

Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*

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We tested whether the age-related differences in reproductive success in male American Redstarts are caused by differences in date of arrival on the breeding grounds. By relating arrival date to three measures of reproductive success we determined what stage of the breeding cycle is affected by date of arrival. Adult male redstarts were more successful than subadults at obtaining mates. Adult males were also more likely than subadults to have nests built in their territories, and to fledge young. Among mated males, neither age class was significantly more likely to obtain nests. However, among males that nested, there were significant age-related differences in fledging success. Adult males arrived on the breeding grounds before subadults. Within both age classes, males that mated had arrived significantly earlier than those that did not mate. Similarly, males that nested had arrived significantly earlier than those that did not. There were no significant differences in arrival date between males that fledged young and those that did not. Finally, adult males were more likely to renest after nest failure. Therefore, we conclude that reproductive success in male redstarts is independently affected by both arrival date and age, and that the lower success of subadults may not be a consequence solely of their age and late arrival, but also of their lack of experience in selecting territories early in the breeding season.

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In many birds reproductive success increases with age (e.g., Perrins and Moss 1974, Afton 1984, Smith 1993, Black and Owen 1995, Pugsek 1995). Three general explanations have been proposed to interpret this phenomenon. First, the correlation between age and reproductive success may be a statistical consequence of poor breeders also having lower survivorship (Curio 1983). This explanation is refuted by the finding in several species that individuals increase their reproductive success in successive reproductive bouts (e.g., Pyle et al. 1991, Forslund and Pärt 1995). Second, the restraint hypothesis, based on the theoretical trade-off between current and future reproduction (Williams 1966, Pianka and Parker 1975), predicts that current reproduction is more valuable for older individuals because they have a lower residual reproductive value (Curio 1983). Older individuals are therefore more apt to put greater effort

into reproduction. Finally, the constraint hypothesis argues that younger individuals cannot reproduce as well as older ones because they are at a disadvantage in obtaining breeding opportunities or raising offspring. The two latter hypotheses are not mutually exclusive, and separating them can be difficult because it requires finding out whether younger individuals are unable or unwilling to reproduce as well as older ones.

The restraint hypothesis is based on life-history theory; thereby, age *per se* is used to explain age-related differences in reproductive success. On the other hand the constraint hypothesis predicts that younger individuals are disadvantaged when compared to older individuals at one or several stages of the breeding cycle. Therefore, when testing the constraint hypothesis it is not sufficient to show that younger birds are disadvantaged, but we must also determine the ecological vari-

ables responsible for these differences, and how events earlier in the breeding season affect subsequent events.

In many species of birds older males arrive on the breeding grounds earlier and are more successful breeders than yearling males (e.g., Flood 1984, Francis and Cooke 1986, Hill 1988, Enstrom 1992). Earlier arrival times may lead to greater territory and/or mate availability, earlier breeding, longer available breeding season, greater possibility of reneesting, and other factors that may ultimately affect reproductive success. Therefore, it is seldom clear whether differences in reproductive success are caused by differences in age *per se*, or are a consequence of differences in arrival times.

In this paper we examine this question using male American Redstarts *Setophaga ruticilla*. The American Redstart is a small (10 g) passerine that breeds in North America and winters in the Neotropic. Males in their first potential breeding season (SY or subadult) have a plumage distinct from older (ASY or adult) males. Subadult males arrive on the breeding grounds later than adult males. Females start to arrive at the same time as subadult males, choose mates from among the already-settled males, and build nests (Ficken and Ficken 1967, Francis and Cooke 1986). The distribution of territories with respect to male age is not random. Adult territories are clustered around each other. Subadult territories are also clustered, but in different areas, or are located peripherally to areas containing adult territories (Ficken and Ficken 1967, Howe 1974, Morris and Lemon 1988). Despite these differences, Morris and Lemon (1988) failed to find any differences in the number of offspring fledged between nests attended by adult males and subadult males. In a subsequent analysis, resampling nests of the same males was avoided by randomly selecting a single nest from each male, regardless of year or nesting attempt within a year, and although nests of adults had more eggs, again, they neither hatched nor fledged more young (Lemon et al. 1992). These analyses did not include males that were unable to obtain a territory or a nest.

