SPECIAL SECTION:
MIGRATION AND STOPOVER ECOLOGY

The Condor 107:193–196

ECOLOGY AND PHYSIOLOGY OF *EN ROUTE* NEARCTIC-NEOTROPICAL MIGRATORY BIRDS: A CALL FOR COLLABORATION

Patricia J. Heglund[1,3] and Susan K. Skagen[2]
[1]*United States Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI 54603*
[2]*United States Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526*

Ornithologists who regularly witness the breathtaking influx of songbirds at stopover sites during spring or fall migration know that birds are tremendously adaptable. Migration encompasses a range of actions distinct from permanent residency but includes altitudinal movements, sporadic irruptions, short-distance flights, as well as obligate long-distance movements (Able 1991). Migration can be acquired, abandoned, or prolonged by a species depending on conditions along their migratory routes (Able and Beltoff 1998). Previously nonmigratory populations may undertake migration where changing conditions become increasingly disadvantageous for the resident population or where interspecific competition becomes more severe. Regardless of the distance or motivation, migration is physiologically demanding and potentially risky.

Nearctic-Neotropical migrants face both ecological and physiological challenges while *en route* from one location to another. Migrants require periodic stopovers to rest and refuel, and during these stopovers, they must cope with the uncertainties of resource abundance and availability, intra- and interspecific competition, and predation pressures in unfamiliar environments (Moore et al. 1995). Physiologically, the size of many Nearctic-Neotropical migrants puts large constraints on fat storage, flight speed, and the ultimate distance a bird is able to travel in one migratory bout. Ecological and physiological hurdles associated with trans- and intercontinental migration in concert with the extensive landscape changes along historical migratory pathways suggest that the migration period poses formidable hardships to many birds.

Quantifying the effects and timing of limiting factors for migratory species is particularly difficult because of the transitory nature of migration (Hutto 2000, Sillett and Holmes 2002), which makes this period a fruitful area for basic and applied research. Songbirds often migrate at night and are broadly and unpredictably dispersed during the day. Further, events or conditions at one stage in the annual cycle can have a powerful influence over a bird's survival and productivity in another stage (Marra et al. 1998, Sillett et al. 2000). Because some migratory bird species have shown regional declines in abundance and therefore are of conservation concern (Sauer et al. 1996, Peterjohn and Sauer 1999), future research and modeling efforts should focus on understanding how events and conditions throughout the annual cycle are interconnected and how limiting factors might work at different scales to influence population size (Sillett and Holmes 2002).

Determining whether populations are limited by events or processes that operate *en route* involves a complex series of tasks that collectively require intensive and extensive research using new and emerging technologies. We now know that rates of lipid deposition, as measured with plasma metabolite profiles, may serve as an indicator of habitat quality (Williams et al. 1999, Guglielmo et al. 2002), and genetics and stable isotope analyses can be valuable tools to elucidate links between breeding and wintering areas

Manuscript received 25 August 2004; accepted 4 February 2005.
[3] E-mail: pheglund@usgs.gov

(Hobson and Wassenaar 1997, Webster et al. 2002, Lovette et al. 2004). Radar imagery (Diehl et al. 2003, Gauthreaux and Belser 2003) and low orbit radar receivers (Cochran and Wikelski, in press) also hold much potential for tracking large-scale movements and habitat use of migrants. Direct information on survival rates during migration or how migratory conditions affect fecundity and overwinter survival is elusive. However, we are now beginning to unravel the mysteries of migration by tracking how birds move from one location to another, understanding what types of habitats and resources birds use, determining whether the timing of migration and migratory pathways is fixed or plastic, understanding the energetic and dietary constraints of long-distance flight, and determining the competing demands on birds during migration.

From a practical perspective, there is a great need for the information necessary to make good choices regarding where, when, and how to place conservation efforts and to ensure those efforts are responsive and effective (Petit 2000). We need to define what constitutes ''important'' or ''good'' *en route* habitat so management agencies and private landowners can develop effective programs at appropriate scales and receive the greatest return for the dollars expended. The habitat selection process of *en route* migrants, according to current theory, occurs on two levels: processes that are intrinsic to, and those that are extrinsic to a stopover location (Hilden 1965, Hutto 1985, 2000, Moore et al. 1995, Moore and Aborn 2000). Thus, effective conservation will require better data on the spatial scale at which migrants assess and use landscapes and a better understanding of evolutionary processes that have resulted in the patterns we see today.

This special section of *The Condor* is based on a symposium held on migration stopover ecology at the 2004 Cooper Ornithological Society meeting in La Crosse, Wisconsin. The symposium was inspired by the volume on stopover ecology edited by Frank Moore (Moore 2000), which stimulated discussions among the authors and other colleagues that continued through a subsequent workshop on migration ecology in western North America (Skagen et al. 2004). During many of our conversations we thought it would be interesting to compare results from studies conducted in eastern, midwestern, and western migration systems. There has been debate over whether or not eastern and western migration systems are ecologically distinct and there have been few comparative studies to examine this question.

