

Fat stores of American redstarts *Setophaga ruticilla* arriving at northerly breeding grounds

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Many long-distance passerine migrants arrive with more fat stores than necessary to have reached their northerly breeding grounds. Researchers have argued for adaptive advantages associated with arriving with 'surplus' migratory fat, including increased breeding performance and insurance against adverse weather, and reduced food resources during the days following arrival. The objectives of this work were to document fat stores in American redstarts *Setophaga ruticilla* arriving to breed in northern Michigan and to test predictions associated with the hypothesis that arrival fat serves an insurance role. Results suggest that redstarts arrived in northern Michigan with fat stores sufficient to have continued migrating an additional distance greater than 1000 km. Significant yearly variation in arrival fat corresponded in part with environmental conditions measured at the breeding grounds. Birds arrived with the most fat in the year with the coolest temperatures and the lowest food abundance at the time of arrival to the site. Further, an inverse relationship between arrival fat and arrival day in males indicated that early arrivals carried more fat than later arrivals. Birds that arrived early faced cooler temperatures and lower densities of terrestrial invertebrates, and arrival fat may have provided a mechanism to overcome poor early season foraging conditions. However, our results are not entirely consistent with the hypothesis that arrival fat serves only as insurance. Arrival fat appeared important even during the most benign year of this study. Further, evidence suggests that females may have derived more benefit from arrival fat than males. These results highlight the connection between phases of a bird's annual cycle. Migrants that do well *en route*, arrive at breeding grounds in better condition, which may contribute to survival and reproductive success.

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Intercontinental landbird migrants often outpace the phenological development of vegetation and terrestrial invertebrates as they move north during spring migration (Slagsvold 1976, Ewert and Hamas 1995), arriving on their breeding grounds well before vegetation is fully leafed out and food becomes abundant (Slagsvold 1976, Nolan 1978, Perrins 1996, Nystrom 1997). Slagsvold (1976) estimated that spring migrants progress northward at a rate approaching twice the speed of vegetation development at high latitudes in Norway. In northern Michigan, breeding birds arrived up to 4 weeks before leaf development was complete (R. Smith unpubl. data).

Early arrival also increases exposure to poor weather, including late season snowstorms, low temperatures, or extended periods of rain (Whitmore et al. 1977, Ewert and Hamas 1995, Aebischer et al. 1996, Merkle and Barclay 1996).

Growing evidence suggests that these same passerine migrants arrive with more fat stores than necessary to have reached their northerly breeding grounds (Ojanen 1984, Sandberg 1996, Fransson and Jakobsson 1998, Widmer and Biebach 2001). Sandberg and Moore (1996) discuss several advantages that might accrue to an individual able to 'overload' (*sensu* Gudmundsson

et al. 1991). One such advantage is that fat stores accumulated during passage might aid in offsetting adverse environmental effects and unpredictable foraging conditions typical of early spring at high latitude breeding areas. Our study of American redstarts *Setophaga ruticilla* in Michigan's eastern Upper Peninsula provided an opportunity to: (1) document fat stores of birds arriving at a northerly breeding location, and (2) test predictions associated with Sandberg and Moore's Insurance Hypothesis.

Prediction 1: Arrival fat stores will be greater in those years when environmental conditions are poor relative to years when environmental conditions are favorable. Yearly variation in mean daily temperature influences the onset and progression of spring. In colder years vegetation and invertebrate development is delayed. Migrants may face depressed food abundance as they approach and arrive at their breeding grounds in colder years while experiencing increased thermoregulatory requirements. In these situations, arrival fat would be advantageous.

Prediction 2: Individuals that arrive at the breeding grounds early carry larger fat stores than those arriving later. Because of the increase in daily temperatures and food abundance associated with the passage of spring (Perrins 1996), early arrivals should benefit more from arrival fat than later arrivals if fat serves as insurance. This prediction is potentially confounded by age effects. Age-dependent differences in arrival dates are known in many migratory species (Francis and Cooke 1986), including redstarts (Lozano et al. 1996, Sherry and Holmes 1997). There may also be age-dependent differences in arrival condition (see Widmer and Biebach 2001). The ease with which Second Year (SY) male redstarts can be distinguished from After Second Year (ASY) males allows checking for potential confounding factors in arrival fat that may be a result of age.

Prediction 3: Fat stores on arrival are not sex-dependent unless members of one sex arrive earlier than the other sex (Prediction 2, see also Sandberg and Moore 1996), or one sex stands to gain more than the other viz. insurance.

Methods

Field work was conducted during the spring migratory and breeding periods at a 5 ha site located on the shoreline of northern Lake Huron in Michigan's eastern Upper Peninsula (46°2'N, 84°35'W). Forest vegetation was a mixture of conifers including balsam fir *Abies balsamea*, northern white cedar *Thuja occidentalis*, white spruce *Picea glauca*, white pine *Pinus strobus*, red pine *Pinus resinosa*, and deciduous species including paper birch *Betula papyrifera*, quaking aspen *Populus*

tremuloides, and balsam poplar *Populus balsamifera*. Relative densities of each species were as follows: northern white cedar =61%, balsam fir =10%, quaking aspen =7%, white spruce =5%, paper birch =2%, white pine 1%, red pine <1%, and balsam poplar <1% (Smith and Moore unpubl. data).

American redstarts were trapped 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 used a combination of passive and active netting to increase the likelihood of capturing birds on the day they arrived. After an initial pilot season (1997), we increased the number of nets and extended the netting period through the end of July to better understand the biology of redstarts breeding in the eastern Upper Peninsula. Except for 1997 when we ran 10 nets, we used 25 to 30 permanently positioned mist-nets to sample the avifauna. During the arrival period we supplemented this netting by intensively searching the area, capturing new arrivals by placing temporary nets in the new arrival's territory and broadcasting song-chip playbacks.

