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33. All animal procedures were approved by Northwestern University's Animal Care and Use Committee. Each chinchilla was deeply anesthetized with diallyl barbituric acid in urethane. The left pinna was resected and the head was attached to a metallic holder. A calibrated miniature microphone, with its tip placed within 2 mm of the eardrum, was used for in situ determination of SPLs (expressed relative to 20 μPa). The auditory bulla was opened widely and a gross electrode, which recorded compound action potential thresholds of responses to tone pips, was placed on the round window. Both middle-ear muscles (cochlea L208) or only the tensor tympani (L199) was detached. Then the surgical preparations necessary for microelectrode recording from auditory nerve fibers (*31*) and for measuring BM vibrations with a laser velocimeter (*32*) were made consecutively. After the otic capsule was opened and reflective microbeads were dropped onto the BM, the otic capsule hole was covered with a window (made from slide coverslip glass) to minimize motion of the perilymph (*7*). Stimuli for BM recordings were 128 to 512 repetitions of gated tones (5 to 100 ms in duration, presented every 53 to 500 ms). BM tuning curves were computed from velocity-intensity functions (resolution: 5 or 10 dB, 100 to 1000 Hz) by interpolating at each frequency the response magnitude corresponding to neural threshold at CF. Frequency-threshold tuning curves of auditory nerve fibers were measured with 50-ms tone pips, presented every 100 ms, by an automated procedure (*11*). They had a resolution of 32 frequency steps per octave near CF and 8 steps per octave at lower frequencies.
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Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes

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For migratory birds, early arrival and physical condition on the breeding grounds are important determinants of reproductive success and fitness. Differences in arrival times often exceed a month, and later arriving individuals are often in poorer condition. Habitat-specific isotopic signatures indicate that the quality of winter habitats occupied by American redstarts (*Setophaga ruticilla*) determines their physical condition and spring departure dates, which in turn result in variable arrival schedules and condition on temperate breeding grounds. These findings link events in tropical winter grounds with those in temperate breeding areas for a migratory songbird and provide evidence that winter habitats may be limiting.

Natural selection acts on individuals throughout the annual cycle. For migratory animals, understanding these selection processes has been limited by our inability to follow individuals yearround, yet events during each phase of the annual cycle are likely to influence those in subsequent phases. Many long-distance migratory birds, such as the American redstart, spend 3 to 5 months on their temperate breeding grounds, 1 to 2 months on autumn migration, 6 to 7 months on tropical wintering areas, and another month on spring migration (*1*).

For many migratory species, males arrive at breeding habitats before females (*2*), and breeding success and physical condition decline with arrival date (*3, 4*). Early arrival appears to be advantageous because it gives access to the best breeding sites and mates, as well as additional time to replace lost clutches (*5*). Declining reproductive success for late arriving birds is also attributed to poor physical condition of these individuals (*4*). Factors that determine arrival time and physical condition of birds in breeding areas are poorly understood.

To test the hypothesis that winter events influence arrival dynamics on the breeding grounds, we studied American redstarts in two habitats in southwestern Jamaica: a black mangrove (*Avicennia germinans*) forest in which males predominated (65% male and 35% female) and a drier, second-growth scrub habitat in which females were more abundant (30% male and 70% female). Sexual habitat segregation is common in redstarts during the winter period (*6*) and is produced by the dominance behavior of older males forcing most females and young males into habitats of poorer quality (*7–9*). In autumn 1995 and 1996, redstarts were captured with mist nets, measured, bled for hormone and stable-isotope assays, color-banded, and released. In late March and early April, those individuals that remained on territory over the winter were recaptured for remeasurement. We found that individuals wintering in the forest habitat, regardless of sex, maintained or gained body mass, whereas individuals in scrub habitat lost up to 11% of their body mass [0.06 ± 0.05 g (mean ± SE) compared with −0.24 ± 0.07 g; two-way analysis of variance: sex $F = 0.09$, $P = 0.77$; habitat $F = 15.1$, $P = 0.0004$; sex by habitat $F = 2.56$, $P = 0.12$]. Individuals in scrub habitats showed other signs of deteriorated physical condition, including elevated plasma corticosterone concentration (*9*).

The poor physical condition of redstarts in scrub habitat did not lead to lower overwinter survival (*8*), but it did result in a delay in departure schedules (*10*). Both males and females departed significantly later from scrub habitat in both years (Fig. 1). Furthermore, departure time was inversely correlated with change in body mass (Fig. 2), implying that redstarts in better physical condition were able to leave sooner.

