

ON THE IMPORTANCE OF *EN ROUTE* PERIODS TO THE CONSERVATION OF MIGRATORY LANDBIRDS

RICHARD L. HUTTO

Abstract. In the annual cycle of a migratory landbird, *en route* periods provide unique challenges and selective pressures. The importance of these periods is not yet reflected in the amount of attention this period gets from either research biologists or conservation organizations. Several issues suggest that these annual periods will be important in any program to conserve migratory landbirds: (1) the routes birds take during migration are relatively restricted, implying that some geographic locations may be more critical than others; (2) the habitats migrants use are also relatively restricted and differ between migratory periods, implying that managers will need to know such details to successfully manage for any one species; (3) the migratory periods probably act to limit populations at times, and may be the critical period contributing to long-term declines in some species; and (4) these periods are the source of stories that capture the imagination of humans, implying that basic research during these periods may contribute substantially toward the development of a conservation ethic.

Key Words: conservation, *en route* ecology, habitat selection, neotropical migrants, population regulation, stopover ecology.

In terms of current efforts toward the conservation of migratory landbirds, I propose that the *en route* periods are worthy of considerably more attention than they currently get from research biologists and conservationists. My reasoning involves a discussion of four topics: (1) patterns of geographic distribution of birds while *en route*, (2) patterns of habitat use while *en route*, (3) a possible relationship between changing conditions at stopover sites and population trends, and (4) the way the public at large is captivated by questions and answers associated with *en route* ecology.

GEOGRAPHIC DISTRIBUTION OF *EN ROUTE* MIGRANTS

Geographically speaking, stopover opportunities would appear to be less restricted for landbirds, which can refuel above or within a wide variety of vegetation types, than for other species such as shorebirds, which tend to concentrate in relatively small areas for brief periods of time while *en route* (Myers et al. 1987). Even European migrants that cross the Sahara Desert appear to migrate in broad fronts across the entire expanse of desert rather than within narrowly restricted travel routes (Biebach 1990).

Nonetheless, even though most migratory landbird species can be found over broad fronts during passage, they are not equally abundant in all locations. Moreover, areas of concentrated movement may change from spring to fall, as evidenced by (1) site-specific capture or detection rates, which differ more between migratory seasons than expected due to annual recruitment of young or due to annual mortality (Lavee and Safriel 1989; Winker et al. 1992b,c; Rappole and Ramos 1994, Finch and Yong *this volume*); and by (2) the innovative use of data from museum

specimen records, which reveal, for example, that several western hummingbird species migrate up the Pacific coast and back down the Rocky Mountain chain (Phillips 1975; Fig. 1), or that male Hammond's Flycatchers (*Empidonax hammondi*) come up the Pacific coast and females take a more direct inland route later (Johnson 1965). In other words, just because a bird species has been sighted most everywhere at some time or another during migration and, therefore, occurs on spring and fall check-lists across the United States, it does not mean all areas are equally important to the species.

PATTERNS OF HABITAT USE WHILE *EN ROUTE*

Within a fairly restricted geographic location, there are demonstrated nonrandom patterns of habitat use for virtually any landbird species that has ever been studied during either spring or fall migration (e.g., Parnell 1969, Bairlein 1983, Hutto 1985a, Moore et al. 1990, Weisbrod et al. 1993, Winker 1995c, Yong and Finch 1997a, Petit *this volume*). Patterns of habitat use also vary significantly among species (Bairlein 1983, Hutto 1985a, Moore et al. 1995); habitats that receive relatively heavy use by one species are not necessarily the same ones that receive relatively heavy use by other species (Fig. 2). Moreover, because patterns of habitat use while *en route* may differ from patterns of habitat use during the nonmigratory breeding or wintering periods for any given species (Faaborg et al. 1996, Parrish *this volume*), we cannot determine its *en route* needs on the basis of habitat use patterns during one or the other nonmigratory period. As an extreme example, most western species that breed in association with high-elevation and high-latitude conifer forest habitats