Nets were opened shortly before sunrise, remaining open through early afternoon, were reopened in early evening and closed at dusk. Nets were closed if the temperature dropped below 3°C, or in the event of high wind or rain. Standard measurements taken from each bird included body mass and unflattened wing chord. Visible, subcutaneous fat deposits were quantified using a six-point ordinal scale (Helms and Drury 1960). This commonly used procedure (Bairlein 1985, Woodrey and Moore 1997, Gosler and Harper 2000) provides a repeatable method of indexing fat stores as long as comparisons are made within species (Krementz and Pendleton 1990). All measures were performed by trained individuals who were periodically tested to ensure validity and repeatability of measures. Each bird was aged and sexed according to characteristics outlined in Pyle (1997), fitted with a USFWS aluminum band, and individually color-banded. If an individual was recaptured, body mass, wing chord and visible fat deposits were measured without reference to previous records.

While we made a concerted effort to ensure we captured birds on the day they arrived, we cannot rule out the possibility that birds were resident at our site for a few days prior to capture. To minimize this possibility, we limited our study area to 5 ha so that we were intimately familiar with when birds arrived and who those individuals were. Further, every day during the arrival period, between 5 and 8 field assistants searched the study area for new arrivals. When a new arrival was identified, we augmented our permanent netting array with temporary nets in the area of the new arrival until it was captured. Further, we saturated our study area with

nets (approx. 1 net per 0.2 ha) to maximize probability of capturing new arrivals soon after they arrived. Finally, field observations indicated that newly arrived individuals (observed without bands) were typically confirmed as captured (observed with bands) within a few hours of the original observation.

We grouped individuals as either breeders or migrants based on daily searches of both the study site and adjacent areas (up to 2 km distant). We used several types of evidence to identify local breeders, including morphological evidence of breeding on recapture, and observation of reproductive behaviors including nest construction/attendance, incubation, brooding, carrying food/feeding nestlings or fledglings, or evidence of territoriality.

Because so few breeding redstarts were captured in 1997, we excluded these data from analyses comparing sex and yearly variation in arrival fat. However, to gain insight into how birds responded to environmental variation in 1997, the year with the poorest arrival conditions (see below), we performed a separate set of analyses on migrant redstarts. Further, redstarts gained mass throughout the day (reflecting addition of fat stores, see Smith 2003), so we limited statistical analyses to captures before 12:00 pm, a period when there was no influence of time of day on mass change (Smith and Moore unpubl. data).

We estimated field metabolic rate (*FMR*) using the allometric equation of Williams et al. (1993):

$$\log_{10} FMR = 0.981 + 0.689(\log_{10} m)$$

where *FMR* is in kJ/d and *m* is body mass in grams. *FMR* estimates the total daily energy cost of a wild animal and includes basal metabolism (*BMR*), thermoregulatory costs, movement, feeding, digestion, growth, reproduction and any other energy expenditures (Nagy 1987). For each fat score, we estimated the average amount of fat available (in grams) by subtracting fat free body mass (from Odum 1993), and converting the energy available from arrival fat (assuming 1.0 gram of fat equals 9.0 kcals, 37.683 kJ/g; Blem 1990) into time that could be spent without feeding by dividing available fat energy by *FMR* and multiplying by 24 hours.

Average flight range was calculated according to Pennycuick's flight mechanical model (Pennycuick 1998). Maximum range speed was used to estimate flight-range and depends mainly on body mass and wing morphology (Pennycuick 1975, 1989, 1998). For wingspan measurements we used data supplied by Woodrey and Moore (1997). We determined fat stores available for migration by calculating average body mass for each sex, then subtracted the average fat-free body mass (Odum 1993). Calculations of flight range were made under still air conditions (0 m/s wind speed) with the assumption that migrating American redstarts travel

at an average altitude of 500 m (air density = 1.17 kg/m³; Pennycuick 1989).

We sampled the arthropod fauna every sixth day throughout the duration of the netting effort in 1997–1999 and every third day in 2000–2001 using a 'grab' sampling technique adapted from Cooper and Whitmore (1990). During each sampling round, we randomly selected 3 locations, collecting one sample for each tree species common to the study area, namely white cedar, balsam fir, white spruce, at each location resulting in 9 samples per round. Because most quaking aspens within the study site were fully mature (average height = 15.1 m), we were unable to sample this species within the study area. We collected aspen samples from a young aspen stand 7.2 km east of the study area. We chose these species for invertebrate sampling because trees with relative density estimates of <5% rarely occurred at the randomly chosen sampling locations.

Sample height was randomly selected, ranging from 1 to 5 m above the ground. A closable bag was placed over a selected branch, the bag sealed, the bag clipped and the contents fumigated with insecticide. All arthropods were collected and sorted to size and order except for Dipterans, which were differentiated as either Chironomidae or Dipteran. We used the equations of Hóðar (1996) to estimate biomass for each group of arthropods. To correct for differences in vegetation amount between samples, we weighed all clipped branches and report biomass estimates as milligrams biomass per 100 grams vegetation. Finally, because the study area was relatively unique in its abundance of early spring midges (Diptera: Chironomidae) due to proximity of Lake Huron (Dallman and Smith 1995, Ewert and Hamas 1995, Smith et al. 1998), we report results of arthropod sampling performed inland, away from the influence of the lake. Inland arthropod data are more representative of what migrants encounter as they move through inland forested habitat during spring migration. The definition of inland followed that of Ewert and Hamas (1995), where inland habitats were greater than 0.4 km from Lake Huron. We controlled for differences in vegetation by sampling in areas that had previously been demonstrated similar in vegetation composition to the shoreline site (Smith and Moore unpubl. data).

