

AGE-DEPENDENT ASPECTS OF STOPOVER BIOLOGY OF PASSERINE MIGRANTS

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Abstract. Most studies of the behavior and ecology of birds address questions at the species level without assessing the effects of factors such as age, sex, or age-sex classes, although variation observed within species can be at least partly attributed to these factors. My objective is to synthesize known information concerning aspects of age-dependent *en route* ecology and behavior, emphasizing long-distance, intercontinental passerine migrants. Adults and yearlings show differences in the amount of fat stores carried during migration, in food acquisition rates in some species, and in the effect of differential social dominance on foraging sites used during migration. Foraging sites influence predation risk incurred by individuals, and young birds typically vary more in their ability to orient during migration than experienced birds. Results presented here emphasize the need to consider intra-specific, age-dependent effects on the behavior and ecology of migratory birds.

Key Words: age-dependent, competition, energetics, foraging, migrants, migration, orientation, passerine, predation, social dominance, stopover.

Migration is an ecological strategy evolved in response to temporal and spatial environmental heterogeneity that allows organisms to exploit seasonal resources (Baker 1978, Dingle 1980). For example, nearctic-neotropical (Hayes 1995) migratory landbirds leave their breeding sites in temperate regions before their food resources become scarce, travel thousands of kilometers in uncertain weather over ecological barriers, stop periodically to (re)build fat deposits, and finally arrive in tropical wintering habitats different from those in the temperate zone. After residing for five or six months in tropical communities, they return north again to their temperate breeding areas.

Despite renewed interest in the biology and conservation of long-distance passerine migrants (see Keast and Morton 1980, Hagan and Johnston 1992, Crick and Jones 1992, Finch and Stangel 1993, Martin and Finch 1995, and references therein), relatively few aspects of the stopover biology of passerine birds have been examined. Topics such as migrants and their relation to stopover habitats (Bairlein 1992a, Winker et al. 1992a), effects of habitat suitability on migrant stopover biology (Moore and Simons 1992a, Winker et al. 1992a), species-specific migration strategies (Bairlein 1992b), genetic control of migration (Berthold and Helbig 1992), energetic condition and its consequences (Biebach et al. 1986, Biebach 1992, Woodrey and Moore 1997), and conservation and management of migratory birds (Wood 1992, Moore and Woodrey 1993; Moore et al. 1993, 1995) have been investigated. Unfortunately, few studies have addressed age-specific aspects of migrant ecology and the possible consequences for a successful migration.

RATIONALE FOR FOCUS ON AGE-DEPENDENT STOPOVER BIOLOGY

The rationale for a focus on age-dependent stopover biology is two-fold. First, a migrant's fitness is enhanced by surviving in the best possible condition to maximize the probability of a successful migration. A successful migration is dependent upon how effectively the bird offsets the costs of migration (i.e., satisfies energy demand and meets *en route* contingencies; Alerstam and Lindström 1990). Regardless of whether benefits of migration accrue through increased productivity, increased probability of surviving an unfavorable season, or both, they must be balanced against increased mortality experienced during migration (e.g., Fretwell 1980, Alerstam and Högstedt 1982). The mortality associated with intercontinental migration, though difficult to estimate, is probably substantial (Lack 1946, Moreau 1972, Ketterson and Nolan 1982), and because this cost (reduced fitness, increased mortality) is absorbed largely by the hatching-year age-class (Nisbet and Medway 1972, Johnson 1973, Alerstam 1978, Greenberg 1980, Goss-Custard and Dit Durell 1983; Ketterson and Nolan 1982, 1983, 1985; DeSante 1983, Ramos 1988), differential costs should be reflected by age-dependent differences in stopover ecology.

Second, individuals with different levels of migratory experience can be expected to respond differently to the exigencies of migration (Ketterson and Nolan 1985, 1988; Terrill 1988). In addition to the energetic costs of transport (see Pennycuik 1975), migrants must (a) deal with unfamiliar habitats, which often differ in suitability (Bibby et al. 1976, Mehlum 1983, Moore and Simons 1992a), (b) resolve the conflicting demands of predator avoidance, food ac-

quisition, and timely arrival on the breeding and wintering grounds (Metcalf and Furness 1984, Lindström 1989, Moore et al. 1990, Moore 1994), (c) compete with other migrants and resident birds for limiting resources (Rappole and Warner 1976, Alerstam 1978, Bibby and Green 1980, Lindström and Alerstam 1986, Hansson and Pettersson 1989, Moore and Yong 1991), (d) respond to adverse weather conditions (e.g., Richardson 1978, 1990), and (e) correct for orientation errors (Ralph 1978; Moore 1984, 1990a; Alerstam 1990). Moreover, favorable *en route* habitat, where energy stores can be rapidly accumulated, is probably limited for migrants (Martin 1985, Martin and Karr 1986), or effectively so because migrants do not have the luxury of searching for the "best" stopover site (see Hutto 1985a, Moore et al. 1993). These problems are presumably magnified for hatching-year birds on their first migration due to their lack of experience (Ralph 1978, Alerstam 1978, Goss-Custard and Dit Durell 1983, Gauthreaux 1982a, DeSante 1983, Moore 1984, Lindström and Alerstam 1986, Terrill 1987) and socially subordinate status (Gauthreaux 1978, Terrill 1987, Marchetti and Price 1989, Sherry and Holmes 1989, Woodrey 1995).