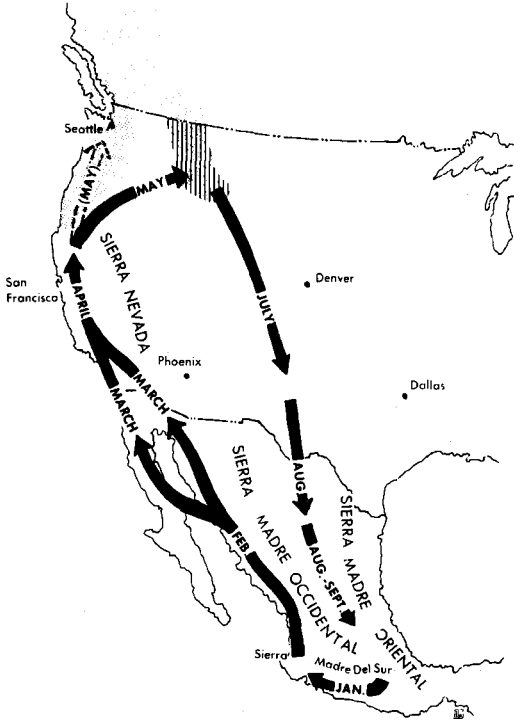


FIGURE 1. The migratory route of the Rufous Hummingbird is not only relatively restricted during a given migratory period, but differs between seasons as well. This pattern was uncovered by plotting the locations of museum specimens that were collected during a given month. Figure taken from Phillips (1975).

can be found in good numbers in the Sonoran Desert in spring (pers. observation). Indeed, it is an amazing spectacle to see species like Townsend's (*Dendroica townsendi*) and Hermit (*Dendroica occidentalis*) warblers, which nest high in mature conifer trees, foraging a meter off the ground in creosote bushes in spring!

In addition to nonrandom use of available habitat types, there is also evidence that some species use only those patches that exceed some minimum size, as Cox (1988) has shown with patterns in the springtime use of maritime hammocks in Florida by Black-and-white Warbler (*Mniotilta varia*), Ovenbird (*Seiurus aurocapillus*), Northern Parula (*Parula americana*), and Summer Tanager (*Piranga rubra*), and as Martin (1980, 1981) has shown for shelterbelts of different sizes in South Dakota. There is also evidence that the particular configuration of habitats in the broader landscape may influence the probability that a given patch is used (Simons et al. *this volume*).

En route patterns are generally consistent from year to year (Fig. 3; see also Bairlein

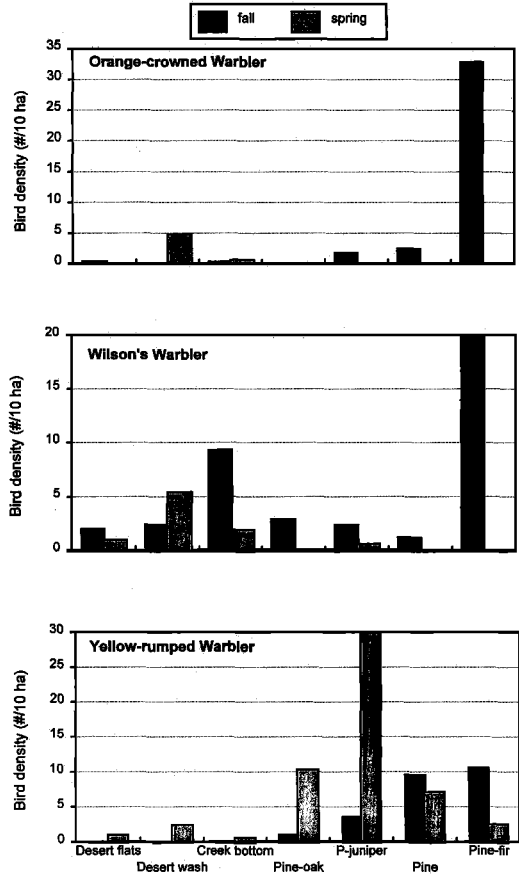


FIGURE 2. Several examples of patterns of habitat use in the Chiricahua Mountains of southern Arizona during both the spring and fall migratory periods. Note that the patterns differ among species, and the patterns differ between seasons for any one species. Data taken from Hutto (1985a).