Weather at the breeding grounds can influence arrival timing (Møller 1994a, b) and possibly arrival condition, so we included weather data collected either at the study site or from a nearby weather station (Mackinac Bridge – approx. 11 km west of the study site). Further, we tracked spring progression by scoring quaking aspen leaf development using the methodology of Ewert and Hamas (unpubl. data). Leaf development was assessed by randomly selecting ten trees every 3 to 4 days during the leaf-out period. We subjectively classified each tree into 1 of the following categories: (1) leaves in bud

(2) leaves emerging from bud and bud scales shed (3) leaves unfurled but not fully expanded (4) leaves fully expanded. Categories were assigned to each tree based on the stage most leaves were in. To remove among-observer bias, the same person (RJS) collected these data in all years.

Data were analyzed using SPSS 9.0 (Spss 1998). Distributions of relevant variables were examined for departures from normality and non-parametric statistics used when transformations did not bring data into compliance with parametric testing assumptions (Siegel and Castellan 1988, Zar 1996). We used a chi-square test to check for year-to-year differences in number of precipitation events and a General Linear Model (GLM) to assess yearly variation in amount of precipitation. We examined yearly variation in arthropod biomass using a GLM on natural log transformed data followed by Tukey *post hoc* comparisons. We assessed yearly variation in arrival date using Kruskal-Wallis ANOVA followed by Dunn's *post hoc* tests (Zar 1996). We made within year sex comparisons of arrival date using Mann-Whitney tests. Because fat score was not normal, we ran General Linear Models on ranks to make multifactorial comparisons (Zar 1996), and Kruskal-Wallis ANOVA followed by Dunn's *post hoc* tests to assess yearly variation in arrival fat (Zar 1996). We used parametric correlations to explore relationships between date, invertebrate abundance, and mean daily temperature. We calculated Kendall partial rank-order correlations, a nonparametric method that removes the effect of a third variable on the relation between the variables of interest (Siegel and Castellan 1988), to examine relationships between arrival fat and arrival date, controlling for year.

Results

Environmental conditions during arrival

Environmental conditions improved through the course of the redstart arrival period regardless of year. Average daily temperatures increased ($r_p = 0.138$, $n = 10571$, $P < 0.001$) and insect biomass increased ($r_p = 0.156$, $n = 214$, $P = 0.023$) with the passage of spring. Birds arriving later in Michigan experienced moderating temperatures and increasing food.

Environmental conditions varied from year-to-year. For instance, quaking aspen was leafed-out by 15 May (Julian day 135) in 4 of the 5 years. However, in 1997 completion of leaf-out was delayed by approximately 20 days (Fig. 1). During this same year approximately 60% of all days during the arrival period (1 May through 12 June) had average daily temperatures less than 10°C (Fig. 1). Environmental conditions in 1997 were poor relative to all other years of this study. There was not, however, any difference in the number of precipitation

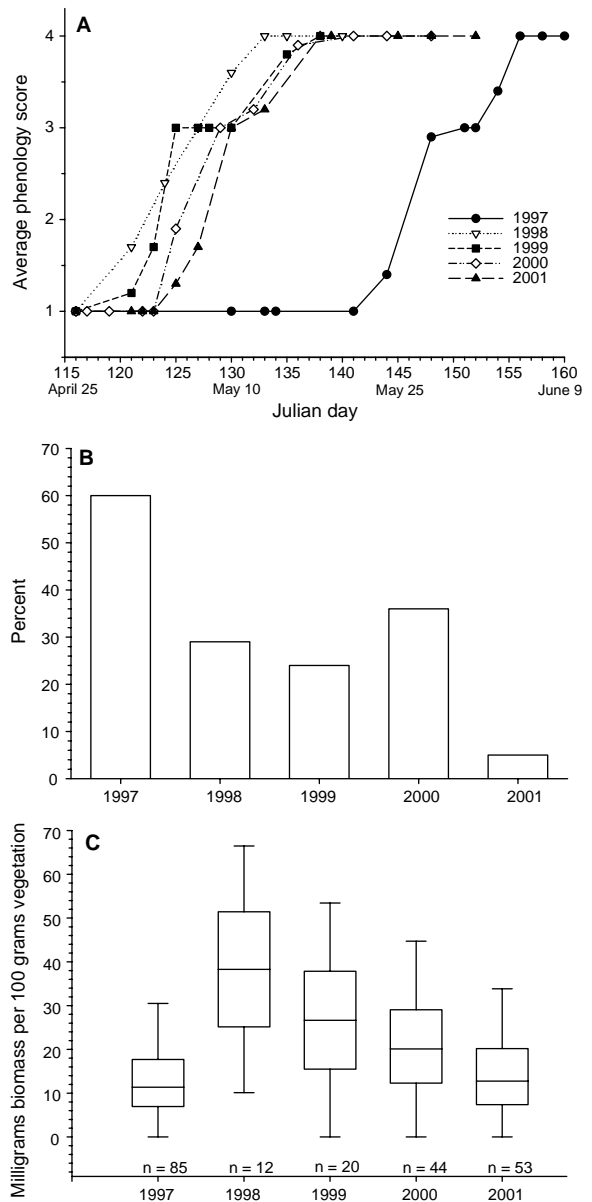


Fig. 1. Yearly variation in environmental conditions during the arrival of American redstarts at Pontchartrain Shores, Michigan. Graph A tracks the onset of spring by assessing progression of leaf development in Quaking Aspen. Phenological scores are an average of subjectively scoring 10 trees during each sampling period. The symbols mark days when sampling occurred. Graph B indicates the percentage of days with average daily temperature less than 10°C during the period from 1 May through 1 June. Graph C represents yearly biomass estimates of inland arthropods for the month of May. Solid line represents mean, box ± 1 SE and whiskers ± 1 SD.

events between years during May ($\chi^2 = 9.195$, $df = 12$, $P = 0.686$) nor was there any difference in the amount of total precipitation between years ($F_{4, 29} = 1.958$, $P = 0.132$).