In this volume we have brought together six papers on North American Nearctic-Neotropical migration ecology. The first two papers are simple, yet elegant efforts to synthesize and interpret data from a much larger perspective providing a frame of reference for more local investigations. Kelly and Hutto (2005) lay the groundwork for comparing U.S. western and eastern migration systems by examining their biogeography, evolutionary relations, and present-day *en route* ecology of wood warblers. They conducted an innovative study using several lines of evidence and postulate that eastern wood warblers and western wood warblers are geographically isolated from one another throughout the annual cycle. This isolation results in the potential for differences in timing, rate of passage, habitat use, and diet. Indeed, they provide several examples wherein these two groups differ in age ratios, body condition, and diet.

Long-distance migration requires enormous amounts of energy and birds vary in their ability to acquire and store the energy needed. Stopover habitats provide varied opportunities for migrants to rest and refuel, and we have little ability to identify quality habitat let alone understand how migrants function relative to habitat features. Skagen et al. (2005) explore relations among species biogeography, habitat affinity, and patterns in migration among short- and long-distance migrants by examining abundance and capture data from the borderlands region of the United States and Mexico. They demonstrated the role of biogeography and its influence on migration patterns among species.

The next paper, by Deppe and Rotenberry (2005), also includes an examination of the roles of biogeography, diet, and competition and their relation in shaping the timing of migration and patterns of species turnover within sites on the Yucatan Peninsula, Mexico. They compared patterns in arrival during the fall with those from other studies in the midwest and eastern U.S. and in relation to the locations of wintering areas and differences in diet among species. Studies like these provide us with views of the rapid changes within a local stopover area and offer insights into the complexities of migratory *en route* ecology in general.

Carlisle et al. (2005) looked at the ecology of fall *en route* migrants in the Boise Foothills of southern Idaho and compared fall migrant use of a riparian draw with that of a nearby montane-shrub habitat. Over the seven years of this study, Carlisle et al. reported high capture rates for a variety of species. They compared recapture rates, stopover duration, and changes in energetic condition between the two habitat types and found that the montane habitats in general were suitable refueling sites for *en route* migrants. These results suggest that future studies of *en route* migrants might benefit from a broader examination of all available habitats (See Kelly and Hutto 2005).

Rodewald and Matthews (2005) looked at spring migrant use of mature-forest upland sites versus lowland-riparian sites in Ohio. Small woodlots (upland, mature forests) and riparian forests are the primary forested habitats within agricultural and urban landscapes. Whereas in the West, riparian vegetation is an extremely important habitat type for migrants (Yong et al. 1998), especially in the spring (Kelly and Hutto 2005, Skagen et al. 2005), Rodewald and Matthews (2005) provided evidence that mature upland sites in Pennsylvania hosted more species and more individuals during spring migration. Thus, we need to increase our understanding of how and when birds are moving across the landscapes, what habitats they use, and what these habitats provide before we can truly make progress in conserving and protecting species during all phases of their annual cycle.

Understanding the physiology of intercontinental flights is logistically challenging. That fact continues to promote important technological advances in the areas of avian physiology and biochemistry, among others, in relation to migration (See Kelly and Hutto). The primary fuel for migration is adipose tissue, but when fat stores are depleted, birds will burn protein at the expense of their muscle tissue and digestive organs (Piersma and Jukema 1990, McWilliams and Karasov 2001). The paper by Pierce and McWilliams provides insights into the ecology of refueling by examining changes in the biochemistry of body fat in association with migration. They begin to tease apart the question of whether birds selectively forage for foods high in certain fatty acids while *en route*, whether they undergo selective metabolism in lieu of changing their diet, or whether they use a combination of both strategies in the acquisition and storage of body fat.

The six papers in this section all lend support to the symposium participants' collective call to develop coordinated, collaborative research efforts that allow us to develop a better understanding of patterns in migration pathways, habitat use, and the energy constraints of migrants. Recent improvements in techniques and technologies hold promise for an explosion of new information from migration research. Coordinated efforts to further examine and synthesize the similarities and differences among Nearctic-Neotropical migrants would provide a better understanding of the ecology of migration and help guide coordinated conservation efforts. Through a series of short-term coordinated efforts over large spatial scales, coupled with long-term targeted programs, we can rapidly strengthen the knowledge base needed by land managers and conservation organizations to protect or restore habitats and habitat conditions for migratory birds in the future.

ACKNOWLEDGMENTS

We thank all the participants in the May 2004 symposium for their enthusiasm and willingness to share ideas. We also extend our gratitude to Melissa Meier for assisting with the development of the symposium and for her efforts to shepherd all the manuscripts through the review process to timely publication. Comments by M. Meier, F. Knopf, J. Kelly, J. Cox, and an anonymous reviewer greatly improved this manuscript. Funding for this symposium was provided by the U.S. Geological Survey and the U.S. Fish and Wildlife Service.

LITERATURE CITED

ABLE, K. P. 1991. Common themes and variations in animal orientation systems. American Zoologist 31:157–167.

