Understanding the Stopover of Migratory Birds: A Scale Dependent Approach[1]

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Abstract

The development of comprehensive conservation strategies and management plans for migratory birds depends on understanding migrant-habitat relations throughout the annual cycle, including the time when migrants stopover *en route*. Yet, the complexity of migration makes the assessment of habitat requirements and development of a comprehensive conservation strategy a difficult task. We emphasize that development of a comprehensive conservation strategy depends on understanding that migrant-habitat relations during passage are scale dependent, and we outline a practical framework for the study of migrants during stopover that reflects spatial scale and allows us to draw stronger inferences about the behavior, ecology and conservation of migratory birds. This framework is organized into four components, each providing an increasing degree of resolution and information at different ecological scales from gross patterns of habitat availability and use by groups of migrants to finer-scale information on habitat suitability and consequences of *en-route* habitat use for individual birds. Combining information from these components with remote-sensing technology and Geographic Information Systems [GIS] places us in a position to develop conservation initiatives and management plans that are focused explicitly on migration and the stopover biology of migratory birds.

Key words: Migration, stopover ecology, scale, habitat selection

Introduction

Migration is a fundamental characteristic of the life history of many organisms from monarch butterflies to marine mammals and is surely one of the most fascinating of all behaviors. Over two-thirds of all the landbirds that breed in temperate North America, for example, migrate long distances to nonbreeding areas in Mexico, Central and South America and the islands of the Caribbean (Keast and Morton 1980, Rappole 1995). Some have argued that these long-distance, intercontinental migrants experience the better of two worlds by virtue of their migratory strategy: increased reproductive success by breeding in food rich, competitor poor temperate areas and increased survival by spending temperate winter in tropics (Greenberg 1980). Be that as it may, traveling long distances across areas that vary physiographically comes with considerable risks, and the mortality associated with intercontinental migration may be substantial, especially among young-of-the-year birds (Lack 1946, Greenberg 1980, Ketterson and Nolan 1983, 1985; Sillett and Holmes 2002). Hence, the migration period is likely to have an important role in limiting migratory landbird populations (see Sherry and Holmes 1995, Hutto 2000), and should factor into the development of conservation strategies aimed at protecting these populations (Moore et al. 1995).

Although many landbird migrants are capable of making spectacular, non-stop flights over ecological barriers, few migrants actually engage in nonstop flights between points of origin and destination. Instead, migration is divided into alternating phases of flight and stopover, with each stopover lasting a few hours to a few days. In fact, the cumulative amount of time spent at stopover sites far exceeds time spent in flight and largely determines the total duration of migration (Alerstam 1993). The place where a migratory bird pauses between migratory flights is called a stopover site.

When trying to understand how migrants "choose" stopover sites during passage, it is important to recognize that migration occurs over a broad geographic scale, but over a relatively short temporal scale, which necessarily limits time and information available to migrants to evaluate different sites. Moreover, migrants almost invariably finds themselves in unfamiliar surroundings (Moore et al. 1990, Petit 2000) at a time

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when energy demands are likely to be high (e.g., Loria and Moore 1990), often faced with the need to acquire food in a short period of time, while balancing often conflicting demands between predator avoidance and food acquisition (e.g., Lindström 1990, Moore 1994, Cimprich and Moore 1999), competition with other migrants and resident birds for limited resources (e.g., Moore and Yong 1991, Carpenter 1993a,b), unfavorable weather (e.g., Gauthreaux and Belser 2000), not to mention the need to make accurate orientation decisions (e.g., Sandberg and Moore 1996a). How well migrants "offset" the costs of migration depends on how well they solve the problems that arise during passage. Solution of *en route* problems determines the success of a migration, while a successful migration is ultimately measured in terms of survival and reproductive success (Sandberg and Moore 1996b, Smith and Moore 2003).