To determine if habitat segregation during winter influences the arrival schedules of birds

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onto breeding sites, we used $\delta^{13}C$ signatures in redstart tissue as an indicator of habitat occupancy. Stable-carbon isotopes are suitable for such applications because the rate of diffusion of ^{13}C from the atmosphere into plant tissues differs between plants with C_3, C_4, and Crassulacean acid metabolism (CAM) photosynthetic pathways (C_3 and C_4 plants produce a three-carbon or four-carbon acid, respectively, as the first product of photosynthesis). C_3 plants are typically associated with cooler, moister habitats and have more depleted $\delta^{13}C$ values, whereas C_4 and CAM plants are often associated with hotter and drier environments and have more enriched $\delta^{13}C$ values (*11*). Similar ^{13}C enrichment patterns in C_3 plant tissues may also result from differences in plant water use efficiency (*11*). Mangrove (*12*) and tropical lowland forests are both C_3 habitats (*13, 14*). More xeric tropical habitats containing grasses (for example, our scrub habitat in Jamaica) typically have more C_4 plants (*11, 14*). These relations were substantiated with isotopic assessments of insects collected from the two Jamaican habitats (*15*).

Previous studies have shown that animal tissues reflect the isotopic composition of their supporting food web (*14, 16*). Thus, we expected American redstarts as obligate insectivores (*1*) to incorporate a habitat-specific $\delta^{13}C$ signature into their tissues from the phytophagous insects they consumed. An analysis of $\delta^{13}C$ values in tissue (*17*) collected from redstarts in Jamaica and in a second geographically distinct locality in Honduras revealed that individuals in wet, forested habitats had significantly depleted $\delta^{13}C$ values relative to individuals in drier, scrub habitats, regardless of sex or locality (Fig. 3).

To determine if habitats occupied in winter influence arrival dates in North America, we collected tissue from American redstarts as they arrived in spring 1997 and settled on breeding areas at the Hubbard Brook Experimental Forest, central New Hampshire, U.S.A. We found that later arriving redstarts had tissue $\delta^{13}C$ values more enriched relative to earlier arrivals (Fig. 4) (*18*). This suggests that males arriving on breeding grounds early were those originating from wetter tropical habitats, whereas those arriving later were from drier tropical habitats (Fig. 4). The period of arrival that we sampled may have been too short to adequately test this for females. Using body mass corrected for skeletal size as an index to physical condition, we also found that the physical condition of redstarts arriving on the breeding grounds declined from early to later arrival ($r = -0.52$, $P = 0.016$, $n = 21$) (*19*).

The specific winter ground origin of redstarts breeding at Hubbard Brook is not known (*1*). However, because habitat segregation is pervasive throughout most of the winter range of redstarts (*9*), we believe the carbon isotope signatures from Jamaican and Honduran habitats to be representative of the major habitat types occupied by redstarts throughout their winter distribution. The application of stable-carbon isotope methodology has allowed us to link two separate periods in the annual cycle of this migratory species.