My purpose is, first, to synthesize and evaluate current knowledge about age-dependent aspects of migration, and, second, to identify areas of stopover biology where age-dependent information is lacking. The focus of this review is primarily on passerine migrants because of the growing interest in this group of birds in North America and Europe (see Keast and Morton 1980, Hagan and Johnston 1992, Crick and Jones 1992, Finch and Stangel 1993, Martin and Finch 1995, and references therein). This assessment of age-dependent stopover biology begins by addressing differences in the timing of migration between age classes, then discusses *en route* challenges facing migratory birds, including energetics, food acquisition, competition and social dominance, predation, and orientation. I conclude with a summary of the significance of age-dependent research and provide direction for future research.

AGE-DEPENDENT DIFFERENCES IN TIMING AND LOCATION OF MIGRATION

Although differential timing of migration by age has been documented, the proximate causes for differences have not been thoroughly investigated and interpreted. Early studies showed that in many cases hatching-year (HY: yearling) individuals were the first to leave their natal territories because after-hatching-year (AHY: adult) individuals were delayed until they completed their prebasic molt (reviewed by Gauthreaux 1982b).

Numerous studies indicate that during fall migration adult passerines precede immatures (Hussell et al. 1967, Ely 1970, Leberman and Clench 1973, Johnson 1974, Seel 1977; Hussell 1980, 1981, 1982, 1991; Woodrey and Chandler 1997), while others indicate that immatures precede adults (Magee 1924, cited in Gauthreaux 1982a; Leberman and Clench 1973, Woodrey and Chandler 1997), while yet others found no age difference in timing (Murray 1966, Woodrey and Chandler 1997). Thus, no consistent pattern emerges within or between groups of species in age-specific timing of migration. Note however, that the lack of temporal overlap is important when discussing the role of intraspecific competition on the behavior of migrants during stopover (see COMPETITION AND SOCIAL DOMINANCE below).

Age-classes of passerines often migrate along different routes, with juveniles concentrated along coastal areas. During fall migration, young birds comprise 85–95% of the birds captured along the Atlantic coast (Drury and Keith 1962, Murray 1966, Ralph 1981, Morris et al. 1996) and Pacific coast (Ralph 1971, Stewart et al. 1974). In contrast, only 65–70% of the birds captured at inland sites are young birds (Stewart et al. 1974, Ralph 1981). This "coastal effect" might be the result of different migratory routes followed by young and adults (Leberman and Clench 1975), or the high percentages of young could denote the periphery of a species' migration route (Ralph 1981). Four of six species studied by Woodrey and Moore (1997) along the northern coast of the Gulf of Mexico showed more balanced age-ratios (69.7% young birds). Species studied by Ralph (1981) follow more restricted routes and generally move parallel to the coast line, whereas birds migrating through the central portion of the United States display a more broad-front migration (i.e., less geographically restricted) than coastal migrants. Furthermore, birds moving south in the fall are traveling perpendicular to the east-west orientation of the northern Gulf coastline. Thus, more adult and juvenile birds encounter the Gulf coast, resulting in more balanced age-ratios.

EN ROUTE CHALLENGES

The variety of problems or contingencies faced by migratory landbirds during the *en route* period of their annual cycle may be classified, somewhat arbitrarily, into five topics: (a) the energetic cost of transport, (b) food acquisition, (c) competition and social dominance, (d) predator avoidance, and (e) orientation.

ENERGETIC COST OF TRANSPORT

Before initiating their journey, migratory birds add an average of 30–50% of lean body

mass in fat stores (Blem 1980). During migration, free-ranging birds are capable of replenishing depleted fat stores at rates approaching 10% of body mass/day (Dolnik and Blyumental 1967, Bairlein 1985a, Biebach et al. 1986, Moore and Kerlinger 1987). Fat stores become important when migrants face the heightened energy demand of making long-distance, non-stop flights over ecological barriers such as a large body of water or a desert (Biebach et al. 1986, Moore and Kerlinger 1991).

Visible subcutaneous fat stores are often used as a surrogate measure of fitness in migrating birds because it is difficult, if not impossible, to measure the direct effects of *en route* events on survival or reproductive success. Despite changes in mass due to changes in the flight musculature (Marsh 1984, Lindström and Piersma 1993), I assume here that fat accounts for essentially all mass differences during stopover (Odum et al. 1961, 1964; Rogers and Odum 1966, Child 1969). In addition, the interest here is comparisons of arrival masses between age classes within species, and I assume that any other components contributing to differences in mass is the same across age classes.

Of the 26 cases (21 species) for which age-specific stopover data are available, adults were significantly heavier than young for 13 cases (11 species; Table 1). Inexperience and subordinate social status are implicated as potential causes of greater arrival mass of adult American Redstarts (see Table 1 for scientific names), Swainson's Thrushes, and White-eyed Vireos (Woodrey and Moore 1997), and Bluethroats (Ellegren 1991). These factors also likely influence age-dependent body mass differences in Blackpoll and Yellow-rumped warblers (Murray 1979), Pied Flycatchers (Viega 1986), Sedge Warblers (Spina and Bezzi 1990, Basciutti et al. 1997), Traill's Flycatchers, Red-eyed Vireos, Tennessee Warblers, American Redstarts, and Northern Waterthrushes (Morris et al. 1996).