The development of comprehensive conservation strategies and management plans for migratory birds depends on understanding migrant-habitat relations during stopover. This understanding is best gained by taking a hierarchical approach in which the mechanisms by which habitats are occupied as well as the costs and benefits of habitat use are studied at different ecological scales. Our objectives are two fold: (1) Emphasize that migrant-habitat relations during passage are scale dependent and (2) outline a practical framework for the study of migrants during stopover that reflects spatial scale and allows us to draw stronger inferences about the conservation of migratory birds.

Migrant-Habitat Relations

Although we might expect migrants to settle in habitats based on relative suitability, where suitability is tied to why the migrant stops over in the first place (Petit 2000), that outcome is not assured. Favorable *en route* habitat, where a fat-depleted migrant can rapidly meet nutritional needs, for example, is probably limited in an absolute sense, or effectively so because migrants have limited time to search for the "best" stopover site (Hutto 1985, Martin and Karr 1986). Intrinsic constraints on habitat use are those factors thought to determine habitat quality and upon which migrants make decisions about habitat use at a fine spatial scale – factors such as food and presence of predators (see Hutto 1985, Moore et al. 1995). As the spatial scale broadens, factors intrinsic to habitat give way to factors largely unrelated to habitat (see Gauthreaux 1980, Kelly et al. 1999). Indeed, at a broad spatial scale, habitat use is largely under control of factors extrinsic to habitat per se such as weather.

The study of landbirds during migration should reflect the hierarchical nature of a migrant's relationship to habitat (Moore et al. 1995), and should "focus" on the migrant-habitat relationship at different scales. Imagine an intercontinental songbird migrant traveling northward across the Gulf of Mexico. At this broad geographical scale, the hypothetical migrant might stop on East Ship Island off the Mississippi Gulf Coast rather than along the coast of Louisiana by virtue of prevailing winds alone (*fig. 1a*). That "decision," influenced as it is by extrinsic factors, is likely to have consequences for the migrant. For example, when stopover biology of migrants was studied simultaneously in spring at two sites along the northern coast of the Gulf of Mexico, White-eyed Vireos (*Vireo griseus*) were more likely to replenish depleted fat stores and stay for a shorter time if they stopover in a chenier in southwestern Louisiana (*fig. 2*), where food abundance was estimated to be greater, than on East Ship Island (Kuenzi et al. 1991).

