation of migratory landbirds during migration. We hope that it will serve to inform the collective network of individuals and organizations working on bird conservation and lead to successful conservation of these species.

The conceptual framework presented here is designed for forest-dwelling, nocturnally migrating landbirds relying on stopover habitats in Canada and the United States east of the 100th meridian. In certain regions, the ecology of this group of species during the migratory period is sufficiently understood to provide an adequate scientific basis to begin conservation action. Our conclusions, with necessary modifications, should be applicable to other geographic regions, to other groups of migratory birds, and, ultimately, to other groups of migratory animals.

FRAMEWORK FOR STOPOVER SITES

Stopover sites vary across a range of intrinsic (e.g. resource availability) and extrinsic (e.g. landscape context) factors. This ecological variability, combined with weather and a given migrant's condition, determines how a particular stopover site will contribute to a successful migration. We hypothesize that stopover sites can be defined on the basis of their capacity to meet migrants' needs at a given point in space and time. Capacity can be conceived as facilitating an individual's survival, its need to complete short migratory flights to the next stopover site, or its ability to perform long-distance flights over barriers or to a final destination. On the basis of this hypothesis, we have developed a conservation framework for categorizing stopover sites into three functional types, recognizing that these categories represent points on a continuum of the function of stopover sites. To simplify the communication of these concepts to scientific, conservation, and public audiences, we use the terms "fire escapes," "convenience stores," and "full-service hotels" to denote the function of each type of stopover site.

At one end of the continuum are "fire escape" stopover sites. These are infrequently used, but are utterly vital in emergency situations, analogous to fire escapes in human habitations. If a fire escape is not available at the critical place and time, migrants are not likely to survive to continue migration (see Spendelov 1985). Resource availability at the site may be too low to allow birds to replenish fat stores or recover muscle mass, but the stop allows them to survive and to continue migration from the site. Fire escape sites are typically adjacent to significant barriers, such as large bodies of water, deserts, or intensively altered landscapes, and are typically small and isolated habitat patches surrounded by unusable habitat. Because weather is such an important factor in determining when these sites are used, intra- and interannual variation in migrant density at these sites is high. However, given the importance of extrinsic factors in determining use of fire escapes, the situations in which high densities of migrants are observed at fire escape sites may be fairly predictable. Given the small size of most fire escapes and the inhospitable surrounding matrix, predation pressure may be relatively high in these habitats. Survivorship at fire escapes may be density-dependent or density-independent, depending on the relationship between available resources, particularly shelter, and migrant numbers at a given time. Examples of fire escape sites include islands in the Gulf of Mexico (e.g. Dauphin Island, Alabama; Dry Tortugas, Florida) and unforested islands or tips of peninsulas in or along the Great Lakes (e.g. Long Point, Ontario [Dunn 2001]). Although migrants are known to stop on ships and oil rigs, such structures can be considered fire escapes only if migrants are able to survive the stop and continue migration. Ideal fire escapes are those best located to serve as refugia for migrants when the surrounding landscape is completely unsuitable. Conservation plans should identify the existing networks of fire escape sites along the coasts of the Great Lakes, the Atlantic Ocean, and the Gulf of Mexico, as well as sites within urban or agricultural landscapes. Efforts should be made to fill in the largest spatial gaps within these networks through acquisition, easements, restoration, and management agreements to encourage compatible use. With intense development pressure in coastal areas (National Oceanic and

Atmospheric Administration 1998), all currently unprotected fire escapes would be considered valuable additions to the continental stopover network.