ABLE, K. P., AND J. R. BELTHOFF. 1998. Rapid 'evolution' of migratory behavior in the introduced House Finch of eastern North America. Proceedings of the Royal Society of London Series B 265: 2063–2071.

CARLISLE, J. D., G. S. KALTENECKER, AND D. L. SWANSON. 2005. Stopover ecology of autumn landbird migrants in the Boise Foothills of southwestern Idaho. Condor 107:244–258.

COCHRAN, W. W., AND M. WIKELSKI. In press. Individual migratory tactics of New World Catharus thrushes: current knowledge and future tracking options for space. *In* P. Marra and R. Greenberg [EDS.], Birds of two worlds. Princeton University Press, Princeton, NJ.

DEPPE, J. L., AND J. T. ROTENBERRY. 2005. Temporal patterns in fall migrant communities in Yucatan, Mexico. Condor 107:228–243.

DIEHL, R. H., R. P. LARKIN, AND J. E. BLACK. 2003. Radar observation of bird migration over the Great Lakes. Auk 120:278–290.

GAUTHREAUX, S. A., JR., AND C. G. BELSER. 2003. Radar ornithology and biological conservation. Auk 120:266–277.

GUGLIELMO, C. G., P. D. O'HARA, AND T. D. WILLIAMS. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western Sandpipers (*Calidris mauri*). Auk 119:437–445.

HILDEN, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53–75.

HOBSON, K. A., AND L. I. WASSENAAR. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia 109:142–148.

HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory landbirds, p. 455–476. *In* M. L. Cody [ED.], Habitat selection in birds. Academic Press, Inc., Orlando, FL.

HUTTO, R. L. 2000. On the importance of *en route* periods to the conservation of migratory landbirds. Studies in Avian Biology 20:109–114.

KELLY, J. F., AND R. L. HUTTO. 2005. An East-West comparison of migration in North American wood warblers. Condor 107:197–211.

LOVETTE, I. J., S. M. CLEGG, AND T. B. SMITH. 2004. Limited utility of mtDNA markers for determining connectivity among breeding and overwintering locations in three neotropical migrant birds. Conservation Biology 18:156–166.

MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282: 1884–1886.

MCWILLIAMS, S. R., AND W. H. KARASOV. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. Comparative Biochemistry and Physiology 128:577–591.

MOORE, F. R. [ED.]. 2000. Stopover Ecology of Nearctic-Neotropical landbird migrants: habitat relations and conservation implications. Studies in Avian Biology 20.

MOORE, F. R., AND D. A. ABORN. 2000. Mechanisms of *en route* habitat selection: how do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

MOORE, F. R., S. A. GAUTHREAUX JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: important link in conservation, p. 121–144. *In* T. Martin and D. M. Finch [EDS.], Ecology and management of Neotropical migratory birds. Oxford University Press, New York.

PETERJOHN, B. G., AND J. R. SAUER. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, p. 27–44. *In* P. D. Vickery and J. R. Herkert, [EDS.], Ecology and conservation of grassland birds of the western hemisphere. Studies in Avian Biology 19:27–44.

PETIT, D. R. 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. Studies in Avian Biology 20:109–114.

PIERCE, B. J., AND S. R. MCWILLIAMS. 2005. Seasonal changes in composition of lipid stores in migratory birds: causes and consequences. Condor 107: 269–279.

PIERSMA, T., AND J. JUKEMA. 1990. Budgeting the flight of a long-distance migrant: changes in the nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. Ardea 78:315–337.

RODEWALD, P. G., AND S. N. MATTHEWS. 2005. Landbird use of riparian and upland forest stopover habitats in an urban landscape. Condor 107:259–268.

SAUER, J. R., G. W. PENDLETON, AND B. G. PETERJOHN. 1996. Evaluating causes of population change in North American insectivorous songbirds. Conservation Biology 10:465–478.

SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71: 296–308.

SILLETT, T. S., R. T. HOLMES, AND T. W. SHERRY. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288: 2040–2042.

SKAGEN, S. K., J. F. KELLY, C. VAN RIPER III, R. L. HUTTO, D. M. FINCH, D. J. KRUEPER, AND C. P. MELCHER. 2005. Geography of spring landbird migration through riparian habitats in southwestern North America. Condor 107:212–227.

SKAGEN, S. K., C. P. MELCHER, AND R. HAZLEWOOD. 2004. Migration stopover ecology of western avian populations: a southwestern migration workshop. U.S. Geological Survey Open-File Report No. 2004–1452.

WEBSTER, M. S., P. P. MARRA, S. M. HAIG, S. BENSCH, AND R. T. HOLMES. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

WILLIAMS, T. D., C. G. GUGLIELMO, O. EGELER, AND C. J. MARTYNIUK. 1999. Plasma lipid metabolites provide information on mass change over several days in captive Western Sandpipers. Auk 116: 994–1000.

YONG, W., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. Auk 115:829–842.