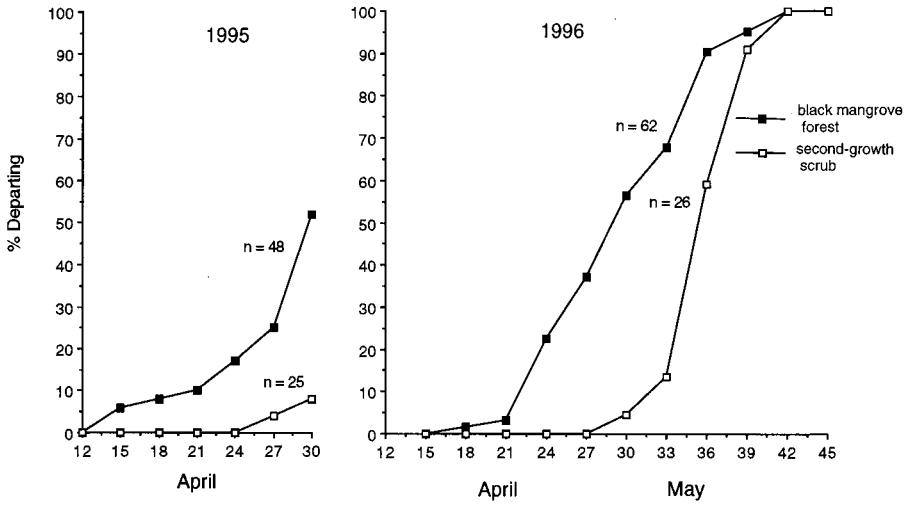

Fig. 1 (top). Spring departure schedules of color-banded American redstarts from their wintering territories in Jamaica, West Indies. In 1995 and 1996 redstarts departed significantly earlier from black mangrove forest compared with second-growth scrub [Kaplan-Meier survivorship analysis (*23*); 1995, $P = 0.0006$; 1996, $P = 0.0002$]. In 1995, there were no significant differences in departure schedules between sexes within a habitat (forest, $P = 0.923$; scrub, $P = 0.34$), but in 1996, males from forest departed before females ($P = 0.004$) and before both males and females from scrub ($P = 0.001$). Females from forest (1996) departed significantly earlier than both females ($P = 0.04$) and males ($P = 0.008$) from scrub.

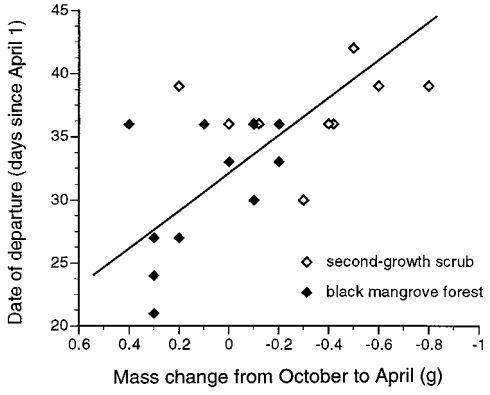

Fig. 2 (bottom). The relation between winter mass change (in grams) of color-banded American redstarts captured in October and then recaptured in April and the number of days until they departed on spring migration (Pearson's $r = 0.60$, $P < 0.004$).

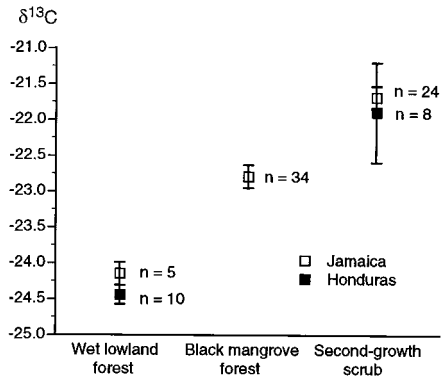

Fig. 3. Stable-carbon isotope values ($\delta^{13}C$) (mean ± SE) taken from blood samples of American redstarts in three habitat types in Jamaica, West Indies, and in two habitat types in Honduras, Central America. These habitats contained different sex ratios of wintering American redstarts (wet lowland forest, 95% male; black mangrove forest, 65% male; second-growth scrub, 30% male). In both localities, isotope values differed significantly across habitat types ($F = 77.34$, $P < 0.0001$) but did not differ between geographic localities ($F = 1.91$, $P = 0.20$). No effects of sex were found within a habitat when comparing isotope values of redstarts in mangrove forest versus scrub ($F = 0.16$, $P < 0.69$).

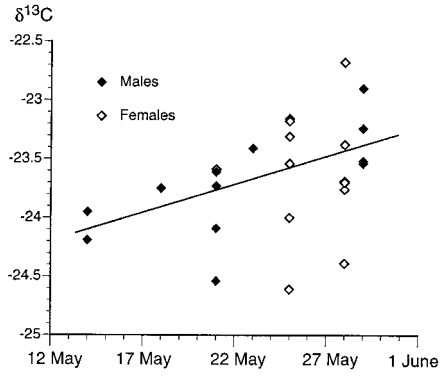

Fig. 4. Stable-carbon isotope values ($\delta^{13}C$) taken from muscle tissue of American redstarts as they arrived in spring at the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, U.S.A. (sexes combined: Spearman $\rho = 0.47$, $P = 0.01$; males only: Spearman $\rho = 0.80$, $P = 0.002$; females only: Spearman $\rho = 0.11$, $P = 0.72$).

These results implicate events during the preceding winter, namely intraspecific competition for optimal winter habitat mediated through behavioral dominance (*8, 20*), as an important factor determining arrival times and condition upon arrival of redstarts in their north temperate breeding areas. This finding is important because arrival time at the breeding ground is a major determinant of fitness in migratory birds (*3, 21*). Furthermore, our evidence that later arriving birds wintered in drier habitats and that physical condition declined with arrival date suggests that optimal winter habitats for redstarts may be saturated and therefore limiting. If optimal winter habitats (more mesic sites) were always available, then all redstarts should have occupied them, and we would have found no relation between $\delta^{13}C$ values and the physical condition of redstarts over the arrival period. This conclusion, that winter habitats are limiting, has important conservation implications for the long-term stability of migratory bird populations, many of which are declining and of conservation concern (*22*).