More central along the continuum are “convenience store” stopover sites. They are habitat patches of varying size, such as a park, woodlot, or small forest block, in a generally inhospitable landscape matrix. We define these sites as places where birds can briefly rest (i.e. stopover of two days or less) and easily replenish some fat or muscle or both. Sites of this type function to support birds between short flights to higher-quality sites or when migrants’ fuel needs are moderate. A given convenience store may better serve the needs of some species than of others (Hutto 1985b, Moore and Aborn 2000, Petit 2000). As with fire escapes, predation risks and resource depletion may make stopover periods shorter than “optimal” for individual migrants. Given that convenience stores are relatively small and isolated, migrants stopping at these sites may be vulnerable to density-dependent limits to food and shelter. Convenience stores may be the most common stopover sites in many parts of the agriculturally altered Midwest and in the urban corridors of northeastern North America but relatively scarce along the northern coast of the Gulf of Mexico. Examples of convenience stores include forested patches in central Illinois, and parks and cemeteries in many large cities of eastern North America (e.g. Central Park, New York City; Mt. Auburn Cemetery, Boston, Massachusetts; Jackson Park, Chicago, Illinois [Brawn and Stotz 2001]). The ideal convenience store is structurally heterogeneous, contains fresh water, and provides a variety of food resources (e.g. fruits and insects). As with fire escapes, there is no minimum size restriction on convenience store sites, but as they increase in size and heterogeneity, they merge into the next category of stopover site. Inventory efforts should identify small habitat patches and naturally vegetated riparian corridors within larger areas of unsuitable habitat that may function as convenience store sites. Protection, restoration, and habitat management efforts to encourage compatible use should be used to establish networks of convenience store sites to fill gaps between large protected sites.

At the other end of the continuum, a “full-service hotel” stopover site is an extensive

area of predominantly forested habitat. These are places where all necessary resources (i.e. food, water, shelter) are relatively abundant and available and that serve many individuals of many species. Individuals may remain at these sites for one to several days, because essentially all immediate resource needs are supplied and associated risks are relatively low, which allows individuals to attain top physiological condition and continue their migration to their next stop or final destination. Full-service hotels may be less susceptible to strong fluctuations in resource availability, because of lack of competition attributable to their size and inherent heterogeneity. Migrants use full-service hotels in great numbers, though observed densities may be relatively low (Gauthreaux and Belser 1998). Examples include the DeSoto National Forest and Pascagoula River bottomlands in Mississippi; Hiawatha National Forest, Michigan; and Great Smoky Mountains National Park and surrounding national forests in North Carolina. Ideal full-service hotels are ecologically heterogeneous, with a variety of food resources across environmental gradients (e.g. wetlands, streams, and uplands). A continental network of stopover sites would include full-service hotels consisting of large tracts of forest land in public and private ownership stratified across ecoregions. Areas in eastern North America with few large forest tracts pose the greatest challenge to establishing and protecting a network of full-service hotels. Regional-scale landscape alteration has left significant areas of the central Midwest (e.g. portions of Illinois, Indiana, Ohio, Ontario), the mid-Atlantic (e.g. urban corridors of the Piedmont and Coastal Plain), and Southeast (e.g. Mississippi Alluvial Valley) with few or no full-service hotels.

IDENTIFYING AND PRIORITIZING SITES

Conservation of stopover habitat requires an understanding of what makes a site “important” for migratory birds. We view importance as consisting of two components: (1) the function of a site as defined by the continuum of categories from fire escape to full-service hotel and (2) the relative value of a site within a category. Important stopover habitat is not easily identified. Currently, there is no objective way to rank stopover sites that adequately accounts

for the tremendous spatial and temporal variation in use and resource availability within and between seasons and years. Recognizing the differences in stopover site function is a significant step toward meaningful accounting of the inherent variability of migration. We suggest that the first step in classifying and prioritizing stopover sites can be based on three criteria, each of which represents an integration of multiple factors: (1) ecological context (e.g. extrinsic factors such as proximity to ecological barriers and degree of spatial isolation); (2) intrinsic characteristics (e.g. diversity and abundance of resources); and (3) migrant use (e.g. relative abundance, including frequency and consistency of use as a stopover site).

A key attribute of this framework is that it allows conservation planners to evaluate site quality within rather than across functional categories, thus avoiding the problem of unsuitable and inappropriate comparisons among sites during the process of prioritizing areas for conservation. Each category has its own value for migratory birds and its own set of criteria for assessing importance and priority. For example, fire escape sites will not be discounted for inconsistent migrant use compared with full-service hotel sites. To meet the goal of a trans-continental safety net for migrating landbirds, conservationists need to ensure the protection of examples of all appropriate categories of stopover sites. When decisions are made about where to direct scarce conservation resources, site prioritization should be considered within each category.