The delayed leaf-out and colder temperatures in 1997 were reflected in arthropod biomass estimates from May. Average abundance of all arthropods was less in 1997 than other years except 2001 (Fig. 1). There were yearly differences in total arthropod biomass ($F_{4,209} = 6.501$, $P < 0.001$) with 1997 having significantly less biomass than 1998 ($P < 0.001$), 1999 ($P = 0.045$), and 2000 ($P = 0.040$). Further, arriving birds found more food available in 1998 than 2001 ($P = 0.009$). Arriving redstarts in 1997 encountered both cold weather and depressed prey conditions while birds arriving in 1998 encountered perhaps the most favorable environmental conditions during the entire study period (1997–2001). During 1998 ambient air temperatures were benign, there was a slight advancement in leaf-out of aspen and food was relatively abundant (Fig. 1).

Arrival timing

Arrival timing of confirmed breeders varied significantly by year ($\chi^2 = 21.428$, $df = 4$, $n = 440$, $P < 0.001$). Average arrival date was later in 1997 relative to other years, though multiple comparisons tests only revealed significant differences when comparing arrival date in 1997 vs 1998 ($P = 0.008$), and 1997 vs 2000 ($P = 0.045$). Further, average arrival day for breeding individuals was earlier in 1998 than all other years. Multiple comparisons tests indicated significant differences between 1997 vs 1998 ($P = 0.008$), 1998 vs 1999 ($P = 0.010$), and 1998 vs 2001 ($P \leq 0.001$). Birds also arrived significantly earlier in 2000 vs 2001 ($P = 0.010$). We found no difference by sex in arrival timing for verified breeding redstarts (Table 1).

Arrival timing of birds classified as migrants also varied significantly by year ($\chi^2 = 54.815$, $df = 4$, $n = 678$, $P < 0.001$; Table 1). Birds classified as migrants arrived significantly later in 1997 than in all other years (all $P < 0.035$) and significantly earlier in 1998 than all other

years (all $P < 0.004$). Arrival in 1999 was also significantly later than in 2000 and 2001 ($P \leq 0.005$). While there was no sex difference in arrival timing in 1997, males preceded females in all other years (Table 1).

Arrival fat

Both sexes, on average, arrived at the breeding grounds with fat (Table 2). There was no effect of male age on arrival fat (Breeder: $Z = 0.204$, $n = 300$, $P = 0.838$; Migrants: $Z = 0.204$, $n = 409$, $P = 0.301$). Of those individuals verified as breeders, 51% of males and 62% of females arrived with visible fat stores (Table 2). Binomial tests indicated no difference between males arriving with or without fat ($P = 0.796$) whereas significantly more females arrived with fat than without ($P < 0.001$). Females arrived at the breeding grounds with more fat than males ($F_{1,296} = 22.828$, $P < 0.001$) and arrival fat varied significantly among years ($F_{3,296} = 36.570$, $P < 0.001$). There was no sex by year interaction ($F_{3,296} = 1.574$, $P = 0.196$). Females arrived with significantly more fat than males in 1999 and 2000, with the relationship approaching significance in 2001 (Fig. 2).

Arrival fat varied significantly among years for both breeding females ($\chi^2 = 19.237$, $df = 3$, $P < 0.001$), and breeding males ($\chi^2 = 27.510$, $df = 3$, $P < 0.001$; Fig. 2). Female fat stores differed in 1998 from 1999 ($P < 0.001$), 2000 ($P < 0.05$), and 2001 ($P < 0.001$; Fig. 2). Males arrived with more fat in 1998 than 1999 ($P < 0.001$), 2000 ($P < 0.001$) and 2001 ($P < 0.001$; Fig. 2).

We computed non-parametric partial correlations between arrival date and arrival fat stores, controlling for year. There was a negative relationship between arrival date and arrival fat in breeding males (Kendall's partial $T = -3.786$, $n = 239$, $P < 0.001$), but no relationship in breeding females (Kendall's partial $T = 0.786$, $n = 173$, $P = 0.422$). To account for possible age effects

Table 1. Average arrival dates¹ for American redstarts known to have bred within our study area and those individuals not resighted during the breeding season.

Year		Breeders	SE	N	Z	P	Migrants	SE	N	Z	P
1997	Overall	148.77	1.36	13			147.85	0.32	40		
	Male	149.63	2.20	8			148.07	1.12	26		
	Female	147.40	0.51	5	-0.223	0.833	147.85	1.22	14	-0.564	0.585
1998	Overall	143.68	0.67	123			141.70	0.53	126		
	Male	141.60	1.01	73			140.58	0.86	62		
	Female	143.14	0.85	50	-0.753	0.451	142.78	0.61	64	-3.125	0.002
1999	Overall	145.78	0.75	122			145.94	0.53	169		
	Male	145.05	1.05	78			143.71	0.90	75		
	Female	147.07	0.89	44	-1.652	0.098	147.71	0.58	94	-4.209	<0.001
2000	Overall	144.21	0.69	82			143.28	0.48	173		
	Male	144.17	0.10	48			141.98	0.74	93		
	Female	144.27	0.89	34	-0.160	0.873	144.81	0.52	80	-3.136	0.002
2001	Overall	147.53	0.96	86			144.10	0.53	168		
	Male	146.45	1.37	53			141.65	0.66	80		
	Female	149.03	1.28	38	-1.218	0.223	146.33	0.75	88	-3.136	0.002

¹Mann-Whitney tests were used to make sex comparisons of arrival day within years.

