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ABSTRACT.—We examined the pattern of American Redstarts (*Setophaga ruticilla*) migrating through and arriving in breeding areas in northern Michigan to evaluate factors that may influence arrival of redstarts. Variation in arrival schedules coincided with variation in endogenous and exogenous factors. Redstarts arrived 3 to 7 days later during a year characterized by cold temperatures and low resource abundance as compared to years in which environmental conditions during the arrival period were more benign. Further, males verified as breeding at our site arrived 2 to 4 days before breeding females while males classified as migrants preceded migrant females by 4 days. Finally, older birds preceded younger for both verified breeders (7 days) and migrants (6 days). These findings demonstrate behavioral plasticity within the constraints of optimal migration theory which places high value on early arrival in breeding areas. Our results suggest that some species of long-distance migrants may adjust spring migration rates in response to environmental conditions. *Received 20 March 2008. Accepted 17 September 2008.*

Migratory timing is a consequence of endogenous and exogenous factors (Berthold 1996). For example, genetic control mechanisms influence factors including onset of migratory restlessness, temporal pattern of migratory activity, migratory direction, and annual patterns of body mass cycles (Berthold 1996). Events that occur during passage also influence migratory timing, such as competing with other migrants for limited resources (Moore and Wang 1991), satisfying nutritional demands under time constraints (Loria and Moore 1990), and avoiding predation while balancing conflicting demands between predator avoidance and food acquisition (Moore 1994). Additionally, migrants must adjust to unfamiliar surroundings (Aborn and Moore 1997, Petit 2000), cope with unfavorable weather (Richardson 1978) and choose the appropriate direction for the next migratory flight (Moore 1990). Further, exigencies in wintering areas may influence migratory timing. Age and gender-related dominance asymmetries, via influencing winter habitat occupancy, have been related to northerly departure time and timing of arrival in breeding areas (Marra et al. 1998, Norris et al. 2004, Norris and Marra 2007). A successful migrant integrates these factors, tai-

loring its migratory strategy in an effort to optimize efficiency and speed of movement (Ålerstam and Lindström 1990, Mabey 2002) because time and condition upon arrival at the migratory destination may have fitness consequences (Rowe et al. 1994, Moore et al. 2005, Smith and Moore 2005a).

Intrinsic factors also have a role in defining migration patterns, passage rates, and arrival timing. Migratory strategies within-species may diverge leading to intra-specific differential migration and/or differential passage (e.g., Bensch et al. 1999). Differential migration arises when migratory patterns vary intra-specifically, leading to geographic or habitat segregation of gender or age classes during the non-breeding season (Terrill and Able 1988, Cristol et al. 1999). Differential passage is defined as the temporal segregation of gender or age classes during migration. The classic example of differential passage is early migration and arrival of territorial individuals (generally males in North American landbirds) in breeding areas (Francis and Cooke 1986), which is considered advantageous for gaining access to the highest quality territories (Bensch and Hasselquist 1991, Aebischer et al. 1996, Lozano et al. 1996, Smith 2003). Differential passage may be a consequence of differential migration patterns, for example, if all individuals of a species initiate migration within the same time frame but must travel different distances. Alternatively, it may be an integral part of intra-specific differences in optimal migration strategies that balance the ex-

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penditure of time and energy to maximize fitness and shape departure timing and/or rate of migration (Sandberg and Moore 1996, Mabey 2002, Smith 2003). Given well-documented intra-specific differences in migration patterns and our general lack of understanding of the ultimate and proximate causes driving those differences, there is need to examine variability in migratory timing not just across species but also within species across age and gender.

Our work on stopover and breeding ecology of landbird migrants (Smith and Moore 2003, 2005a, b) in Michigan's eastern Upper Peninsula provided an opportunity to examine the patterns of American Redstarts (*Setophaga ruticilla*) passing through and arriving at a northerly stopover and breeding site, and to assess arrival timing in response to annual variation in environmental conditions. Our objectives were to: (1) compare arrival pattern by age and gender in redstarts that arrived at our site to breed, (2) compare passage pattern by age and gender in redstarts stopping to rebuild fat stores prior to continuing migration, and (3) relate extrinsic factors such as weather and food abundance to patterns of arrival and passage.