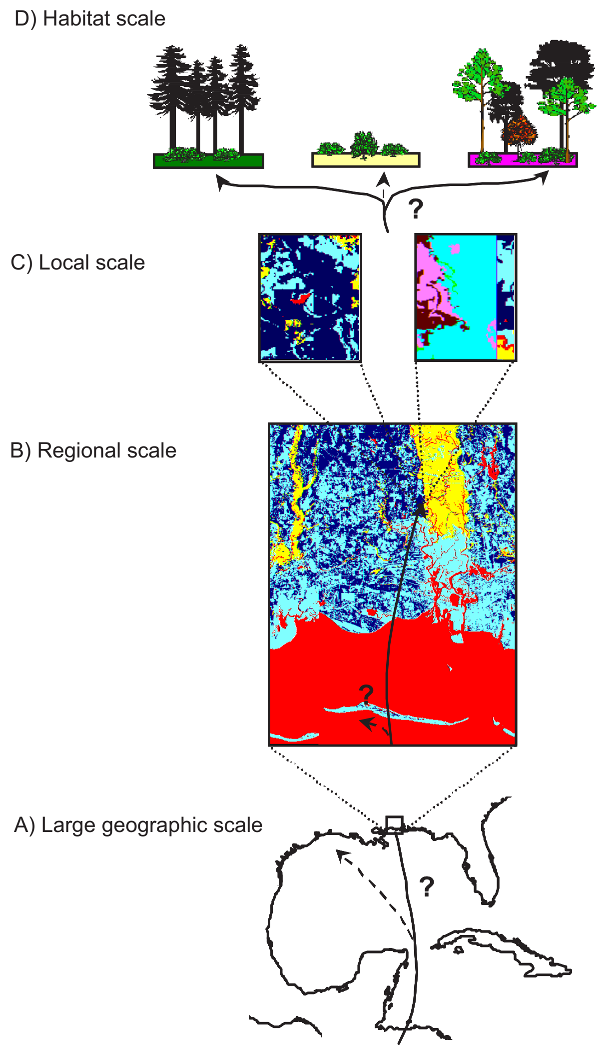

Figure 1— Conceptual hierarchy of en route habitat use by migratory landbirds making landfall after a trans-Gulf migratory flight in spring at various spatial scales.

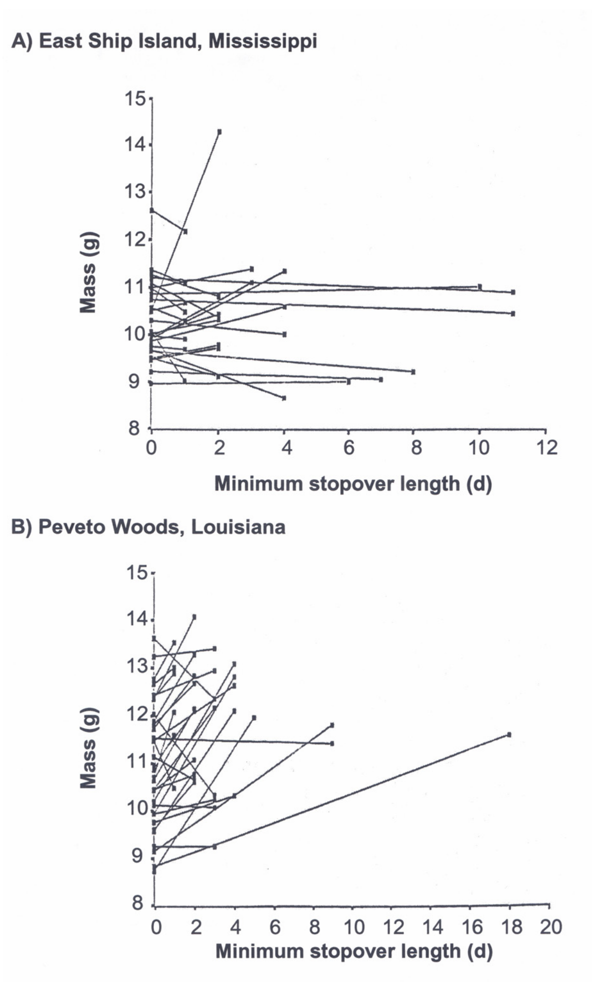

Figure 2— Mass change of White-eyed Vireos from first capture to last capture at A) East Ship Island, Mississippi (mean = 0.00 ± 0.08 g/d, N = 30), and B) Peveto Woods, Louisiana (mean = 0.33 ± 0.08 g/d, N = 33) in 1988.

Our hypothetical migrant may fly inland and make landfall in a patch of hardwood forest rather than land in coastal woodland or on barrier island, a decision that is probably influenced by the migrant's energetic condition as well as wind and other weather conditions (see Lowery 1945, Gauthreaux 1971, Moore and Kerlinger 1987, Gauthreaux and Belser 2000). The result of the "decisions" that migrants make at this broad geographic scale is reflected, for example, in data collected from surveys stratified into three latitudinal bands from the immediate coast up to 85 km from the coast in southern Mississippi[1] (*fig. 3a*). In general, more individual migratory birds were observed inland away from the coast during spring migration.

When our hypothetical bird makes landfall, she encounters a landscape of different habitats at a local scale (*fig. 1c*). Observations of migrants arriving along the northern coast of the Gulf of Mexico following a trans-Gulf crossing suggest that migrants assess alternative habitats (*fig. 1d*) during an initial exploratory phase shortly after arrival (Aborn and Moore 1997). An "exploratory phase" to habitat selection would be adaptive when migrants encounter a variety of habitat types and the availability of suitable habitat is unpredictable. Although migrants could arrive at a stopover site with prior information about the distribution of resources and habitats, migrating birds experience a variety of unfamiliar habitats and usually spend little time at one location, circumstances that reduce the value of prior information.