Table 2. Summary of Field Metabolic Rate (*FMR*) calculations based on first captures for female and male American redstarts breeding at Pontchartrain Shores, Michigan 1997–2001. Fat-free body mass¹ estimates are from Odum (1993).

Fat score	N	Percent of total captures	Average body mass (g) ± SE	Average arrival fat (g)	Average FMR (kJ/day)	Average energy from fat (kJ)	Average fast time (h)	Percent reduction in foraging	
								1 Day	4 Days
Female									
0	58	38	7.46 ± 0.07	1.11	38.22	41.83	26.27	109	27
1	44	29	7.44 ± 0.05	1.10	38.15	41.50	26.11	109	27
2	51	33	7.98 ± 0.11	1.60	40.04	60.30	36.14	151	38
3	6	4	8.23 ± 0.46	1.84	40.90	69.34	40.69	170	43
Overall	154		7.66 ± 0.05	1.30	40.90	49.00	28.75	120	30
Male									
0	116	50	7.75 ± 0.03	1.11	39.24	41.83	25.59	105	26
1	50	22	7.84 ± 0.05	1.20	39.55	45.22	27.44	114	29
2	56	24	8.06 ± 0.06	1.41	40.32	53.13	31.63	135	34
3	8	4	8.16 ± 0.11	1.52	41.66	57.28	33.00	160	40
Overall	231		7.86 ± 0.03	1.22	39.62	45.97	27.85	116	29

¹Odum (1993) provides a compilation of avian body mass and composition collected mostly from birds killed during spring and fall migration at a television tower located in Leon County, Florida. Briefly, (see Odum 1993 for details) specimens were sexed by plumage or gonadal inspection and aged via degree of skull ossification. Specimens were weighed, dried, pulverized, and the fat extracted using petroleum ether. Fat-free mass was calculated as the difference between wet mass and extracted fat mass. We calculated *FMR* using average body mass for each category of birds captured in Michigan and estimated average arrival fat by subtracting Odum's fat-free estimates from these masses (see text for details).

we ran partial correlations between arrival date and fat stores within male age class. There continued to be significant associations between fat stores and arrival date in SY males ($T_K = -2.664$, $n = 165$, $P = 0.008$), and ASY males ($T_K = -2.110$, $n = 101$, $P = 0.035$).

For redstarts classified as migrants, 52% of males and 60% of females arrived with visible fat stores. Binomial tests indicated no difference between males arriving with or without fat ($P = 0.551$) whereas significantly more females arrived with fat than without ($P < 0.001$). There was no effect of male age on arrival fat ($F_{1,275} = 0.492$, $P = 0.483$) although a male age-by-year interaction was significant ($F_{4,275} = 3.938$, $P = 0.004$). Migrant females arrived with more fat than migrant males ($F_{1,616} = 15.467$, $P < 0.001$), and arrival fat varied significantly among years ($F_{4,616} = 27.064$, $P < 0.001$). There was no sex-by-year interaction ($F_{4,616} = 1.415$, $P = 0.227$). Females arrived with significantly more fat than males in 1997, 1999 and 2000 (Fig. 2). Arrival fat varied significantly among years for both migrant females ($\chi^2 = 36.147$, $df = 4$, $P < 0.001$), and migrant males ($\chi^2 = 16.026$, $df = 4$, $P = 0.003$; Fig. 2). Dunn's *post hoc* tests indicated that females arrived with more fat in 1997 compared with other years (all $P < 0.001$) except 1998 ($P < 0.10$) and more fat in 1998 than in 1999, 2000 or 2001 (all $P < 0.02$; Fig. 2). Males arrived with more fat in 1997 than in 1999 ($P < 0.05$), with the difference between 1997 and 2000 approaching significance ($P < 0.1$). Males arrived with more fat in 1998 than in 1999, 2000 and 2001 (all $P < 0.001$; Fig. 2).

In evaluating that relationship between arrival date and arrival fat stores, controlling for year, we found a negative relationship between arrival date and arrival fat in migrant males ($T_K = -2.998$, $n = 340$, $P = 0.003$) and