METHODS

Study Site.—The study was conducted during the spring migratory and breeding periods at a 5-ha site on the shoreline of northern Lake Huron in Michigan's eastern Upper Peninsula (46° 2' N, 84° 35' W). Forest vegetation at this site was a mixture of conifers including 61% northern white cedar (*Thuja occidentalis*), 10% balsam fir (*Abies balsamea*), 5% white spruce (*Picea glauca*), and deciduous species including 7% quaking aspen (*Populus tremuloides*) and 2% paper birch (*Betula papyrifera*) (Smith 2003). Vegetation composition was representative of the lowland coniferous forests common in shoreline habitats throughout the entire eastern Upper Peninsula of Michigan (Smith et al. 1998).

Bird Sampling.—We trapped American Redstarts daily using mist-nets (12 × 2.6 m, 30 mm mesh) from 7 May through 6 June in 1997, 4 May through 28 June in 1998, 30 April through 23 July in 1999, 27 April through 29 July in 2000, and 27 April through 26 July in 2001. We operated between 25 and 30 permanently positioned mist-nets with the exception of 1997 in which we had 10 nets.

We augmented netting during the arrival period by intensively searching the study area, capturing new arrivals (both males and females) not caught in permanent nets by placing temporary nets in the new arrival's territory and broadcasting song-chip playbacks. We began netting well before redstarts arrived, but our 1997 data are truncated because of a shortened pilot season. The effect of delayed spring in 1997 on arrival timing (Smith and Moore 2005b) precluded capturing as many individuals as in following years. Thus, our estimates of arrival dates are likely skewed toward earlier arrival (i.e., actual arrival dates in 1997 were likely more delayed than our results indicate).

Nets were opened shortly before sunrise, and remained open through early afternoon. We reopened nets in early evening, closing at dusk. Nets were closed in the event of excessively low temperatures, high wind or rain. We restricted analyses for this paper to first captures of birds prior to 12 June to ensure capture data accurately reflected day of arrival. Birds were classified to gender and age following Pyle (1997). If we could not reliably assign age as either a bird in its second calendar year (SY), or at least its third calendar year (After Second Year, ASY) we assigned the age category After Hatch Year (AHY). The AHY categorization indicated the bird was in at least its second calendar year. Birds were fitted with a USGS aluminum band and individually color-banded.

We monitored color-banded American Redstarts during the migratory and breeding periods, and were able to categorize individuals as either breeders or migrants. We searched the immediate study area daily throughout the duration of our study as well as adjacent areas (circles with a radius of 2–2.5 km with occasional searches extending to 5 km) looking for color-banded birds. We used several types of evidence to identify individuals as local breeders: capture or observation during the breeding season, morphological evidence of breeding on recapture (i.e., brood patch or obvious cloacal protruberance), or evidence of nest attendance.

Environmental Conditions on Arrival.—We included weather data collected either at our study site or from a nearby weather station (Mackinac Bridge, ~11.3 km west of the

study site). We tracked the progression of spring each year by collecting data describing quaking aspen leaf development. We selected 10 trees during the leaf-out period at 3–4 days intervals, classifying each into one of four categories: 1 = leaves in bud; 2 = leaves emerging from bud; 3 = leaves unfurled but not fully expanded; 4 = leaves fully expanded. Categories were assigned based on the stage for most of a tree's leaves. The same person (RJS) collected these data in all years.

Invertebrate Sampling.—We sampled the invertebrate fauna using a technique modified from Cooper and Whitmore (1990) every 6 days, except in 2000 and 2001, when we sampled every 3 days. We randomly selected 3 locations during each sampling round, collecting one sample for each of the common tree species at each location.