Yearling migrants are likely at a competitive disadvantage, as mentioned previously, because of their inexperience and socially subordinate status relative to adults. Younger, less experienced birds are typically less efficient at procuring resources (Burger 1988, Wunderle 1991), and are usually subordinate to adults during the nonbreeding season (Terrill 1987, Sherry and Holmes 1989). Social status could handicap yearling migrants if their subordinate status affects access to resources and the subsequent opportunity to deposit necessary fat reserves (cf. Ekman and Askenmo 1984, Piper and Wiley 1990).

Age-dependent differences in body mass likely have profound consequences for migrant pop-

ulations. Although the effects of fat stores on survival and reproduction are difficult to measure directly, we can speculate as to their effects. For instance, Woodrey and Moore (1997) calculated flight range estimates by age-class for each of the six species they studied. In a species where adults were significantly heavier than young birds upon arrival along the northern coast of the Gulf of Mexico, adult American Redstarts with an average mass of 9.4 g can fly 1,400 km, whereas an average immature bird has a 950 km flight range (average mass = 8.4 g). Approximately 47% of immature American Redstarts have inadequate stores to complete a successful trans-Gulf crossing, which could result in death due to starvation during the 1,200 km non-stop flight over the Gulf of Mexico.

In addition to starvation, there may be more subtle and less dramatic consequences of age-specific fat deposits. Young migrants in a fat depleted state have a smaller margin of safety to buffer the effect of adverse weather on the availability of insect prey during stopover (*sensu* Moore and Kerlinger 1991). Also, the need of young birds to satisfy energetic demands of migration through increased foraging (equals increased activity) may expose them to increased predation relative to adults (Metcalf and Furness 1984, Moore 1994, Woodrey 1995). Further, because of increased duration of stopover, as required to replenish depleted stores, the migration of young birds may be slowed, which may jeopardize opportunities to secure suitable winter territories (Stutchbury 1994).

Differing flight morphologies are known to affect the aerodynamics of migratory flight. Long-distance migrants typically have wings with a high aspect ratio and low loading, which reduces drag and the energetic cost of powered flight (Pennycuik 1975; Rayner 1988, 1990). Differences in wing lengths of adult and juvenile birds within a species have been noted for a variety of species. Almost without exception, young passerine birds have shorter wings than adult birds (Alatalo et al. 1984). Thus, given the same mass and wing shape, young birds have a shorter flight range compared to adults because of the greater mechanical efficiency of flight and lower cost of transport in longer-winged birds (Rayner 1990). Shorter wings, in combination with lower fat stores for migration, further decrease the probability of a successful migration for young migratory passerines.

Unlike species discussed previously, yearling Gray Catbirds, Magnolia Warblers (Woodrey and Moore 1997), and Chaffinches (Å. Lindström, unpubl. data) were significantly heavier than adults upon arrival at a particular stopover site (Table 1). This unexpected result for Gray

TABLE 1. SUMMARY OF SELECTED RESULTS FROM STUDIES OF AGE-SPECIFIC STOPOVER BIOLOGY OF LONG-DISTANCE PASSERINE LANDBIRDS

Species	Fat stores	Body mass	Length of stopover	Mass change ^a	Reference
Eastern Wood-Pewee <i>Contopus virens</i>	NS ^b	NS	(?) ^c	NS	Morris et al. 1996
Trail's Flycatcher <i>Empidonax traillii</i>	NS	AHY>HY ^d	(?)	NS	Morris et al. 1996
Yellow-bellied Flycatcher <i>E. flaviventris</i>	NS	NS	(?)	NS	Morris et al. 1996
Bluethroat <i>Luscinia svecica</i>	AHY>HY	(?)	HY>AHY	NS	Ellegren 1991
Veery <i>Catharus fuscescens</i>	NS	NS	NS	NS	Morris et al. 1996
Swainson's Thrush <i>Catharus ustulatus</i>	NS	NS	(?)	NS	Morris et al. 1996
Sedge Warbler <i>Acrocephalus schoenobaenus</i>	AHY>HY	AHY>HY	(?)	(?)	Spina and Bezzi 1990
Pied Flycatcher <i>Ficedula hypoleuca</i>	(?)	AHY>HY	HY>AHY	NS	Veiga 1986
Gray Catbird <i>Dumetella carolinensis</i>	NS	HY>AHY	NS	NS	Woodrey and Moore 1997
White-eyed Vireo <i>Vireo griseus</i>	AHY>HY	AHY>HY	NS	(?)	Woodrey and Moore 1997
Red-eyed Vireo <i>Vireo olivaceus</i>	NS	AHY>HY	NS	NS	Morris et al. 1996
Tennessee Warbler <i>Vermivora peregrina</i>	NS	NS	(?)	(?)	Woodrey and Moore 1997
Cape May Warbler <i>Dendroica tigrina</i>	AHY>HY	AHY>HY	NS	NS	Morris et al. 1996
Magnolia Warbler <i>Dendroica magnolia</i>	NS	NS	(?)	NS	Morris et al. 1996
Yellow-rumped Warbler <i>Dendroica coronata</i>	NS	HY>AHY	(?)	(?)	Woodrey and Moore 1997
Bay-breasted Warbler <i>Dendroica castanea</i>	(?)	AHY>HY	(?)	(?)	Murray 1979
Blackpoll Warbler <i>Dendroica striata</i>	NS	NS	NS	NS	Morris et al. 1996
Black-and-white Warbler <i>Mniotilta varia</i>	NS	NS	(?)	NS	Morris et al. 1996
American Redstart <i>Setophaga ruticilla</i>	(?)	AHY>HY	(?)	(?)	Murray 1979
Northern Waterthrush <i>Seiurus noveboracensis</i>	NS	NS	(?)	NS	Morris et al. 1996
Wilson's Warbler <i>Wilsonia pusilla</i>	AHY>HY	(?)	HY>AHY	NS	Yong et al. 1998
Chaffinch <i>Fringilla coelebs</i>	AHY>HY	AHY>HY	HY>AHY	NS	Morris et al. 1996
	HY>AHY	HY>AHY	(?)	(?)	Å. Lindström, unpubl. data