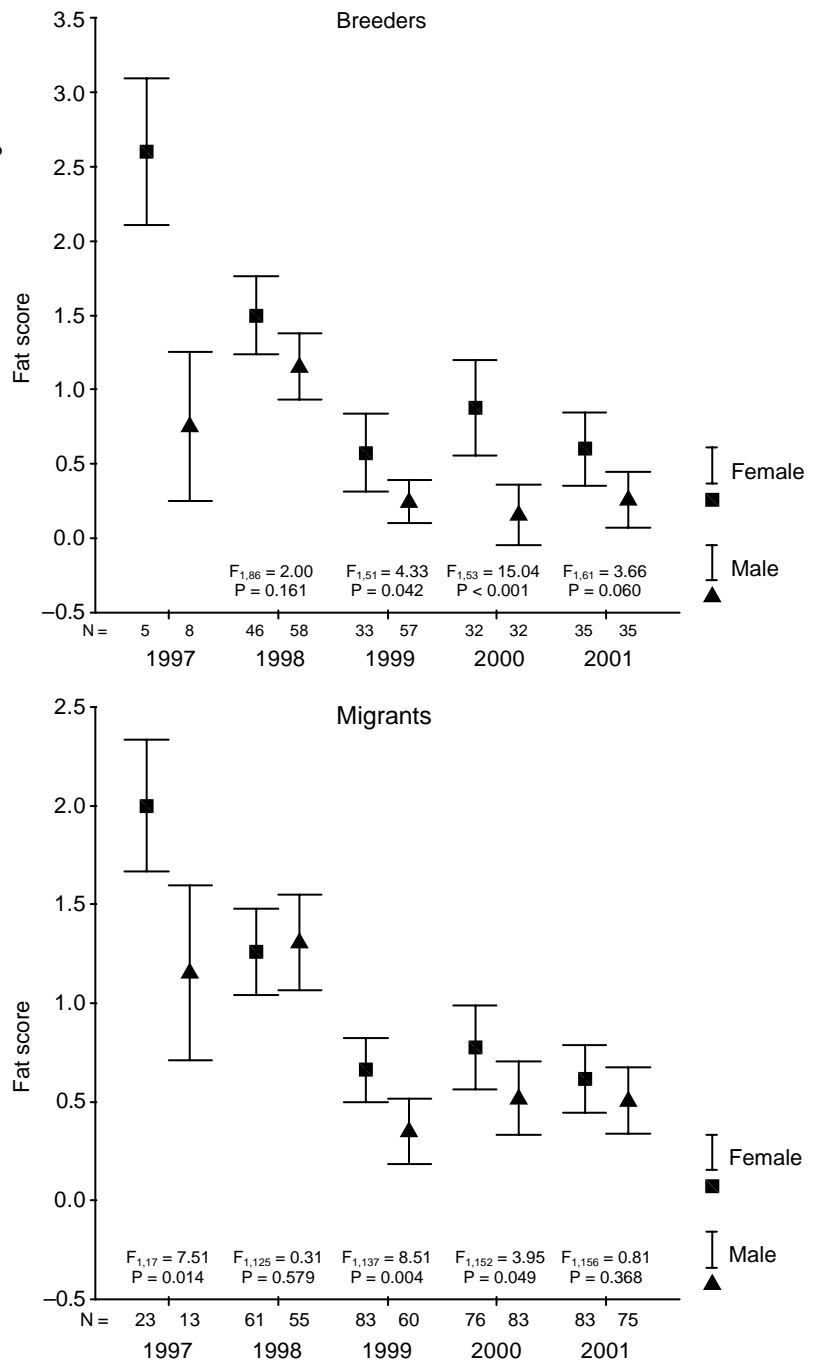
in migrant females ($T_K = -4.427$, $n = 349$, $P < 0.001$). Examination of males by age revealed no relationship between arrival day and fat stores in ASY males ($T_K = -1.435$, $n = 115$, $P = 0.150$) though early arriving SY males carried more visible fat stores ($T_K = -2.537$, $n = 224$, $P = 0.011$). The sex-related and yearly variation in migrant redstart arrival fat stores paralleled what was found in redstarts that bred within the study area.

It is important to point out the limitations of our breeding/migrant categorization. While we are confident in our classification of breeding redstarts, we cannot rule out the possibility that an individual classified as a migrant simply passed through and terminated migration within close proximity to our study area. Our reason for including migrants (unverified breeders) in our analyses was to gain added insight into the influence of environment on arrival condition, especially in 1997 when, for logistical reasons, we were only able to capture a small number of verified breeders. We point out that we are not making comparisons between groups, rather that we analyzed migrants in hopes of reinforcing our findings with breeding birds. Our results indicate that timing of arrival in both groups varied between years in a similar manner and migrants generally patterned breeders in variation of visible fat stores.

Discussion

American redstarts arrived at their breeding grounds in Michigan's eastern Upper Peninsula with fat stores sufficient to have allowed continued migration of greater than 1000 km. Further, estimates of *FMR* suggest that females arrived with enough fat to sustain normal

Fig. 2. Arrival fat score for breeding and migrant American redstarts, Pontchartrain Shores, Michigan. Whiskers encompass ± 1 SE. Due to small sample sizes for breeding individuals in 1997, we did not compute statistics comparing female to male arrival fat.



activity without foraging for 26–41 hours, and males for 26 to 33 hours. Our finding that redstarts arrived with fat stores coincides with the findings of other researchers (Ojanen 1984, Sandberg 1996, Fransson and Jakobsson 1998, Widmer and Biebach 2001), suggesting that the advantages associated with ‘overloading’ (*sensu* Gudmundsson et al. 1991) offset costs of depositing or carrying these fat stores. These costs may include increased susceptibility to predation (Houston et al.

1993, Witter and Cuthill 1993), increased flight costs (Hendenström 1992), or time delays associated with fat deposition (Alerstam and Lindström 1990).

Evidence for the insurance hypothesis

Arrival fat stores were higher in 1997 when birds encountered colder temperatures and lower food

abundance. Our data suggest that birds were carrying more fat in 1997 in response to the relatively poor environmental conditions characteristic of that year. Furthermore, birds delayed arrival during the most unfavorable year, and appeared to advance arrival in the most benign year of the study.

Further evidence in support of the Insurance Hypothesis is found in the negative relationship between arrival day and arrival fat in both age categories of breeding males, first year migrant males and migrant females, which is consistent with Prediction 2. This finding corresponds with a general increase in overall favorableness in environmental conditions with the passage of spring. Early arrivals encountered cooler temperatures and low densities of terrestrial invertebrates. Arrival fat may have provided a mechanism to overcome these poor foraging conditions (Sandberg and Moore 1996). Interestingly, even with the significant year-to-year variation in females that patterned yearly environmental conditions, female arrival fat did not vary significantly through the course of the arrival period. This finding suggests that arrival fat may be important to females for reasons in addition to insurance.