Within-category prioritization requires selection of reasonable criteria for measuring the relative value of a given stopover site. The ultimate measure of a stopover site's value would be its contribution to maintenance of a population. Theoretically, we would classify a stopover site as having high conservation priority when elimination of a site would directly or indirectly affect the global abundance of one or more migratory species. Operationally, this is not yet possible. With the improvement and wider application of field and modeling techniques for linking populations of migrants across the annual cycle (Erni et al. 2002, Kelly et al. 2002, Webster et al. 2002, Hobson et al. 2004), estimating the relative value of a stopover site to a given species may become feasible. For most species, it is likely that the importance

of any given site can only be determined when considered in the context of the potential loss of various combinations of other sites (Farmer and Wiens 1998, 1999; Weber et al. 1999). In the interim, it is necessary to consider alternative metrics that can help rank stopover sites of varying quality and value.

Criteria that can be used for prioritizing important stopover sites within functional categories include use by a relatively high proportion of a species' population; use by relatively large numbers of migrants; and consistency of use between seasons, years, or both. Duration of stopover, site-specific survival rates, and rate of energetic gain are also possible measures of stopover site quality (Dunn 2002), though these parameters are difficult to measure accurately (Dunn 2000, Schaub and Jenni 2001, Schaub et al. 2001, Schilch and Jenni 2001, Jones et al. 2002, Morris et al. 2004). Moreover, given that migrants' resting and refueling requirements at a particular stopover site may vary among individuals both within and between species, it would be difficult to define a single optimal stopover length or fattening level to use as a basis for a habitat-quality metric. Finally, some sites, such as places where birders and the public can observe and learn about migrants, have a high degree of educational significance and may therefore have enhanced value for protection (e.g. High Island, Texas).

FUTURE RESEARCH PRIORITIES

This stopover-site conservation framework is intended to help clarify those factors that combine to make stopover sites "important" from a migrant's perspective. It is our hope that this framework stimulates discussion around the problem of how stopover sites contribute to a bird's ability to successfully negotiate migration. A large number of research priorities follow from this question.

Research on all the components of stopover site value is still needed. A suite of descriptive questions will require original research and synthesis of existing data. For example, there is no definitive agreement on best descriptors of ecological context (i.e. best predictors of migrant use) or the most salient intrinsic characteristics of stopover sites (e.g. primary productivity, insect and fruit availability, shelter). Furthermore, there is a need to understand both

the spatial (i.e. landscape, regional, continental) and temporal (i.e. within and between seasons and years) variation in ecological context and resources. Identifying the best standard method for measuring relative cumulative use of stopover sites by migrating birds, including frequency and consistency of use during and among seasons and years, remains a priority that will allow for measures of variation in use over space and time.

Beyond these fundamental questions, basic research is needed to understand whether and how these factors relate to one another. Moreover, it is essential to establish how factors including landscape context, resource availability, competitor density, and predation risk translate into ecologically meaningful parameters, such as body-condition recovery (e.g. fattening), overall pace of migration, probability of survival now and in the future, timing of breeding activities, and reproductive success. Attention must also be given to the patterns and consequences of differential migration (Cristol et al. 1999). Intraspecific differences in migratory routes and timing could translate into systematic differences in resource availability and risk for males and females or juveniles and adults (Mabey 2002). Ultimately, research in these areas will help connect migration stopover biology to population dynamics.

CONCLUSION

This framework reflects our experiences in eastern North America. In other parts of North America or the Neotropics, important stopover sites may have other distinctive attributes. For example, many migrants in western North America use riparian corridors in both spring and fall (Finch and Yong 2000). During fall migration, high-elevation sites are also important (Hutto 1985a). In southwestern deserts, the density of migrants at even small oases rivals that in riparian corridors along the San Pedro River (Skagen et al. 1998). We intend to modify this framework in the future and encourage others to do so by expanding its geographic scope and making more explicit recommendations. The strength of the framework is that it is based on the function of sites from the migrants' perspective. This foundation allows for the flexibility necessary to easily refine the framework as research on migration ecology advances.