^a Based on data from recaptured birds.

^b NS = non-significant difference between adult and yearling birds.

^c (?) indicates that data were insufficient to draw biological or statistical conclusions, results were not reported, age comparisons not made, or variable not measured as part of study.

^d AHY = after-hatching-year bird (adult); HY = hatching-year bird (yearling); AHY>HY or HY>AHY = significant difference between adult and young birds.

Catbirds may be related to its migration strategy, which is to migrate around, rather than across, the Gulf of Mexico (Eddins and Rogers 1992). Furthermore, Christmas Bird Count data show that Gray Catbirds winter abundantly from Florida to southern Texas (Root 1988). This tendency for many catbird individuals not to cross the Gulf of Mexico may explain why few individ-

uals arrive with sufficient fuel to complete a trans-Gulf crossing (Woodrey and Moore 1997). Nevertheless, age differences in fat stores could be important if catbirds exhibit age-dependent habitat or geographic segregation in winter (e.g., Ketterson and Nolan 1983). Apparently, yearling Magnolia Warblers and Chaffinches compensate in some way for their lack of experience and

their socially subordinate status so as to maintain greater fat stores than adults. At present we do not understand the mechanism for such high yearling fat stores.

FOOD ACQUISITION

Acquisition of adequate food resources to meet the anticipated energy demand of migration is possibly the most important constraint on migratory birds during their annual cycle. Two factors that may influence the foraging behavior of passerine birds are experience and social dominance (Gauthreaux 1978, Burger 1988, Wunderle 1991; see COMPETITION AND SOCIAL DOMINANCE below). Experience can affect how, when, and where a bird might forage. Many studies concerning age-related (i.e., experience) foraging behavior focus on the structure of the foraging bout (e.g., Ziegler 1976, Lovette and Holmes 1995). A change in feeding bout structure, caused by changes in, for example, search time, handling time, inter-food interval, or bout length could lead to a change in the food intake rate for an individual.

When food is plentiful, even a less efficient forager may have few problems finding enough food to deposit sufficient lipid stores. However, any decrease in the foraging efficiency (e.g., foraging rate) could be critical to a juvenile migrant about to cross an ecological barrier because experience and/or social dominance may affect the opportunity to secure adequate resources for fat deposition (Ekman and Askenmo 1984, Lindström et al. 1990). Because yearling migrants are inexperienced and often socially subordinate to adults, they might be expected to satisfy the energy requirements and meet *en route* contingencies less effectively than adults (e.g., HY migrants deposit fat at a slower rate than AHY migrants).

Only four studies provide any empirical evidence relevant to the expectation of slower rates of fat deposition in yearling migrants (Table 1). Fat deposition rates for adult and juvenile Bluethroats migrating through Sweden were almost identical (adults = 0.089 g/d, juveniles = 0.092 g/d; Ellegren 1991). However, adults put on more fat than juveniles in a given stopover period because adults were more likely not to lose mass at the beginning of the stopover period. During stopover, young Bluethroats lost mass initially and then began gaining mass on the third day of the stopover period. Adult Bluethroats tended not to lose mass at any time, and they showed consistently higher rates of mass gain for any particular day (Fig. 1), although this was not statistically significant. Fat deposition data, based on recaptured individuals, showed no significant difference between adult

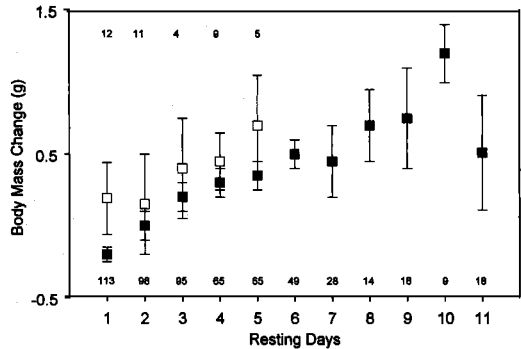


FIGURE 1. Pattern of fat deposition of fall migrating Bluethroats indicated by the average change in body mass as a function of the number of days from banding to recapture. The vertical lines represent ± 1 SE. The open squares are adults, the filled squares immatures. Sample sizes are represented by numbers above (adults) and below (juveniles) (from Ellegren 1991).

and yearling Wilson's Warblers (Yong et al. 1998), American Redstarts and White-eyed Vireos (Woodrey and Moore 1997), Pied Flycatchers (Veiga 1986), nor any of the 14 species studied by Morris et al. (1996; Table 1).