In this study we extend the analysis to include all banded males. First we examine whether subadults are less successful breeders than adults. Second, we test whether arrival date is associated with male reproductive success. We then establish whether the disadvantage of the subadults is still present once effects of arrival dates are statistically removed. Finally we test whether reproductive success of males is affected by the arrival date *per se*, or merely the number of nesting attempts.

Methods

Data were collected from 1982 to 1989 at St. Andrews, New Brunswick, Canada (45°05'N, 67°04'W). The

study area is described in detail by Morris and Lemon (1988). Data from 1985 and 1986 were excluded because censuses were not performed throughout the entire breeding season. The study area was surveyed daily during the breeding seasons and searched thoroughly for nests. All the nests found were checked daily in 1982, 1983 and 1984, and at least once every three days in the other years.

After a territory was established, it was surveyed at least once every three days. Some males had been banded in previous years; the others were usually banded within a few days, and aged according to their plumage. Arrival dates were estimated in two ways. Some males had not been seen before they were trapped; for these, banding date was used as an estimate of arrival date. For other males the day of territory establishment was used as the arrival date. While unbanded, these males were identified by their location, plumage and song characteristics. Birds were captured using mist nets and each bird was banded with a standard USFWS aluminium band and three coloured plastic bands.

Three categorical measures of reproductive success were used. First, a male was scored as "mated" if a female was seen in his territory. The presence of a female in a territory is a purely operational measure of the male's ability to attract a potential mate. It is also possible that more than one female was seen in a particular territory, or that the same female was seen in several territories. Second, a male was scored as having "nested" if a female was observed building a nest and at least the beginnings of a nest were found on his territory. This measure does not imply that the nest was completed, eggs were laid, or young fledged, and it should not be confused with the commonly used term "nesting success". The measure simply indicates a decision by a female to attempt to breed with a male. Eleven percent of males that fledged young did so without the nests being found, but these males were accredited with a nest nonetheless. Finally, the third categorical measure of reproductive success was whether a pair fledged any young, regardless of the number of young fledged.

Age-related differences in reproductive success were tested by constructing 2×2 contingency tables (success vs. male age) for each of the three estimates of reproductive success. For $n \leq 20$ Fisher's exact tests were used. For n between 20 and 40, χ^2 tests were used if all expected frequencies were 5 or more, and Fisher's exact tests if any expected frequency was less than 5. For $n \geq 40$ χ^2 tests corrected for continuity were used (Cochran 1954, Fienberg 1977, Siegel and Castellan 1989).

Fledging young requires a nest, which, in turn, requires having obtained a mate. Therefore, the data were analyzed in two ways. First, all individuals were included. Then, comparisons of fledging success were also

Table 1. Reproductive success versus age of male American Redstarts. Three estimates of reproductive success were used, and each was analyzed separately using continuity-adjusted χ^2 tests of 2×2 contingency tables, by year first, and then using totals (expected frequencies in parentheses).