Our findings do not appear confounded by age effects (Widmer and Biebach 2001), at least in males. While older male redstarts did arrive first (Smith 2003), we found no age difference in fat stores for either breeding or migrant males. Further, examination of correlations between arrival day and fat stores within age class indicated negative relationships between arrival day and fat stores for both age categories of breeding males and for SY males categorized as migrants.

Our results do not accord with Prediction 3, namely that males and females arriving at the breeding grounds at the same time should have similar fat stores if arrival fat serves primarily an insurance role. Migrant females arrived with more fat than migrant males in 1997, 1999 and 2000. Breeding females arrived with more fat than breeding males in 1999 and 2000. Finding sex-dependent differences in arrival fat would be consistent with the Insurance Hypothesis if males preceded females such that the two sexes encountered differences in food abundance during passage (Sandberg and Moore 1996). However, examination of all known breeding redstarts revealed no difference in arrival timing by sex. Further, in the one year when migrant males and females did not differ in arrival timing, females carried more fat than males. Finally, if females were fatter by consequence of later passage we would expect a positive relationship between arrival day and arrival fat, which was not the case. There was no relationship between fat and date of first capture in breeding females and there was a negative relationship between arrival day and fat stores in migrant females.

Our data are not entirely consistent with the Insurance Hypothesis. For instance, males and females arrived with

larger fat stores during 1998, the year with the most favorable arrival conditions. If arrival fat were used solely as insurance, we would expect lower levels during this favorable year, especially when considering the negative influence migratory delays may have on territory quality (Francis and Cooke 1986, Francis and Cooke 1990, Aebischer et al. 1996, Lemon et al. 1996, Kokko 1999, Smith 2003). Additionally, we would not expect differences by sex in arrival fat stores when the sexes arrive at the same time (Sandberg and Moore 1996).

Besides insurance against poor environmental conditions, other advantages may accrue to an individual able to arrive with fat (see Sandberg and Moore 1996). Although it is unlikely that female redstarts used some of the added energy as a direct aid in forming eggs, or increasing egg size (Perrins 1970, Meijer and Drent 1999, Klaassen et al. 2001), our data are insufficient to rule out this possibility. It is more likely, however, that arrival fat has indirect effect(s) on reproductive performance. For instance, arriving with fat may provide birds with an advantage during the period immediately following arrival by allowing more time to devote to breeding activities rather than foraging behavior. Our estimates suggest that, when the energy available from arrival fat is apportioned equally over a 4-day period, newly arrived males would have been able to decrease required foraging time by 29% and females by 27%. This time could instead have been dedicated to breeding activities.

Our results suggest that females may derive more benefits from arrival fat than males. Breeding females arrived with more fat than breeding males in 2 of 4 years, and migrant females arrived with more fat than migrant males in 3 of 5 years. These differences may reflect sex-related differences in time budgets or reproductive costs (see Sandberg and Moore 1996).

Evidence presented here points to adaptive advantages in arriving at the breeding grounds with fat stores, and provides insight into how events during one phase of the annual cycle may influence the biology of migratory birds during subsequent phase(s). The fat a migrant carries to the breeding grounds is deposited *en route*. Hence, the ability to locate suitable stopover habitat to rest and refuel not only influences *en route* survival, but also may affect breeding season performance. Individuals that do well *en route* arrive at the breeding grounds in a timely manner and in better condition, both of which may contribute to survival and reproductive success.