Because few migrants are recaptured during migration (Veiga 1986, Ellegren 1991; Winker et al. 1992a,b; Morris et al. 1996, Woodrey and Moore 1997), Winker et al. (1992b) used linear regression to examine species-specific relationships between body mass and time of day of capture for individuals captured only once. Using this approach to investigate age-specific rates of fat deposition, Woodrey and Moore (1997) found that yearling White-eyed Vireos and American Redstarts showed a significant positive relationship between body mass and time of day whereas adults showed no significant relationship. These contradictory results, in conjunction with the fact that for this analysis no study showed a significant age difference in mass change, suggest that the expectation of greater rates of fat deposition for yearlings may not be valid. Although Woodrey and Moore (1997) found a statistically significant relationship for yearlings, the mass gained per day resulted in little increase in estimated flight ranges for these migrants (White-eyed Vireo = 4.68 km, American Redstart = 7.30 km). The results from these studies are clearly ambiguous with regards to rates of fat deposition for different age classes of migrant passerines.

Few studies have dealt with foraging behavior of passerines during migration and even fewer have looked at age-related differences during stopover. However, Woodrey (1995) compared the foraging behavior of HY and AHY Ameri-

can Redstarts during stopover. Both adult and yearling redstarts frequently moved forward while foraging, though they sometimes made acute turns to the side or to the rear. The angular movements of yearling and adults did not differ significantly, nor did the rate or speed at which they foraged. Young redstarts did show greater variation in the rate and speed at which they foraged.

One possible explanation for the lack of observed differences in the foraging rates and patterns of adult and immature redstarts may be related to experience and learning in juvenile birds. Whenever the foraging ability of adult and full-grown juvenile birds have been compared, the former typically have greater success (Burger 1988, Marchetti and Price 1989, Wunderle 1991). However, it is possible that an age-related disparity in foraging success may disappear by the onset of migration (Sullivan 1988, Weathers and Sullivan 1991). In their discussion of developmental constraints on age-related foraging differences in birds, Marchetti and Price (1989) concluded that young birds appear to be under strong selection to reach adult form and function as rapidly as possible. Thus, any age-related disparity in foraging efficiency of migrant passerines could disappear before they begin their migration.

Another aspect of foraging with respect to age-classes of birds is neophobia (Greenberg 1983, 1984a,b,c, 1990). Neophobia occurs when a bird responds to novel situations with acute stress, which leads to avoidance (Greenberg 1990). If young birds are less likely to approach novel prey items or novel microhabitats, then fewer opportunities will be available for HY foraging repertoires, resulting in reduced ecological plasticity. Neophobia in juvenile birds could play an important role in shaping the use of microhabitat sites and the exploitation of unfamiliar habitats during migration, resulting in young birds being less efficient at satisfying the energetic demands of migration.

COMPETITION AND SOCIAL DOMINANCE

One prerequisite for competition is that potential competitors, for example different age classes, should overlap temporally. As noted previously however, many species exhibit age-specific differential timing of passage (see AGE-DEPENDENT DIFFERENCES IN TIMING AND LOCATION OF MIGRATION above). However, despite age differences in the mean passage times of birds, yearlings and adults often occupy the same stopover site simultaneously (e.g., Woodrey and Chandler 1997, Woodrey and Moore 1997), increasing the potential for competitive interactions among migrants. Com-

petition for food resources may reduce fat deposition rates during stopover, particularly considering the energetic demand of migration (Moore and Yong 1991). In addition, migrants concentrated in unfamiliar habitats where resources are limited must contend with other individuals that have similar dietary requirements. Some evidence, albeit mostly circumstantial, is consistent with the occurrence of food-based competition during migration (reviewed by Moore and Yong 1991): (1) observations of territoriality among migrants, (2) density-dependent settlement during migration, and (3) habitat selectivity in relation to food availability. Moore and Yong (1991) provide direct evidence for competition with a predator-exclosure experiment, which indicates that passerine migrants depress food abundance during stopover, and that migrants replenish fat stores at rates inversely proportional to migrant densities.

What are the possible effects of food-based competition in combination with the differing dominance relationships among age-classes of passerine migrants? Social dominance, which may affect an individual's foraging behavior, frequently confers priority of access to resources (Gauthreaux 1978; see also Piper 1997 for review of social dominance in birds). Individuals may have a different social status depending on characteristics such as sex, age, size, and aggressiveness (Thompson 1960; Brown 1963, 1975; Waite 1987). Many studies of nonbreeding birds have documented differences among age and sex classes in resource use (reviews by Selander 1966, Morse 1980a, Grubb and Woodrey 1990, Wunderle 1991), and the mechanism of interference competition through social dominance is often implicated in differences in resource use. To compensate for their lower social status, subordinate individuals have two choices: use non-preferred resources or adopt other compensatory behaviors. In an observational study of free-ranging American Redstarts during stopover along the northern Gulf coast, Woodrey (1995) found that age-classes of foraging American Redstarts differed significantly in use of trees: HY birds used slash pines (*Pinus elliottii*), adults used sand live oaks (*Quercus geminata*; Woodrey 1995). Hatching-year birds gleaned insects from needle clusters located near the outer portions of the branches, up to a relative height in trees of 3/4, whereas adults typically hawked insects from the middle areas of the lower branches of tall pine trees. These observations led Woodrey (1995) to hypothesize that social dominance is the mechanism responsible for the differential use of microhabitats by adult and juvenile redstarts. In addition, Woodrey (1995) showed that social interactions (intraspecific