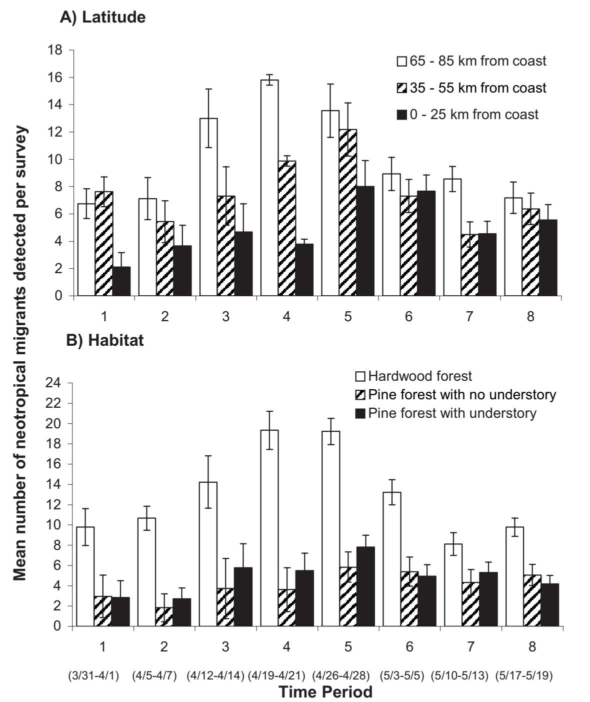

Figure 3— Mean number (±se) of neotropical migratory landbirds detected per survey at coastal sites (N = 6 sites per treatment) of A) different distances from the coast and B) various habitat types within Mississippi during spring 1993.

Nevertheless, several lines of evidence suggest that migratory species exhibit selective use of locally available habitats during stopover (Moore et al. 1995, Petit 2000): (1) Use of habitat out of proportion to its availability (*fig. 3b*; see also Moore et al. 1990, McCann et al. 1993); (2) Species-specific patterns of distribution among different habitats (e.g. Bairlein 1983); (3) Habitat use correlated with food availability (e.g., Hutto 1985, Martin 1985, Martin and Karr 1986, Yong et al. 1998); (4) Shifts in habitat use correlated with changes in dietary preferences (Moore et al. 1990, Moore and Woodrey 1993); (5) Habitat use in relation to energetic condition (Aborn and Moore 1997, Moore and Aborn 2000). What cues

[1]unpublished data, Moore and Simons.

migrants use to select among alternative habitats are poorly understood (Moore and Aborn 2000).

Scale-Dependent Framework

The study of migrants during stopover should reflect their scale dependent relationship with habitat. We begin with a regional habitat map of the landscape in question based on land cover classification of a multi-spectral remotely-sensed image. The abundance and spatial pattern of habitat types of the study landscape are derived using a geographic information system (GIS) (e.g. Simons et al. 2000). We use this map as a setting or geographic framework in which to develop our study design. We organize our study design into four components, each providing an increasing degree of resolution and information at different spatial scales of a migrant's relationship to habitat; from gross patterns of habitat availability and use by groups of migrants, to finer scale information on habitat suitability and consequences of *en-route* habitat use for individual birds.

Radar Component - Weather surveillance radar is a useful tool for the detection, monitoring and quantification of the movement of birds in the atmosphere (Gauthreaux and Belser 2000, 2003; Diehl et al. 2003). As such, radar is capable of addressing questions about broad geographic scale movements over various time scales. Over the course of a migration season, for example, radar provides an indication of where and how frequently migratory flights are made. Although weather surveillance radar can be used to determine areas where migrants stopover, it provides only a rough indication of density in relation to habitat type and little, if any, information on species, much less age, sex or energetic condition. Consequently, radar information is most valuable when integrated with data at the next level of analysis.