We randomly selected sample height (1 to 5 m above ground level), placing a bag over a representative branch, clipping the branch and fumigated it. Invertebrates were collected and sorted to size and Order with the exception of Diptera, which we differentiated as either chironomid or dipteran. We used the equations of Hóðar (1996) to estimate biomass for each group of arthropods. We weighed branches and report arthropod biomass estimates as milligrams biomass/100 g foliage.

Statistical Analysis.—Data were analyzed using SPSS 9.0 (SPSS Institute Inc. 1998). Distributions of relevant variables were examined for departures from normality and we used non-parametric statistics when transformations did not bring data into compliance with parametric testing assumptions (Zar 1996). We used Chi-square tests to compare number of precipitation events between years and a General Linear Model (GLM) on ranked data to look for differences in precipitation amount by year. We used a Kruskal-Wallis nonparametric analysis of variance along with Dunn's post hoc comparisons to examine year effects on arthropod biomass and mean daily temperature, and used Spearman rank correlations to assess the relationship between invertebrate biomass and aspen leaf development.

We calculated average arrival temperature, invertebrate biomass, and aspen phenology during the arrival period for each year and used Spearman rank correlations to assess relationships

with mean redstart arrival day. We used a GLM for factorial comparisons of arrival day (Zar 1996) with Games-Howell multiple comparison tests. The Games-Howell procedure is specifically designed for situations when population variances differ (Field 2003). We used Chi-square tests to assess age-related capture ratios and compared arrival day by gender within age categories using *t*-tests.

RESULTS

Environmental Conditions.—Invertebrate abundance was associated with aspen leaf development ($r = 0.521$, $n = 112$, $P < 0.001$). Further, in 4 of 5 years aspen completed leaf-out by 15 May (Julian day 135). However, in 1997 leaf-out was delayed by 18 days relative to 1999, 2000, and 2001, and 23 days relative to 1998 (Smith and Moore 2005a: figure 1). This delay was presumably in response to depressed temperatures; the spring arrival/passage period in 1997 was the coldest of the 5 years of study (Table 1). Environmental conditions during the 1997 arrival/passage period were poor relative to other years. Spring during 1997 was colder and remained colder for longer. There were no differences in the number of precipitation events between years during May ($\chi^2 = 1.29$, $df = 4$, $P > 0.05$) nor was there any difference in amount of precipitation between years ($F_{4,29} = 1.96$, $P = 0.132$).

The delayed leaf-out and colder temperatures in 1997 were reflected in arthropod biomass estimates. Invertebrate abundance was lower in 1997 than other years ($\chi^2 = 32.09$, $df = 4$, $P < 0.001$; Smith and Moore 2005a: figure 1). Sampled biomass in 1997 was significantly less than in 1998 ($P < 0.001$), 1999 ($P = 0.002$), and 2000 ($P = 0.03$). Further, there was a significant difference between 1998 and 2001 ($P = 0.01$). Redstarts using our site in 1997 had both cold weather and depressed prey conditions.

Even as 1997 saw the poorest conditions of all 5 years of study, the following year appeared the most favorable. Ambient air temperatures during the 1998 arrival/passage period were benign, there was a slight advancement in leaf-out of aspen throughout the study area relative to all other years, and food was more abundant.