Year		Subadult		Adult		χ^2	p
		Yes	No	Yes	No		
1982	Mated	19 (25)	16 (10)	43 (36)	7 (14)	8.95	0.003
	Nested	17 (22)	18 (13)	37 (32)	13 (18)	4.70	0.030
	Fledged	6 (11)	29 (24)	20 (15)	30 (35)	4.05	0.044
1983	Mated	5 (7)	15 (13)	38 (30)	8 (16)	17.9	0.000
	Nested	5 (9)	15 (11)	24 (20)	22 (26)	3.15	0.076
	Fledged	3 (4)	17 (16)	11 (10)	35 (36)	0.24	0.627
1984	Mated	14 (16)	9 (7)	39 (37)	12 (14)	1.21	0.272
	Nested	13 (13)	10 (10)	28 (28)	23 (23)	0.00	1.000
	Fledged	2 (5)	21 (18)	15 (12)	36 (39)	2.76	0.096
1987	Mated	6 (12)	11 (5)	26 (20)	2 (8)	14.4	0.000
	Nested	2 (6)	15 (11)	14 (10)	14 (18)	5.18	0.023
	Fledged	1 (2)	16 (15)	5 (4)	23 (24)	0.48	0.488
1988	Mated	12 (16)	9 (5)	20 (16)	0 (4)	0.65	0.003
	Nested	10 (12)	11 (9)	7 (11)	13 (9)	1.59	0.420
	Fledged	2 (4)	19 (17)	6 (4)	14 (16)	46.6	0.208
Total	Mated	56 (83)	60 (33)	166 (139)	29 (56)	9.75	0.000
	Nested	47 (61)	69 (55)	116 (102)	79 (93)	11.2	0.002
	Fledged	14 (26)	102 (90)	57 (44)	138 (150)	8.95	0.001

carried out with data only from those individuals that had obtained a nest, and, similarly, the number of males that nested was examined only among those individuals that had obtained a mate.

Differences in arrival date were tested using Type III sums of squares, unbalanced ANOVAs. Interaction effects were tested for and removed from the model if not significant. All tests were considered significant at $p \leq 0.05$.

Results

Success by age class

In 4 out of 5 years, adult males were significantly more successful than subadults at obtaining mates (Table 1). The results are highly significant when data from all years are pooled. In terms of obtaining a nest and fledging success, the results are not as conclusive in the yearly comparisons, but tests using pooled data also show that adult males were significantly more successful than subadults (Table 1).

However, among males that had mated, there were no significant differences between age classes in the number that nested, neither in yearly comparisons nor using pooled data (Table 2). Among males that nested, adult males were significantly more successful at fledging young overall. In yearly comparisons the pattern was the same 4 out of 5 years but only once was the difference significant, probably because the sample sizes were limited (Table 2).

Arrival date and male fitness

Adult males arrived several days before subadults in all years (Fig. 1). The differences in arrival date by age and year were highly significant (2×5 ANOVA, $F_{1,304} = 119.2$, $p = 0.0001$, and $F_{4,304} = 6.1$, $p = 0.0001$ respectively).

To remove the variance in arrival date due to yearly differences a one-way ANOVA of arrival date versus year was carried out ($F_{4,305} = 3.42$, $p = 0.0094$), and the residuals of this analysis were used in subsequent tests. For both age classes, males that subsequently mated had arrived earlier than those that did not (2×2 ANOVA, Mated $F_{1,307} = 37.88$, $p = 0.0001$; Age $F_{1,307} = 65.90$, $p = 0.0001$) (Fig. 2). Males that nested also had arrived earlier than those that did not (2×2 ANOVA, Nested $F_{1,307} = 17.68$, $p = 0.0001$; Age $F_{1,307} = 103.48$, $p = 0.0001$) (Fig. 2). The pattern was the same for males that fledged offspring, but the difference was not significant (2×2 ANOVA, Fledged $F_{1,307} = 2.41$, $p = 0.1217$; Age $F_{1,307} = 107.09$, $p = 0.0001$) (Fig. 2). Older males always arrived significantly earlier than subadults, regardless of reproductive success.

Subsequently we used pairs of males (one SY and one ASY) with the same arrival dates to test whether adult males had greater success than subadults. Because of the difficulty in finding such pairs, data had to be pooled across all years. Out of 37 such pairs, older males were more successful at attracting a female 11 times and less successful 3 times, with 23 ties (Wilcoxon matched-pairs signed-ranks test, one-tailed $p = 0.0299$). There were no significant age-related differences in the number of

Table 2. Reproductive success versus age of male American Redstarts. In these analyses, only those males that had mated were considered when counting those that nested, and, similarly, only those males that had nested were considered when counting those that had fledged offspring. Depending on the sample size and distribution, continuity-adjusted χ^2 or Fisher's exact tests were used (see methods).