1992a, Winker et al. 1992a), although the pattern during spring passage may differ significantly from the pattern during fall passage (Fig. 2; see also Balda et al. 1975, Winker et al. 1992c, Weisbrod et al. 1993). For a given location, patterns of habitat use may even change with time of day (Moore et al. 1990). We need more information about the patterns of habitat use by migrants during migration. In short, "... we do not know what types of habitat 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 1992a).

That there are nonrandom patterns of habitat use, and that the patterns are consistent from year to year indicate that habitats are differentially useful, and that the birds are not simply

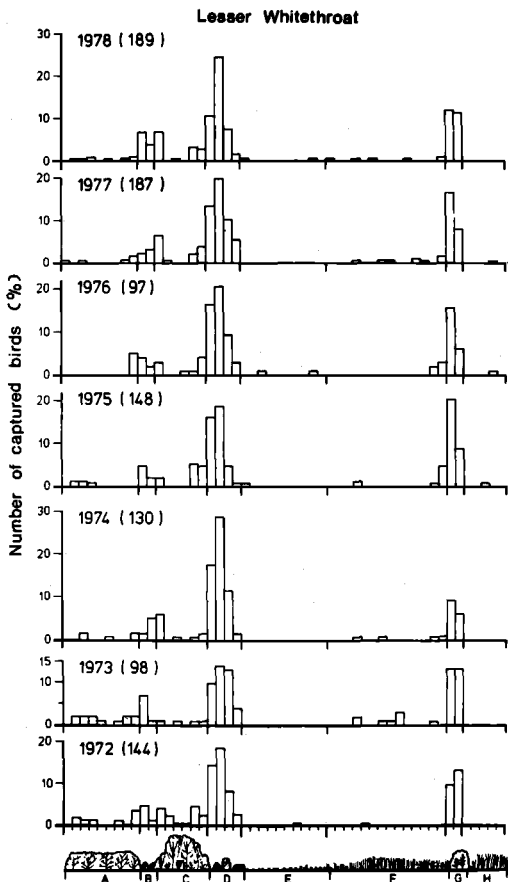


FIGURE 3. Note the remarkable similarity in pattern of habitat use for the Lesser Whitethroat from one year to the next. Letters at the bottom of the figure refer to distinct habitats, as defined by Bairlein (1983).

using whatever they encounter along a known route. So why do we see nonrandom patterns in habitat use? Several lines of evidence suggest that the relative value of an *en route* habitat is most closely related to the rate at which food can be acquired. Migratory landbirds nearly always gain mass at stopover sites (Winker et al. 1992b, Moore and Kerlinger 1987, Moore et al. 1993, Moore et al. 1995, Winker 1995a, Morris et al. 1996). Migrants are also known to reorient toward areas of greater food availability after landing in food-poor sites (Lindström and Alerstam 1986, Wiedner et al. 1992), and are known to orient differently depending on energetic condition (Sandberg and Moore 1996). Shifts in patterns of habitat use from one migratory period to the other are also apparently in response to shifts in relative availability of food both between (Balda et al. 1975; Hutto 1985a,b), and within (Laursen 1978; Bairlein 1983, 1992a)