Arrival and Passage.—Aspen leaf devel-

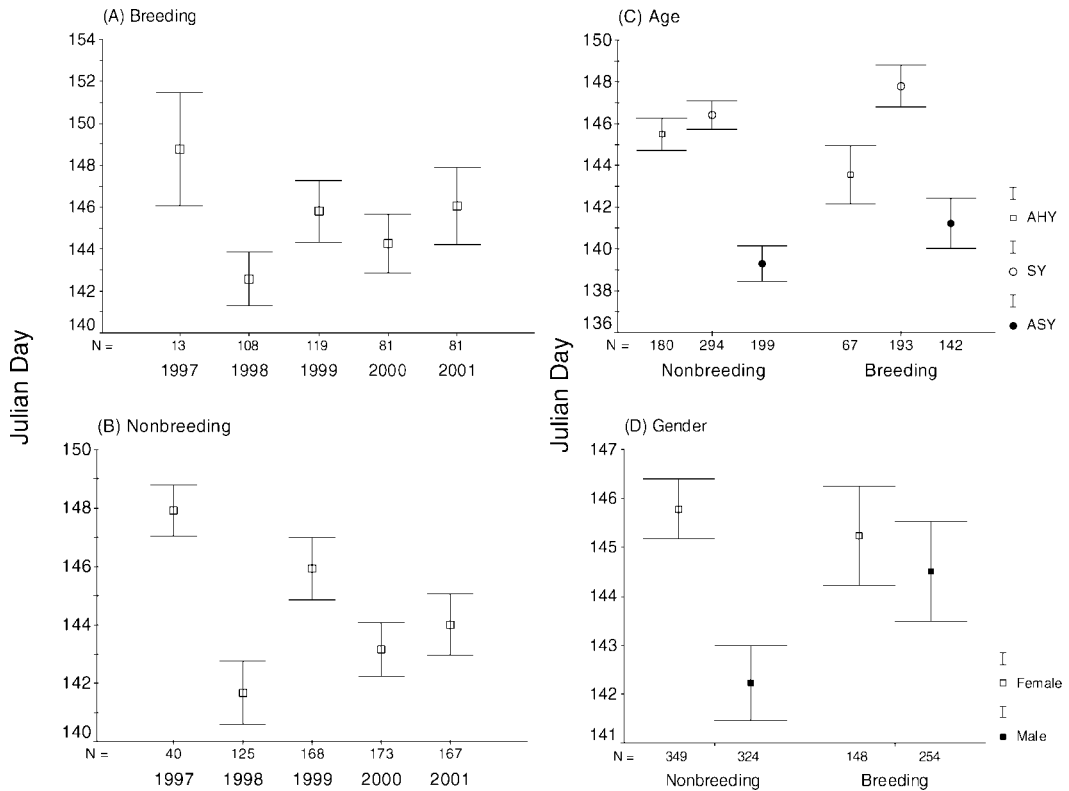


FIG. 1. Annual variation in arrival for breeding (A) and nonbreeding (B) American Redstarts by age (C) and gender (D) at northern Lake Huron, Michigan, 1997–2001. Boxes represent mean and whiskers represent ± 1 SE. Julian date 140 = 20 May.

opment was positively related to arrival day ($r = -0.900$, $n = 5$, $P = 0.037$), although there was no relationship with invertebrate biomass on arrival day ($r = -0.100$, $n = 5$, $P = 0.873$). The relationship between arrival temperature and arrival day approached significance ($r = -0.800$, $n = 5$, $P = 0.104$), even as statistical power was low ($\beta = 0.200$).

TABLE 1. Average daily temperatures by year, northern Lake Huron, Michigan. All means, with the exception of 1998 and 2001, are different (Kruskal-Wallis ANOVA $\chi^2 = 561.413$, $df = 4$, $P < 0.001$; all Dunn's Multiple Comparisons < 0.05).

Year	Average temperature (°C)	SE
1997	7.39	0.56
1998	12.8	0.08
1999	11.45	0.11
2000	10.11	0.10
2001	13.01	0.09

Year ($F_{4,381} = 7.08$, $P < 0.001$) and age ($F_{2,381} = 38.48$, $P < 0.001$), but not gender ($F_{1,381} = 0.88$, $P = 0.35$), influenced when American Redstarts arrived in breeding areas. There were no significant interactions between independent factors (all P 's > 0.60). Birds arrived earlier in 1998 than in all years except 2000 (Games-Howell multiple comparisons, $P = 0.39$; Fig. 1A) and older birds preceded younger individuals ($t = -8.46$, $df = 333$, $P < 0.001$; Fig. 1C).