Year		Subadult		Adult		Test	p
		Yes	No	Yes	No		
1982	Nested	17 (17)	2 (2)	37 (37)	6 (6)	$\chi^2 = 0.00$	1.00
	Fledged	6 (8)	11 (9)	20 (18)	17 (19)	$\chi^2 = 0.98$	0.32
1983	Nested	5 (3)	0 (2)	24 (26)	14 (12)	$\chi^2 = 1.31$	0.25
	Fledged	3 (2)	2 (3)	11 (12)	13 (12)	Fisher's	0.65
1984	Nested	13 (11)	1 (3)	28 (30)	11 (9)	$\chi^2 = 1.55$	0.21
	Fledged	2 (5)	11 (8)	15 (12)	13 (16)	$\chi^2 = 3.88$	0.05
1987	Nested	2 (3)	4 (3)	14 (13)	12 (13)	Fisher's	0.65
	Fledged	1 (1)	1 (1)	5 (5)	9 (9)	Fisher's	1.00
1988	Nested	10 (9)	2 (3)	13 (14)	7 (6)	Fisher's	0.42
	Fledged	2 (3)	8 (7)	6 (5)	7 (8)	Fisher's	0.38
Total	Nested	47 (41)	9 (15)	116 (122)	50 (44)	$\chi^2 = 3.55$	0.06
	Fledged	14 (20)	33 (27)	57 (51)	59 (65)	$\chi^2 = 4.34$	0.04

males that nested (13 cases ASY > SY, 9 cases ASY < SY, and 15 ties, one-tailed $p = 0.2618$). However, older males had greater fledging success (7 cases ASY > SY, 1 case ASY < SY, and 29 ties, one-tailed $p = 0.0293$).

Effect of multiple nestings

The two previous results show that adult males were more successful than subadults in terms of all three measures. However, when only those males that had obtained a female were considered, there were no significant age-related differences in the number that nested. These analyses, however, do not consider re-nesting attempts. Adult males had more nesting attempts in all years, although the difference was significant only in 1982 (Table 3).

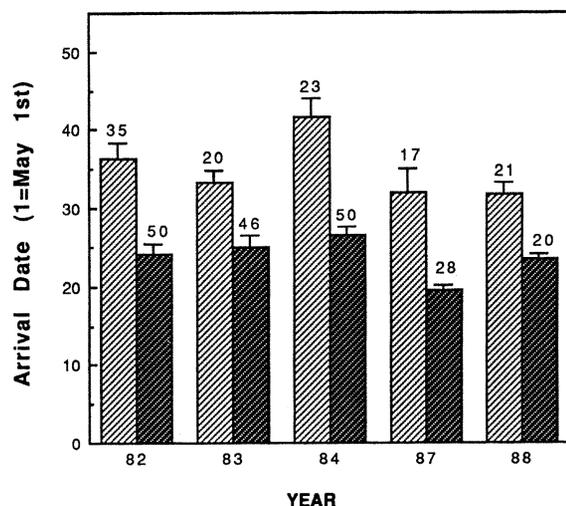


Fig. 1. Male arrival dates by age. Means and standard errors. Dark bars = adults, light bars = subadults. The numbers above the bars represent sample sizes.

Discussion

Age and reproductive success

Our results confirm the findings of Morris and Lemon (1988), who showed that adult male American Redstarts are more successful than subadults at obtaining mates. Females were more likely to build nests in the territories of adult males than in the territories of subadults. Finally, the fledging success of adults was greater than that of subadults.