chases and supplanting attacks) of American Redstarts during stopover along the northern coast of the Gulf of Mexico were correlated with the density of conspecifics. The interactions were facilitated by species-specific agonistic displays, including wingspread and tail-fanning (Ficken 1962, Ficken and Ficken 1962, Holmes et al. 1989), and individuals vocalized with contact call notes throughout the day. In combination, these observations support the hypothesis that social dominance is the mechanism whereby adult American Redstarts meet the contingencies of migration more effectively than yearlings. Thus, social status does appear to affect a yearling redstarts ability to deposit necessary energy stores (e.g., Ekman and Askenmo 1984, Lindström et al. 1990) and it may expose young individuals to increased predation risk (see Piper 1997:167; see also PREDATOR AVOIDANCE below).

The role of intraspecific interference competition in shaping migration strategies is illustrated by studies of Rufous Hummingbirds (*Selasphorus rufus*; Carpenter et al. 1993a,b). Three recognizable age-sex classes migrating through the Sierra Nevada Mountains of California overlapped temporally and defended feeding territories (Carpenter et al. 1993a). These classes differed in their ability to acquire and defend high quality feeding territories, and these differences affected resource use. For example, immature males defended the highest quality patches, whereas young females defended the poorest (Fig. 2). Thus, one would expect females to be less efficient at satisfying the demands of migration. However, immature female hummingbirds gained body mass at the same rate as immature males and adult females. Moreover, departure body masses for females were not significantly different from male hummingbirds (Carpenter et al. 1993b). Carpenter and her colleagues suggest that females may be energetically compensated by (1) lower costs of flight incurred during foraging and defense, a result of their lower wing disc loading, and (2) greater success at robbing nectar from male's energy-rich territories, likely facilitated by duller plumage coloration and, in the case of adult females, greater experience.

PREDATOR AVOIDANCE

Predation pressure on migrating birds can be intense (Rudebeck 1950, 1951; Walter 1979, Kerlinger 1989, Lindström 1990a, Moore et al. 1990, Aborn 1994). Predation can be particularly severe at stopover sites because (1) migrants may find themselves concentrated in unfamiliar habitats, and (2) the passage and concentration of avian predators has been shown to be corre-

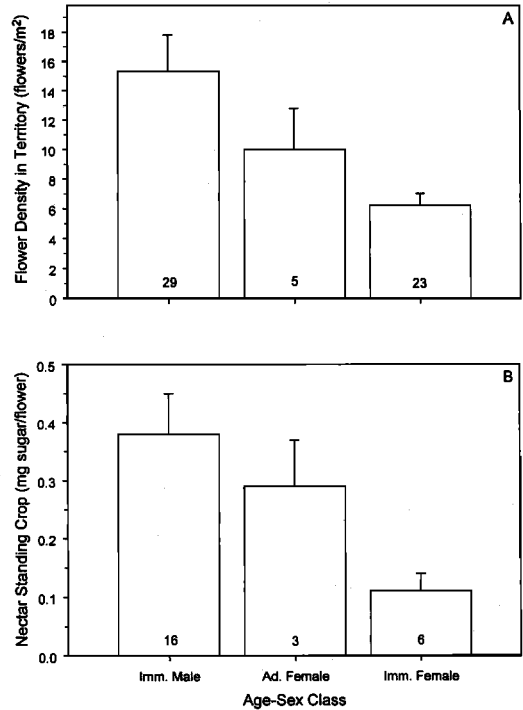


FIGURE 2. Variation in measures of territory quality among different age-sex classes of Rufous Hummingbirds. Means and standard errors are shown, with sample sizes inside the bars. A. Average flower densities in territories pooled across all years (from Carpenter et al. 1993a). B. Nectar standing crop measured on territories in the evening (1930–2030 hrs Pacific Daylight Time) in 1980 (from Carpenter et al. 1993a).

lated with the passage and concentrations of migrants (Kerlinger 1989, Aborn 1994). Predation pressure has been shown to affect the rates of food intake of migratory birds (Metcalf and Furness 1984) and their habitat selection (Lindström 1989). Migratory birds about to embark on a long distance flight must balance the conflicting demands of food acquisition and predator avoidance during stopover (Metcalf and Furness 1984, Moore 1994). Decisions concerning the trade-off between food intake and predation risk depend in part upon both the risk of predation and the cost of lost foraging opportunities (Ydenberg and Dill 1986, cited by Moore 1994). Hatching-year birds face two problems relative to after-hatching-year birds when making this trade-off. First, because HY birds are significantly leaner than adults, the former may have to resume foraging more quickly than adults, thus exposing themselves to increased predation risk (Moore 1994). Second, the subordinate status of HY birds may further expose them to an increased risk of predation because

dominant individuals often force subordinates into riskier foraging sites through interference (Ekman and Askenmo 1984, Koivula et al. 1994, Woodrey 1995; see also Piper 1997:167). Census data of avian predators migrating along Ft. Morgan peninsula in coastal Alabama indicate that bird-eating raptors are found disproportionately in pine-shrub habitats (D. Cimprich and F. Moore, unpubl. data), the same habitat where young, socially subordinate redstarts are found foraging on the outer portions of slash pines (Woodrey 1995). The combination of these observations suggest that young birds are exposed to increased predation risk relative to adults during stopover.