The capture ratio for males was skewed towards SYs, ($\chi^2 = 26.61$, $df = 1$, $P < 0.001$) but not for females ($\chi^2 = 0.15$, $df = 1$, $P = 0.75$). Younger birds of both gender arrived significantly later, consequently the predominance of SY males in our data set skewed the overall male arrival date so the gender effect was not statistically significant (Fig. 1D). We further examined arrival day by gender within age class for known breeding birds. Males of

TABLE 2. Arrival day by age for breeding American Redstarts, northern Lake Huron, Michigan. Years are pooled (1997–2001) and dates are Julian; Day 121 = 1 May, Day 135 = 15 May. Comparisons made using *t*-tests.

	Mean arrival day	Range (days)	Min	Max	SE	<i>n</i>	<i>t</i>	df	<i>P</i>
ASY									
Female	143	19	132	151	0.62	42			
Male	141	31	129	160	0.80	100	2.224	135	0.028
SY									
Female	151	21	140	161	0.92	40			
Male	147	32	130	162	0.57	153	2.824	191	0.002

both age classes (pooled across years) preceded females by ~3 days (Table 2).

Analysis of redstarts classified as nonbreeding also indicated that year ($F_{4,651} = 16.40$, $P < 0.001$), gender ($F_{1,651} = 9.06$, $P = 0.003$), and age ($F_{2,651} = 52.00$, $P < 0.001$) influenced when an individual was captured. There was a significant interaction between age and year ($F_{6,651} = 4.14$, $P < 0.001$). Birds migrated through later in 1997 than in all other years (Games-Howell multiple comparisons, all P 's < 0.035) and earlier in 1998 than 1997 ($P < 0.001$), 1999 ($P < 0.001$), and 2001 ($P = 0.016$), but not 2000 ($P = 0.22$; Fig. 1B). Males preceded females ($t = -6.050$, $df = 491$, $P < 0.001$; Fig. 1D) and older birds preceded younger birds ($t = -13.01$, $df = 491$, $P < 0.001$; Fig. 1C).

DISCUSSION

Extrinsic Factors.—The timing of both passage and arrival at our site appeared to be influenced by onset of spring. Both passage birds and those individuals arriving to breed appeared at our site later during a cold, food-poor spring and earlier during a warm, food-abundant spring (Fig. 1A, B). Further, there was a relationship between arrival timing and aspen leaf development, and possibly between temperature and arrival timing. While estimates of arthropod abundance were unrelated to redstart arrival timing, invertebrate abundance correlated with leaf development, suggesting that leaf development was a reasonable proxy for food abundance during the arrival period. Nolan (1978) attributed some variation in arrival of Prairie Warblers (*Dendroica discolor*) in breeding areas to weather. More recently, Forchhammer et al. (2002) found a strong influence of regional cli-

mate effects associated with the North Atlantic Oscillation on spring arrival in breeding areas by short-distance migrants. These migrants are thought to closely track advancement of spring (Hagan et al. 1991) with less of an effect on arrival of long-distance migrants, which are thought to have a tighter endogenous program for onset of migration (Berthold 1996, Gwinner 2003). Yearly variation in arrival timing has also been demonstrated for male redstarts arriving in breeding areas in New Brunswick, although no attempt was made to relate this variation to environmental conditions (Lozano et al. 1996).