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References

- Aebischer, A., Perrin, M., Krieg, M., Studer, J. and Meyer, D. R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. – *J. Avian Biol.* 27: 143–152.
- Alerstam, T. and Lindström, A. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed.). *Bird migration: physiology and ecophysiology*. Springer-Verlag, New York, pp. 331–351.
- Bairlein, F. 1985. Body weights and fat deposition of Palaearctic passerine migrants in the central Sahara. – *Oecologia* 66: 141–146.
- Blem, C. R. 1990. Avian Energy Storage. – In: Power, D. M. (ed.). *Curr. Ornithol.* 7. Plenum Press, New York, pp. 59–113.
- Cooper, R. J. and Whitmore, R. C. 1990. Arthropod sampling methods in ornithology. – *Studies in Avian Biology* 13: 29–37.
- Dallman, M. and Smith, R. J. 1995. Avian predation on Chironomids along the nearshore waters of Lake Huron. – *Mich. Birds Nat. Hist.* 2: 201–204.
- Ewert, D. N. and Hamas, M. J. 1995. Ecology of migratory landbirds during migration in the Midwest. – In: Thompson, F. R. I. (ed.). *Management of Midwestern Landscapes for the Conservation of Neotropical Migratory Birds*, General Technical Report NC-187. North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Detroit, pp. 200–208.
- Francis, C. M. and Cooke, F. 1986. Differential timing of spring migration in wood warblers (Parulinae). – *Auk* 103: 548–556.
- Francis, C. M. and Cooke, F. 1990. Differential timing of spring migration in rose-breasted grosbeaks. – *J. Field Ornithol* 61: 404–412.
- Fransson, T. and Jakobsson, S. 1998. Fat storage in male willow warblers in spring: do residents arrive lean or fat? – *Auk* 115: 759–763.
- Gosler, A. G. and Harper, D. G. C. 2000. Assessing the heritability of body condition in birds: a challenge exemplified by the great tit *Parus major* L. (Aves). – *Biol. J. Linn. Soc.* 71: 103–117.
- Gudmundsson, G. A., Lindström, Å. and Alerstam, T. 1991. Optimal fat loads and long distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba*, and turnstones *Arenaria interpres*. – *Ibis* 133: 140–152.
- Helms, C. W. and Drury, W. H. J. 1960. Winter and migratory weight and fat field studies on some North American buntings. – *Bird-banding* 31: 1–40.
- Hendenström, A. 1992. Flight performance in relation to fuel load in birds. – *J. Theor. Biol.* 158: 535–537.
- Hódar, J. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. – *Acta Ecologica* 17: 421–433.
- Houston, A. I., McNamara, J. M. and Hutchinson, J. M. 1993. General results concerning the trade-off between gaining energy and avoiding predation. – *Phil. Trans. R. Soc. London* 341: 375–397.
- Klaassen, M., Lindström, Å., Møltøfte, H. and Piersma, T. 2001. Arctic waders are not capital breeders. – *Nature* 413: 794.
- Kokko, H. 1999. Competition for early arrival in migratory birds. – *J. Anim. Ecol* 68: 940–950.
- Krementz, D. G. and Pendleton, G. W. 1990. Fat scoring: sources of variability. – *Condor* 92: 500–507.
- Lemon, R. E., Perreault, S. and Lozano, G. A. 1996. Breeding dispersions and site fidelity of American redstarts (*Setophaga ruticilla*). – *Can. J. Zool* 74: 2238–2247.
- Lozano, G. A., Perreault, S. and Lemon, R. E. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. – *J. Avian Biol.* 27: 164–170.
- Meijer, T. and Drent, R. 1999. Re-examination of the capital and income dichotomy in breeding birds. – *Ibis* 141: 399–414.
- Merkle, M. S. and Barclay, R. M. R. 1996. Body mass variation in breeding mountain bluebirds *Sialia currucoides*: evidence of stress or adaptation for flight? – *J. Anim. Ecol* 65: 401–413.
- Møller, A. P. 1994a. Phenotype-dependent arrival time and its consequences in a migratory bird. – *Behav. Ecol. Sociobiol.* 35: 115–122.
- Møller, A. P. 1994b. *Sexual Selection and the barn swallow*. – Oxford University Press, Oxford.
- Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. – *Ecol. Monogr.* 57: 111–128.
- Nolan, V. J. 1978. Ecology and behavior of the prairie warbler, *Dendroica discolor*. – American Ornithologists' Union, Washington, D.C.
- Nystrom, K. G. K. 1997. Food density, song rate, and body condition in territory-establishing willow warblers (*Phylloscopus trochilus*). – *Can. J. Zool* 75: 47–58.
- Odum, E. P. 1993. Body masses and composition of migrant birds in the Eastern United States. – In: Dunning, J. B., Jr. (ed.). *CRC Handbook of Avian Body Masses*. CRC Press, New York, pp. 313–334.
- Ojanen, M. 1984. The relation between spring migration and the onset of breeding in the pied flycatcher *Ficedula hypoleuca* in northern Finland. – *Ann. Zool. Fenn.* 21: 205–208.
- Pennycuik, C. J. 1975. Mechanics of flight. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds). *Avian Biology*. V. Academic Press, New York, pp. 1–73.
- Pennycuik, C. J. 1989. *Bird flight performance: a practical calculation manual*. – Oxford University Press, New York.
- Pennycuik, C. J. 1998. Computer simulation of fat and muscle burn in long-distance bird migration. – *J. Theor. Biol.* 191: 47–61.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. – *Ibis* 112: 242–255.
- Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. – *Ibis* 138: 2–15.
- Pyle, P. 1997. *Identification guide to North American birds*. – Slate Creek Press, Bolinas, California.
- Sandberg, R. 1996. Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. – *Ibis* 138: 514–524.
- Sandberg, R. and Moore, F. R. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. – *Oikos* 77: 577–581.
- Sherry, T. W. and Holmes, R. T. 1997. American redstart (*Setophaga ruticilla*). – In: Poole, A. and Gill, F. (eds). *The Birds of North America*, No. 277. The Acad. Natl. Sci., Philadelphia.
- Siegel, S. and Castellan, N. J., Jr. 1988. *Nonparametric statistics for the behavioral sciences*. – McGraw Hill, Boston.
- Slagsvold, T. 1976. Arrival of birds from spring migration in relation to vegetational development. – *Norwegian Journal of Zoology* 24: 161–173.

- Smith, R., Hamas, M., Dallman, M. and Ewert, D. 1998. Spatial variation in foraging of the black-throated green warbler along the shoreline of northern Lake Huron. – *Condor* 100: 474–484.
- Smith, R. J. 2003. Resources and arrival of landbird migrants at their northerly breeding grounds: linking en route with breeding season events. – PhD. dissertation, The University of Southern Mississippi, Hattiesburg.
- SPSS. 1998. SPSS base 8.0 for Windows User's Guide. – SPSS Inc., Chicago, Illinois, USA.
- Whitmore, R. C., Mosher, J. A. and Frost, H. H. 1977. Spring migrant mortality during unseasonable weather. – *Auk* 94: 778–781.
- Widmer, M. and Biebach, H. 2001. Changes in body condition from spring migration to reproduction in the garden warbler *Sylvia borin*: a comparison of a lowland and a mountain population. – *Ardea* 89: 57–68.
- Williams, J. B., Roy, S. W., Milton, S. J., Adams, N. J., Dean, W. R. J., Du Plessis, M. A. and Jackson, S. 1993. Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. – *Ecology* 74: 390–404.
- Witter, M. S. and Cuthill, I. C. 1993. The ecological costs of avian fat storage. – *Phil. Trans. R. Soc. Lond. B* 340: 73–92.
- Woodrey, M. S. and Moore, F. R. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. – *Auk* 114: 695–707.
- Zar, J. H. 1996. Biostatistical analysis. – Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

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