ORIENTATION

Numerous studies have shown that experience affects the orientation behavior of migrant passerines (see Gauthreaux 1982a, Moore 1984, Sandberg et al. 1991, and references therein). The majority of studies show that naive migrants consistently display greater angular deviations in orientation when compared to older, more experienced adult birds (Drury and Keith 1962; DeSante 1973, 1983; Able 1977; Ralph 1978, 1981; McLaren 1981, Moore 1984; Sandberg et al. 1988, 1991). For example, adult Savannah Sparrows (*Passerculus sandwichensis*) showed angular deviations half the magnitude of immatures when placed into orientation cages and their nocturnal orientation direction was observed (Moore 1984; Fig. 3). Increased variation in orientation by immature birds means more errors, which will increase the risk of inadequate fat stores for long, non-stop migratory flights (e.g., Woodrey and Moore 1997). Even if the bird survived the extended flight, it would likely be in an energetically depleted state, jeopardizing its ability to secure a suitable overwinter site.

At a broader geographic scale, immatures of many species of wood-warblers (Parulidae) of eastern North America occur regularly in small numbers on the Pacific coast of California during fall migration (DeSante 1973). The regular occurrence of vagrant warblers along the west coast indicates that misoriented warblers have followed a direction that is a mirror image, across the north-south axis, of the correct direction (DeSante 1973). In a second part of DeSante's study, vagrant Blackpoll Warblers in orientation cages showed directed orientation behavior symmetric to both north-south and east-west axes. Such symmetry is compatible with the theory that vagrants display both the correct migratory direction and the mirror image of that direction. Apparently, immature warblers learn the stationary point of the night sky (celestial

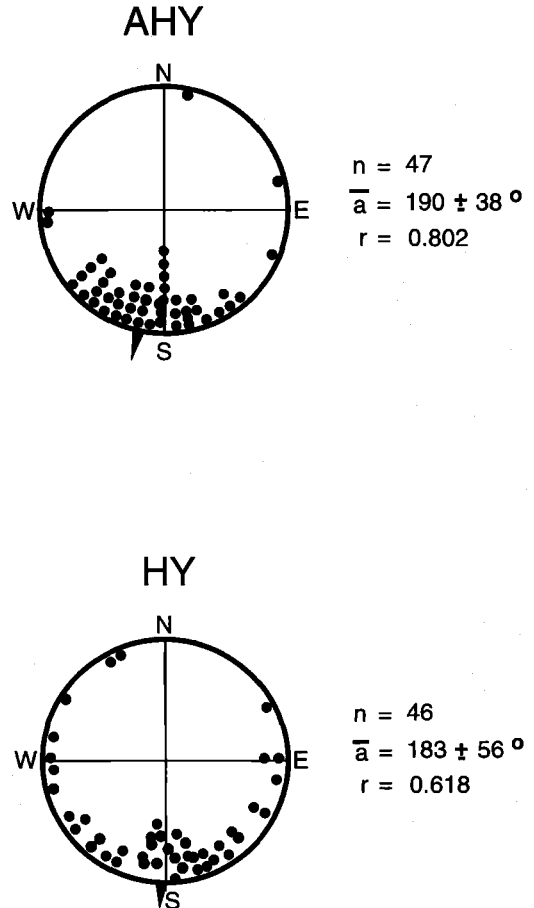


FIGURE 3. Mean orientation headings for experienced (AHY) and naive (HY) individual Savannah Sparrows. The mean headings (\pm angular deviations) and the r-values (measure of concentration of headings; a low value indicates dispersed headings, a high value indicates clustered headings) are given, and the mean headings are shown as arrows on the circumference of the circle. North is at the top (from Moore 1984).

north) as a reference point to which to relate their inherited migratory direction (DeSante 1973). That vagrant migrants are typically immature birds is yet another indication that experience is likely to be important in the development of seasonally appropriate orientation in migratory birds (DeSante 1973).

SIGNIFICANCE OF AGE-DEPENDENT RESEARCH

RESPONSE TO ENERGY DEMAND

The foregoing review of age-dependent research on migrant landbirds demonstrates that age-classes respond differently to the problems

faced during migratory journeys. The *en route* ecology of migratory birds reflects a dynamic interaction between possible behavioral responses and a changing energetic state. For example, Red-eyed Vireos adjust their foraging behavior depending on their energetic status following trans-Gulf migration (Loria and Moore 1990). As a consequence of behavioral adjustments, lean birds are more likely to gain weight than fatter birds. Behavioral plasticity during the migratory period should come as little surprise given the different vegetation structures, wide variations in the resource quality and quantity, and changes in competitive pressures experienced during stopover (Morse 1971, Martin and Karr 1990). If flexibility in the foraging behavior of migratory birds provides a basis for adaptive responses to the energy demands of migration (Parrish *this volume*), a consideration of age as an independent variable becomes essential.