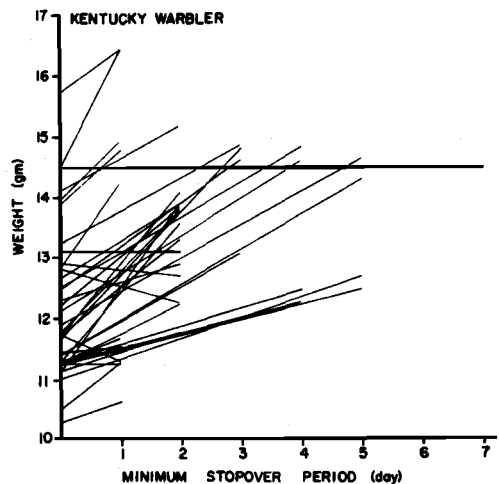


FIGURE 4. Changes in body mass from initial capture to final capture for many individual Kentucky Warblers illustrates the general phenomenon that birds tend to gain mass before departing from a stopover site. Figure taken from Moore and Kerlinger (1987).

seasons. Perhaps the most convincing evidence that the primary value of a stopover site is related to the rate at which a bird can gain mass is that fat birds do not remain in a site as long as lean birds (Dolnik and Blyumental 1967, Yong and Moore 1997), and that most birds leave only after gaining mass, as illustrated by Moore and Kerlinger's (1987) data on Kentucky Warblers (*Oporornis formosus*) that stopover in southwest Louisiana after their trans-Gulf flight in spring (Fig. 4). In addition, Carpenter et al. (1983) have shown that Rufous Hummingbirds (*Selasphorus rufus*) adjust territory size on a daily basis in a way that maximizes the rate of weight gain per day, and Russell et al. (1994) provide evidence that survival of those hummingbirds is related to habitat (food) quality. When results from these studies are taken together, there is ample evidence to suggest that food acquisition rate is of primary importance in explaining nonrandom patterns in habitat use during migration (Alerstam and Lindström 1990), although there may be predation or other constraints that make the suitability of habitats somewhat different from that which would be predicted on the basis of food availability alone (Lindström 1989, 1990b).

Even though food acquisition may contribute disproportionately to the suitability of a site, ranking the suitability of habitats or sites (as may be desired to help set conservation priorities) is probably not as easy as measuring and comparing average fat loads, feeding rates, or stopover durations among sites because (1) fat

birds may use different habitats from lean birds (Biebach et al. 1986); (2) feeding rate depends on current body condition (Rappole and Warner 1976, Yong and Moore 1993, Moore 1994), age (Woodrey *this volume*), and competitive milieu (Moore and Yong 1991); and (3) duration of stay is related to fat level (Cherry 1982, Biebach 1985, Moore and Kerlinger 1987, Lavee and Safriel 1989, Loria and Moore 1990, Kuenzi et al. 1991), age (Ellegren 1991; Morris et al. 1994, 1996; Woodrey and Moore 1997, Woodrey *this volume*), sex (Morris et al. 1994, Otahal 1995), and possibly even the status of a migrant's biological clock (Safriel and Lavee 1988). Thus, significant differences in the "average" age, sex, body condition, or time since arrival among sites will make a meaningful comparison of average fat loads, feeding rates or stopover durations difficult at best. Ranking the relative suitability of habitats or sites using such information will probably necessitate labor intensive capturing, marking, and re-capturing of birds so that confounding variables such as age, sex, body condition, and time since arrival can be factored out before comparing fat loads, feeding rates, or stopover durations among sites.

Even though we are learning what to measure in order to rank habitats according to their suitability, we must also be careful not to get too carried away with thinking we can accurately rank suitabilities of habitats or specific locations for at least two other reasons: (1) different "strategies" of weight gain and load may exist for different-sized birds (Yong and Moore 1994) or for birds of different populations that migrate as little as 150 miles apart (Karlsson et al. 1988); and (2) both intrinsic and extrinsic factors (*sensu* Hutto 1985b) unrelated to food acquisition may contribute to a location's suitability as a stopover site, including low predation rates or its geographic position relative to a migratory route that is restricted for physiographic or climatic reasons. Thus, in terms of food acquisition, a habitat or specific location might rank low in comparison with all others for which there are data, but it may still be the best thing going in certain geographic locations.