It is conceivable that redstarts adjusted migration rate in response to temperature and food abundance encountered *en route*, which in turn reflected conditions in breeding areas. Møller (1994) demonstrated annual arrival variation in Barn Swallows (*Hirundo rustica*) with males arriving at Denmark breeding areas later during cold springs. He suggested that birds could use weather patterns to gauge environmental conditions in breeding area if those patterns operated at a large geographical scale. More recently, Hüppop and Winkel (2006) related first arrival dates of European Pied Flycatchers (*Ficedula hypoleuca*) to temperatures experienced *en route*. They concluded that progression of spring migration may be strongly influenced by temperatures as birds move north. Weather in the United States is often impacted by passage of low- and high-pressure systems affecting large areas. Consequently, both temperatures and onset of spring across large geographical areas is correlated, as has recently been demonstrated in eastern North America by Marra et al. (2005). Further, arthropod abundance is cor-

related with onset of spring (Ratte 1984; Smith and Moore, unpubl. data), possibly in response to increasing daily temperatures (Ratte 1984) and/or availability of leaves as food for leaf-chewing arthropods (Tauber et al. 1986).

Intrinsic Factors.—Differential timing of migration and arrival by age and gender classes at our site was evident in both redstarts arriving to breed and those that continued migration (Table 2, Fig. 1C, D). The pattern of timing was consistent regardless of breeding status; males preceded females and ASY birds preceded SY birds in both migrants and breeders. Similar passage/arrival patterns between breeders and migrants support the assumption that observation of differential passage at a northerly stopover site (e.g., Francis and Cooke 1986, Stewart et al. 2002) results in differential arrival at the migratory destination.

Our results are insufficient to evaluate how intrinsic factors influence arrival in northern Michigan. There are a number of possible reasons for differential arrival by age and gender. For example, differential arrival could be a consequence of classes of individuals differentially departing wintering areas and/or migrating different distances (Ketterson and Nolan 1985, Holberton 1993, Cristol et al. 1999) or at different speeds (Hedenström and Petersson 1987, Ellegren 1990). Age- or gender-related dominance asymmetries might also contribute to differential arrival if subordinates are 'forced' into suboptimal habitats (Woodrey 1995, Mabey 2002, Moore et al. 2003) depressing fat deposition rates and overall speed of migration. Social dominance by age and gender in redstarts has been demonstrated during fall migration (Woodrey 1995), and wintering (Marra et al. 1993, Parrish and Sherry 1994, Marra et al. 1998, Marra and Holberton 1998) and breeding periods (Sherry and Holmes 1997). Finally, there is an increasing body of evidence suggesting that age- and gender-related behavioral asymmetries in American Redstarts, via influencing winter habitat occupancy, affect northerly departure time as well as timing of arrival in breeding areas (Marra et al. 1998, Norris et al. 2004, Norris and Marra 2007).

Redstarts may moderate timing of passage and arrival in response to environmental factors. Furthermore, ASY and SY males and fe-

males respond similarly as males consistently preceded females and older birds consistently preceded younger birds. Questions regarding the ability of migratory birds to moderate timing and rate of their migrations have drawn considerable attention in recent years in view of global climate change (Both and Visser 2001, Winkler et al. 2002, Cotton 2003, Root et al. 2003, Strobe 2003). If arrival in breeding areas is constrained by inflexible endogenous migratory programs, as suggested for some species (e.g., Both and Visser 2001, Hubálek 2004), migrant reproduction and food resources may become asynchronous over time, leading to lower reproductive success (Both and Visser 2001, Winkler et al. 2002). Many long-distance migrants use day length as a primary cue for onset of migration (Gwinner 2003), and modulating rate of passage may be the only avenue for proximate adaptation to temporal changes in resource availability. A number of studies have shown that spring arrival dates for some long-distance migrants have advanced with spring temperatures during the past decades (Both and Visser 2001, Cotton 2003, Hüppop and Hüppop 2003, Root et al. 2003), but there is also evidence that early arrival is limited by as yet unidentified factors (Both and Visser 2001, Winkler et al. 2002). Strobe (2003) suggests that passage resource availability may be delayed relative to advancing availability at breeding sites. Furthermore, if males and females use different migration strategies (Sandberg and Moore 1996), there may be gender-specific constraints on responses to environmental change. Greater attention should be given to possible changes in migratory timing along with the physiological and environmental constraints migrants have as they compensate for climate-driven temporal changes in resource availability.

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