When considering only males that had mated, we failed to find age-related differences in the likelihood of obtaining a nest. This shows that once a female has chosen a male, nest building will likely follow, regardless of the age of the male. However, among males that nested, older males had greater fledging success than subadults, which shows that the greater fledging success of adult males is not just the result of their greater ability to attract females. The mates of adult males were more likely to re-nest after a failed nesting attempt. Therefore, adult males were more successful than subadults partially because of their earlier arrival on the breeding grounds, which led to a longer available breeding season.

Arrival date and reproductive success

In male redstarts, earlier arrival improved the prospects of successful breeding for both age classes. Males that arrived late were less likely to find mates and, consequently, to have a nest. Males that fledged offspring had arrived earlier than those that did not, but the effect was not significant. These effects of arrival date on male reproductive success are independent of male age.

Earlier arrivals not only have a longer breeding season available, but also obtain the best territories;

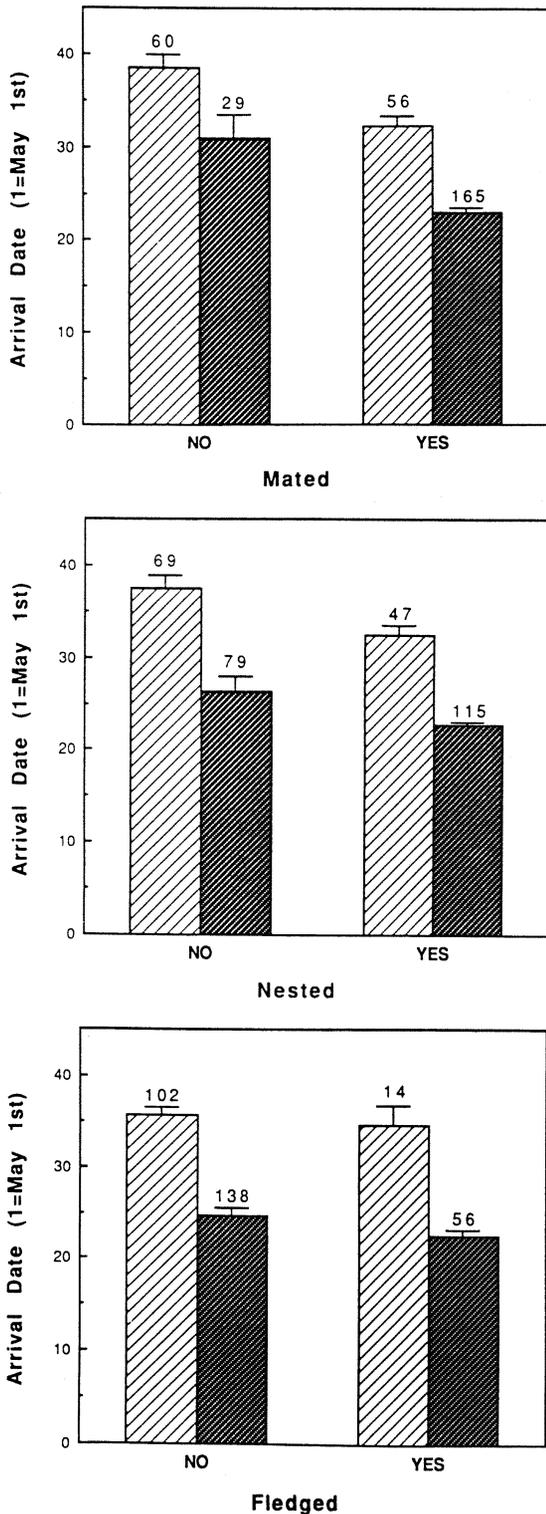


Fig. 2. Arrival date versus age and reproductive success of male American redstarts. Success is measured in terms of having "mated" (top), "nested" (middle), and "fledged" young (bottom). Means and standard errors. Dark bars = adults, light bars = subadults. The numbers above the bars represent sample sizes.