THE IMPORTANCE OF MIGRATORY PERIODS TO POPULATION REGULATION

A key question critical to conservation efforts is: How likely is it that the migratory period contributes to long-term population trends? Even without relevant data, most authors of research proposals and other material involving *en route* ecology generally claim that these periods are critical. Are they? Don't migrants seem to use whatever they come across, occur most everywhere, and do well with whatever exists? Or,

to echo the sentiments expressed by most participants in the first Smithsonian conference on northern migrants in the tropics (Buechner and Buechner 1970): Aren't migrants flexible enough to withstand any change we throw at them?

How do we assess the importance of any season in terms of its contribution to long-term population trends? Over a short period of time, it seems clear that year-to-year trends are controlled by events in different seasons in different years (a summer insect outbreak in one year, a bad winter in another, a springtime storm in another), and that all seasons are important in that sense (Sherry and Holmes 1993). But what about long-term trends? We need to recognize that long-term trends are a separate issue from short-term, year-to-year population fluctuations. While short-term trends are equally likely to be consequences of events in summer, winter, spring, or fall, depending on the year, longer-term population trends can, at the same time, be controlled by events in a single season.

We could evaluate the importance of migratory periods on theoretical grounds, and Sherry and Holmes (1992, 1993, 1995) provide recent reviews of this approach, which generally supports the idea that migratory periods are indeed important. Using a more empirical approach, Svensson (1978) showed that spring numbers predict breeding numbers later on, and suggested that the spring migratory period can be an important contributor to population trends. The problem with the latter approach, however, is if a population is undergoing a long-term change, numbers in *any* season will be correlated with numbers at some later point in time. Ideally, we need population data from just before and just after the season of interest to see if the direction and magnitude of change affects the number seen at some subsequent point in time, year after year (Owen and Black 1991). Unfortunately, it will be difficult to amass such data for at least two reasons. First, it is difficult to define and follow a single population unit year round. For example, it would not be easy to make sense of data from a well defined Montana breeding group that then splits into winter populations scattered from California through Oaxaca. Second, the time period needed for such study is generally beyond the scope of most individual research programs.

A more feasible alternative is to *project* inevitable trends by coupling results from intensive short-term studies of habitat associations with estimates of land-use changes and the anticipated distribution and abundance of habitats into the future. Even here, population projections will be difficult because (1) a habitat that

is not used in one place may be important in another, so the "value" of a habitat may vary from place to place, and will require the development of regional models of habitat use; and (2) human-altered habitats have greater potential than naturally occurring habitats to act as ecological traps (*sensu* Gates and Gysel 1978) because human habitat alteration often uncouples normally co-occurring habitat elements such that proximately and ultimately important factors are no longer linked. Thus, a bird can end up being attracted to a site with appropriate proximate cues but inappropriate ultimately important conditions. This, in turn, means that abundance data alone may not reflect the relative suitabilities of habitats created through a mixture of both natural and unnatural processes. We need data on feeding rates and other characteristics of marked birds, as described earlier, but the collection of such data is labor intensive relative to the collection of data on occurrence among habitats.

So, several lines of evidence suggest that migratory periods are important to the conservation of migrants, but exactly how the management of lands used by migrants *en route* will affect population trends is going to be hard to determine.

STORY-TELLING POWER ASSOCIATED WITH EN ROUTE PERIOD

One last consideration suggests that no matter what role migratory periods play in terms of the regulation of migratory bird populations, stop-over biology and the *en route* periods will still be a key to the conservation of migrants. That consideration involves the story-telling power of this part of the annual cycle of birds, which is immeasurable. For example,

- Why should birds that cross the Sahara stop while *en route*? Because headwinds develop at night, most passerines would not meet the energetic costs of flying both day and night if they stayed at the typical daytime flight altitude of 3000 m. They could fly at a lower altitude during the night, where head winds are less likely; however, they would then move into a warmer zone where the air temperature would cause water loss to become a problem. Thus, the only option is to stop at night (Biebach 1990, Leberg et al. 1996)!