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15. The $\delta^{13}C$ values in insects collected from within the foraging height range of redstarts in two of the habitats in Jamaica differed significantly [$F(1,10) = 15.24$, $P = 0.004$], with $\delta^{13}C$ values of forest insects being more depleted [-25.8 ± 0.44 per mil (mean ± SE)] and insects from scrub territories more enriched (-24.2 ± 0.20 per mil).
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17. Blood tissue samples were collected from redstarts in Jamaica and Honduras, and pectoral muscle tissue was collected from redstarts during the arrival period in New Hampshire. Both types of tissue equally reflect dietary integrations over the previous 6 to 8 weeks (*20*). All samples were freeze-dried and powdered in a dental amalgam mill. About 1 mg of sample was combusted in a Robo-Prep elemental analyzer interfaced with a 20:20 Europa continuous-flow stable-isotope mass spectrometer. Two reference standards were run for every five unknowns, and on the basis of replicate measurements of an egg albumen standard, we estimate our analytical precision to be ±0.1 per mil. All stable-isotope values are reported in δ notation relative to the Pee Dee Belmnite standard: $\delta^{13}C = 1000 \times \{[(^{13}C_{unk}/^{12}C_{unk}) \div (^{13}C_{std}/^{12}C_{std})] - 1\}$. We found no difference in $\delta^{13}C$ values of blood, muscle, and insect samples that were either treated with a 0.5 N HCl solution to remove carbonates or lipid extracted with a chloroform: methanol rinse, so we report here only those values based on replicate measurements of untreated blood, muscle, or insects.
18. The $\delta^{13}C$ values of redstarts arriving in breeding areas should reflect mostly those of habitats occupied on the wintering grounds for several reasons. Although food intake during migration may influence $\delta^{13}C$ values, muscle tissue values have been shown to reflect dietary integrations over the previous 6 to 8 weeks [K. A. Hobson and R. G. Clark, *Condor* **94**, 181 (1992)]. Furthermore, energy demand during migration primarily involves metabolism of fat rather than muscle protein [M. Ramenofsky, in *Bird Migration: Physiology and Ecophysiology*, E. Gwinner, Ed. (Springer-Verlag, Berlin, 1990), pp. 214–231], thus turnover of protein is low. Even if redstarts wintering in scrub habitats had moved into wetter habitats once dominant redstarts left, their muscle $\delta^{13}C$ values would begin to become depleted, not enriched as was found.
19. By controlling for the structural size of individuals and relating this to body mass, it is possible to assess the physical condition of birds. Redstarts with a body mass light for their structural size were considered in poor physical condition relative to those heavy for their structural size. To calculate mass corrected for structural size, we calculated the scores of a principal component analysis on the basis of wing chord, tarsus, and bill length, and then regressed body mass against these scores. The residuals from this regression estimate mass corrected for structural size and provide our index of physical condition.
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Coupling of Mitosis to the Completion of S Phase Through Cdc34-Mediated Degradation of Wee1

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The dependence of mitosis on the completion of the period of DNA replication in the cell cycle [synthesis (S) phase] ensures that chromosome segregation occurs only after the genome has been fully duplicated. A key negative regulator of mitosis, the protein kinase Wee1, was degraded in a Cdc34-dependent fashion in *Xenopus* egg extracts. This proteolysis event was required for a timely entrance into mitosis and was inhibited when DNA replication was blocked. Therefore, the DNA replication checkpoint can prevent mitosis by suppressing the proteolysis of Wee1 during S phase.

Dividing cells depend on ubiquitin-mediated protein destruction for proper cell cycle progression. At least three distinct cell cycle transitions are regulated by proteolysis: passage from the prereplicative phase of growth (G_1) to S phase, passage through metaphase, and exit from mitosis (*1*). Exit from mitosis depends on the proteolysis of the cyclin subunit of the maturation promoting factor (MPF); this is accomplished by the anaphase promoting complex (APC)/cyclosome, a large multi-subunit complex that functions as a ubiquitin ligase. The APC also regulates entrance into anaphase by promoting the separation of sister chromatids that is due to the destruction of the Pds1 (budding yeast) and Cut2 (fission yeast) proteins (*1*). In yeast, the Sic1 protein, an inhibitor of the S phase cyclin-dependent kinase that initiates DNA replication, is degraded to

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