late arrivals have to settle in suboptimal territories (e.g., Wooller and Coulson, 1977, Newton 1986) or may even remain as floaters. Redstarts are occasionally polyterritorial (Secunda and Sherry 1991). Given that polyterritorial males must obtain and defend two non-contiguous territories, arriving before all territories are occupied probably facilitates polyterritoriality. If arrival date is negatively correlated with condition in redstarts, as it is in other species (e.g., Arvidsson and Neergaard 1991, Lozano 1994, Andersson and Gustafsson 1995), early arrivals may also obtain the best mates, which would lead to positive assortative mating. Also, earlier breeders often have larger clutches (e.g., Erikstad et al. 1985, Murphy 1986, Perrins and McCleery 1989). Although the effects of arrival date and age are not easy to separate, the benefits of early arrival are clearly manifold.

The benefits of early arrival must be weighed against the costs. One immediate cost is the increased risk of dying due to exposure to cold weather early in the breeding season (Anderson 1965, Whitmore et al. 1977). The negative effects of cold weather and the risk of predation are increased by the lack of food and shelter early in the spring. Several studies indicate that birds that arrive earlier are older or in better condition than later arrivals (e.g., Arvidsson and Neergaard 1991, Stolt and Fransson 1995). In redstarts, even in the absence of age-related differences in condition, the benefits of an early arrival may be greater for adult than for subadult males.

Redstarts start arriving on the breeding grounds before any foliage has emerged, at a time when it is likely difficult to predict the quality of a territory two or three weeks later. Whereas returning males may use their prior knowledge of the area to select territories, individuals new to the region would not benefit from arriving before any foliage has emerged, as they would be unable to assess territory quality. Males new to the area could delay their arrival until territory quality can be properly assessed. However, they may not need to delay their arrival so long, for they could use the presence of conspecifics as an indirect measure of territory quality (Stamps 1987), and establish themselves in areas adjacent to those occupied by already-settled males.

This idea is similar to that of "local experience", commonly used to attempt to explain age-related philopatry (Hinde 1956, Greenwood 1980). However, here we are suggesting that local experience also increases the benefits of an early arrival. In this case, males new to the area, usually but not necessarily subadults, would be at an even greater disadvantage. Our data show that both age and arrival date affect breeding success. Unfortunately, our data set is not sufficiently large or detailed to compare the arrival dates and subsequent breeding success of individuals with similar local experience.

Table 3. Number of nesting attempts by females of subadult and adult males by year at St Andrews, New Brunswick. Fisher's exact tests were used for the yearly comparisons and a continuity adjusted χ^2 test for the totals.

Year	Subadult		Adult		p
	1	≥2	1	≥2	
1982	17	0	16	22	<0.001
1983	6	0	21	3	1.000
1984	8	5	12	16	0.330
1987	2	0	11	3	1.000
1988	8	2	8	5	0.410
Total	41	7	68	49	0.001

The reproductive disadvantage of subadult redstarts may go beyond arriving late and having to settle on suboptimal territories. A plethora of parentage studies has shown that younger males are more likely than older males to be the victims of cuckoldry (e.g., Westneat 1987, Sherman and Morton 1988, Gowaty and Bridges 1991). When the risk of mortality during migration is also considered, there seems little incentive for yearling males to attempt to breed. However, the disadvantage of subadult males may not be because of their age, but rather because of their lack of familiarity with the breeding area. If this is the case, the trip to the breeding grounds by subadults can be viewed as prerequisite to breeding as adults, an investment in the future.

The constraint hypothesis states that young individuals reproduce poorly because they are at a disadvantage in obtaining breeding opportunities. Our data support this hypothesis, but determining exactly how subadults are disadvantaged will be more difficult. Both arrival time and age affect reproductive success. However, the benefits of arriving early may depend on local familiarity, which is correlated with age. Similarly, the effects of age may be due to breeding experience and local familiarity. Separating the effects of age, breeding experience, and local familiarity will prove to be a difficult task (Forslund and Pärt 1995).

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