Census Component - At a finer resolution, field personnel quantify abundance and diversity of landbird migrants in different habitats and/or in relation to different spatial features by means of surveying protocols (e.g. point counts, line transects). These data can be used to address daily and within-season patterns of migration. For example this approach has been used to examine species-area relationships of migrants *en route* within a single habitat type (see Martin 1980, Blake 1986, Cox 1988).

Telemetry Component - At the local and habitat scale, one can use radio-telemetry to study the movement pattern of migrants in relation to landscape variables. For example, radio-telemetry can be used in conjunction with translocation experiments designed to test predictions about patch occupancy: How do migrants react to patch size, habitat boundaries, habitat type? Radiotelemetry also helps us to understand how migrants make decisions about habitat use during stopover (Aborn and Moore 1997, Moore and Aborn 2000). Radio-telemetry can provide insight into stopover duration, temporary home range size, and exploratory behavior of migrants, as well as whether the factors of habitat patch size and placement within the landscape also affect the availability and suitability of stopover habitat for birds.

Behavioral (Direct Observation) Component - At the habitat scale, the consequences of the migrant-habitat relationship are evaluated by (a) observing how individual migrants use habitat (e.g., Loria and Moore 1990) and (b) using capture-recapture methods in different habitats (e.g., Yong et al. 1998), which allows quantification of the migrant's performance (e.g., energetic status, rates of mass change and length of stopover).

Data derived from the Radar, Census, Telemetry and Behavioral Components are analyzed against the spatial context provided by the regional habitat map. Dynamic spatial models that combine information on migrant stopover ecology (e.g., habitat preferences, energetic condition and flight ranges) with habitat data can be used to simulate how patterns of habitat availability (patch size, shape and distribution) may affect migratory bird populations. For example, Simons et al. (2000) illustrated the application of spatial models to test predictions about how spatial features of the stopover landscape along the northern coast of the Gulf of Mexico might affect habitat suitability, create migratory corridors, or serve as ecological 'traps' for migrants.

Conservation Implications

The spatial scale over which migration occurs, coupled with the variety of habitats migrants encounter during passage make the challenge of conserving stopover habitat for migratory birds uniquely different from that of protecting breeding and wintering habitats (see McCann et al. 1993, Moore et al. 1993, Watts and Mabey 1994, Moore et al. 1995, Petit 2000). The spatial scale presents political and economic difficulties with respect to assigning responsibility for the protection of migratory bird populations, while habitat heterogeneity along migratory routes presents ecological difficulties for understanding what habitats are most important, where they occur, and how their distribution and abundance are changing as a result of development and land conversion (Moore and Simons 1992, Mabey and Watts 2000). However, if the persistence of migratory bird populations depends on birds' abilities to find favorable conditions for survival throughout the annual cycle, factors associated with *en route* ecology must figure in any analysis of population change and in the development of a comprehensive conservation "strategy" for landbird migrants.

A variety of management issues are involved in the conservation of migratory bird stopover habitats. Some conservation issues concerning the integrity and/or suitability of stopover habitat in the southeastern United States include global/climate change, conversion of natural habitats, coastal erosion, bird collisions with communications towers, the role of fire in managing landscapes, livestock grazing and white-tailed deer overbrowsing, the suitability of man-made habitats, invasive exotic plants, and forest management practices (Woodrey et al., in press). Over the past decade, we have gained a deeper understanding of the behavior, ecology and ecophysiology of migratory birds during passage. That understanding, in combination with the recent accessibility of remote-sensing and GIS technology and the scale-dependent approach outlined here, provide us a framework or perspective to identify those issues most-relevant to the development of successful conservation initiatives and management plans that are focused explicitly on migration and the stopover biology of migratory birds.

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