EXPERIENCE AND THE REGULATION OF MIGRATION

Conditions encountered *en route* and experience gained from previous migrations modify behavior and play a role in the regulation of bird migration (Gauthreaux 1978; Ketterson and Nolan 1985, 1988; Terrill 1988). For example, Gauthreaux (1978) and Ketterson and Nolan (1983) found differences in migration distance among age-sex classes of a wide variety of avian species. Ketterson and Nolan (1983) argue that several selective pressures influence such differential migration, including (1) higher mortality in young birds with no previous migratory experience, and (2) age-dependent trade-off between the greater mortality of longer migration and the increased survivorship associated with wintering in more tropical areas (i.e., the trade-off of adult migrants who are more experienced in satisfying energy demand is biased toward avoiding the risks of migration).

Experience, or lack thereof, has been implicated as a cause of age-specific differences in the stopover biology of migratory passerines (Morris et al. 1996, Woodrey and Moore 1997). Yet, distinguishing between lack of experience and constraint (*sensu* Curio 1983) can provide greater insight into the underlying mechanisms influencing age-specific migrant behavior. Whereas some aspects of migration may be endogenously "programmed" (Berthold 1984), young migrants might be constrained either through social dominance relationships or developmental forces (Marchetti and Price 1989). Observations of American Redstarts (Woodrey 1995) and Rufous Hummingbirds (Carpenter et al. 1993a,b) during stopover suggest that social constraints (i.e., density-dependent habitat use) are important in shaping migrant stopover be-

havior. However, regardless of the mechanism, age-related differences during the migration period can lead to differential recruitment into the breeding population.

Populations of long-distance passerine migrants appear to be limited during both summer and winter (reviewed by Sherry and Holmes 1993, 1995). For instance, long-term population data for American Redstarts suggests that breeding season events influence long-term population numbers (Sherry and Holmes 1992). In contrast, Baillie and Peach (1992) found that populations of several species of Palearctic-African migrants depend critically on events during the period between independence-from-parents to the birds' first breeding attempt.

Although the complex annual cycle of migrants makes it difficult to resolve when populations are limited (Morse 1980b, Holmes and Sherry 1988; Sherry and Holmes 1993, 1995), factors connected with migration and the stopover ecology of migrants should figure in any analysis of population limitation (Sherry and Holmes 1993, 1995). Three lines of evidence imply that migration events may limit populations: (1) the observation of territoriality in some species during migration (Rappole and Warner 1976; M. Woodrey, unpubl. data), (2) decreased insect abundance at stopover sites due to the presence of migrants (Moore and Yong 1991), and (3) occurrence of migrants among a variety of stopover habitats (Martin 1980, Moore and Kerlinger 1987, Moore et al. 1990). Further, migrants may be limited by food because of time constraints associated with locating suitable habitats during stopover (Moore and Simons 1992a, Moore et al. 1995). As Sherry and Holmes (1995:95) point out, "Such limitation could cause increased mortality of individuals in proportion to the size of migrants' populations, i.e., to density-dependent mortality during migration, although this phenomenon has yet to be demonstrated at this phase of the annual cycle." Future research in this area should address how different age-classes of migrants select and use stopover habitats, age-specific rates of predation pressure or mortality in habitats migrants select, and identification of intrinsic cues used by migrants to evaluate the suitability of habitats. These as-yet-to-be-collected data will be critical to our understanding of when during the annual cycle populations of birds are limited.

CONSERVATION OF MIGRATORY BIRDS

Stopover biology is critical to the development of conservation strategies for migratory birds. Population declines of long-distance migrant passerines are linked with habitat loss on the wintering grounds (e.g., Wilcove and Ter-

borgh 1984, Kelsey 1992, Sherry and Holmes 1995) and fragmentation of forested breeding habitats (e.g., Wilcove 1988, Bibby 1992; Sherry and Holmes 1992, 1995). The population status of migrants may also be linked to the availability of suitable *en route* habitat (Moore and Simons 1992a, Moore et al. 1993), where energy stores necessary for successful migration are available.

Habitat use during migration has profound consequences for a bird's (1) ability to satisfy the heightened energy demand of migration, (2) vulnerability to predators, and (3) exposure to environmental stress (Moore and Woodrey 1993). Unfortunately, little is known about habitat use by passerine migrants (but see Bairlein 1983, Moore and Kerlinger 1987, Watts and Mabey 1994, Moore and Woodrey 1993). As stop-over habitats are converted or degraded, the cost of migration potentially increases and a successful migration is jeopardized. Protection of stop-

over habitats, used for feeding before and after they cross ecological barriers, is particularly important for the conservation of long-distance migrant passerines (Curry-Lindahl 1981). Because individual behavior influences the dynamics of populations, intensive study of the behavior and ecology of age-classes of intercontinental migrants during stopover is needed if we are to develop a successful conservation strategy for this group of birds.

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