- The same hummingbird that was banded by Elly Jones near Swan Lake, Montana, was caught 10 days later and about 1000 miles south at the Rocky Mountain Biological Laboratory in Colorado by William Calder, the biologist who taught Elly Jones to band hummingbirds!

- While *en route*, many landbird species travel in pairs (Greenberg and Gradwohl 1980) or small groups (Moore 1990b), and may even cop-

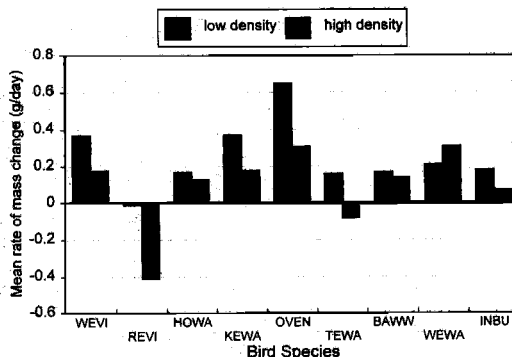


FIGURE 5. The rate of mass gain for a variety of species is inversely related to the density of other migrants in the area, implying that interspecific competition may be important selective pressure during the migratory period. Bird species include White-eyed Vireo (WEVI), Red-eyed Vireo (REVI), Hooded Warbler (HOWA), Kentucky Warbler (KEWA), Ovenbird (OVEN), Tennessee Warbler (TEWA), Black-and-white Warbler (BAWW), Worm-eating Warbler (WEWA), and Indigo Bunting (INBU). Data taken from Moore and Yong (1991).

ulate (Quay 1989, Moore and McDonald 1993) long before they arrive on the "breeding" grounds!

- Recent work suggests that some landbird species may stay for long periods at some "stop-over" sites to molt, before continuing farther south to "winter" (Hedenström et al. 1993).

- Studies of small migratory birds while *en route* provide some remarkably clear demonstrations of resource depletion and competition in bird communities. For example, Pied Flycatchers deplete resources, as evidenced by declining capture rates with time in same area and by increasing feeding rates with time since last visit to a given tree (Bibby and Green 1980). That there may be interspecific effects from such food depletion is also suggested because feeding rates are greater on days when relatively few competitors are present (Fig. 5; Moore and Yong 1991), and diets overlap less when there are more potential competitors present (Laursen 1978).

I hope these examples serve to illustrate that fascinating stories emerge from studies of basic biology of landbirds during migration. My point is that both research biologists and conservation-oriented funding agencies may be putting too much emphasis on conducting or funding conservation projects that involve "high priority" species, and too little attention on other measures of research attractiveness. Our efforts to determine priorities for research that will help conserve migrants will be misdirected if we fail

to consider the story-telling power of proposed research, whether the nature of the work relates directly to saving a high priority species or not! Conservation success is not measured by whether we use limited resources in the right way to save one species; rather, success is measured by how much of the natural world (how many species in total) we can retain. And that is going to be directly related to people's collective attitude about conservation, which may itself be affected less by whether we save a priority species than by whether people have developed a connection between themselves and nature (see also Mabey and Watts *this volume*). That connection to na-

ture, in turn, comes from story telling. Thus, maybe the spending priority of conservation organizations should shift toward support of solid biological research by people who have an eye toward what makes an interesting study, period. Those efforts are most likely to enhance our understanding of the biology of organisms, produce good stories, and change people's attitudes about conservation. Because of the fascinating questions that become apparent to anyone who has read about stopover biology, that area of research should play an integral part in any conservation program that considers an accepting public to be an essential ingredient to success.