We strongly suggest that stopover sites be included in any comprehensive biodiversity planning effort. Preliminary investigations of some of these plans (e.g. Foreman et al. 2000, Groves et al. 2000, Noss 2003) suggest that current or proposed conservation areas selected to protect other components of biodiversity also capture a significant percentage of known and predicted stopover sites (Duncan et al. 2002). However, this may not be true in all geographic areas. In North America, areas that especially need further assessment are the Atlantic Coast, central Midwest, Great Lakes region, Great Plains, western deserts, and the West Coast. Stopover sites most likely to be missed are relatively small sites that are important because of their proximity to ecological or physical barriers (fire escapes) or their position within a matrix of agricultural and urban land use (convenience stores). An excellent example of a strategy that has the potential to enhance fire escapes and convenience stores within large metropolitan areas is the Urban Conservation Treaty for Migratory Birds developed by the U.S. Fish and Wildlife Service (see Acknowledgments). Although the relative numbers of sites to be conserved in each functional category will likely vary among geographic regions, we suggest that fire escapes and convenience stores should receive the most attention, for three reasons. First, these sites are least likely to be identified and managed with conservation objectives in mind. Second, there are few remaining opportunities to protect these types of sites, especially fire escapes. Third, these small remnants of suitable habitat are being rapidly destroyed and degraded (e.g. by invasive species and changes in hydrology). These three characteristics of fire escapes and convenience stores combine to leave them vulnerable to the influences of unpredictable external forces. The landscape-scale nature of full-service hotel sites means that they are likely already either under conservation ownership or have been targeted for conservation action, even if not with migratory birds in mind.

Bird conservation planning efforts have repeatedly identified the imperative need to understand migratory stopover sites from both the research and conservation perspectives (Bonney et al. 2000, Carter et al. 2000, Moore 2000, Donovan et al. 2002, Ruth et al. 2003). Efforts are underway by the conservation and academic research communities to fill these

gaps, typically on a regional basis. One of the goals of this paper is to encourage attention and research on the ecology and protection of stopover habitat, including development of appropriate funding sources. We anticipate that government or private agencies will soon develop the capacity to collate data from diverse geographic areas that will allow us to achieve the systematic hemispheric synthesis we so urgently need.

Ideally, a complete network of migration stopover sites would be identified systematically as part of broad-scale planning efforts. This is difficult, however, given the limited knowledge about migration in many areas and our current inability to estimate how many sites are needed and their spatial distribution. This obliges planners to begin working at smaller spatial scales, using local expertise and readily available, but often anecdotal, information. We recommend including migration stopover needs in site or regional conservation planning efforts that are conducted to design networks or portfolios of conservation areas (see The Nature Conservancy 1999). As our understanding of migration ecology advances, local and regional plans could then be merged into an intercontinental network of protected stopover habitats.

In light of the growing evidence that stopover habitat may be limiting to populations of at least some migratory landbirds (Sillert and Holmes 2002, Berthold et al. 2003; but see Faaborg 2002 for an alternative view) and the certainty of rapid anthropogenic landscape changes in eastern North America (National Oceanic and Atmospheric Administration 1998, Jones et al. 2001), it is critically important that stopover habitat be protected and that this protection occur sooner rather than later. Particular attention needs to be paid to geographic areas where stopover habitat is scarce (i.e. holes in the stopover safety net), where fire escapes are inadequate or lacking, and where sites that receive heavy and consistent use may be lost. Protecting stopover habitat is a proactive conservation strategy that will yield enormous biological and economic benefits well into the future. At the same time, research needs to be directed to understanding the stopover ecology, habitat requirements, and demography of migratory landbirds to ensure that conservation action is based on sound science and is as cost-effective as possible.

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