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Arrival fat and reproductive performance in a long-distance passerine migrant

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Abstract Long-distance passerine migrants deposit substantial fat stores to fuel their migratory journey. Many of those migratory birds arrive at their northerly breeding grounds with larger fat stores than were necessary to reach their breeding area. Both male and female American Redstarts (*Setophaga ruticilla*) arrived to breed in Michigan's Upper Peninsula with fat, and females arrived with more fat than males in 2 out of 3 years. We test the hypothesis that migrants arriving at the breeding grounds with more body fat have higher reproductive success than birds arriving with little or no fat. Females, and to a lesser extent males, that arrive with fat experience gains in reproductive performance as evidenced by increased clutch size, egg volume, and nestling mass. The results have implications for understanding how events occurring during one phase of the annual cycle influence survival and/or reproductive performance in subsequent phases.

Keywords American Redstart · Arrival fat · Landbird migrant · Migration · Reproductive performance

Introduction

Migration is a period of exceptional energy demand (Blem 1980). To fuel this demand, birds deposit fat stores, which may reach 50% of total body mass among intercontinental migrants (e.g., Bairlein 1985; Biebach et al. 1986; Moore and Kerlinger 1987). Whereas adequate fat stores are critical to a successful migration, migrants that arrive on breeding grounds with fat stores to spare may be better able to meet exigencies that arise during the onset of the breeding season and to 'offset' time constraints associated with breeding at boreal latitudes (see Sandberg and Moore 1996).

It is well established that the pre-breeding nutritional condition of parents affects reproductive success (Drent and Daan 1980; Price et al. 1988; Rowe et al. 1994). Such an effect is most dramatic among some waterfowl that breed at boreal latitudes and rely on endogenous stores to produce a full clutch of eggs (e.g., Ankney and MacInnes 1978; McLandress and Raveling 1981). Although it is unlikely that a small songbird migrant could accumulate energy stores sufficient to produce a complete clutch of eggs (Perrins 1970), experiments in which food has been supplemented prior to egg laying provide compelling evidence that parental condition influences clutch size and laying date in passerines (reviews in Davies and Lundberg 1985; Arcese and Smith 1988; Daan et al. 1988). Arriving with fat may be directly advantageous if these stores are used to offset even a part of the energy expenditure of egg production (but see Winkler and Allen 1996; Klaassen et al. 2001), or indirectly advantageous if arrival fat improves reproductive performance in ways not related to formation of gametes directly from fat deposits. Indirect advantages (see Sandberg and Moore 1996) include better ability to offset time constraints, evidenced by accelerating the start of reproduction (time constraint hypothesis); fat stores used to sustain an individual when environmental conditions on arrival at the breeding grounds are poor (insurance hypothesis); and fat stores acting to buffer time budgets in relation to accumulation of limiting nutrients specific to the breeding process (foraging shift hypothesis). Hence, the availability of resources in the form of endogenous fat stores acquired during passage should improve parental condition and influence reproductive success among landbird migrants.

Despite the intuitive appeal of the latter argument, empirical support is lacking. King et al. (1963) speculated that substantial lipid accumulation for spring migration in the White-crowned Sparrow (*Zonotrichia leucophrys gambelli*) represented an adaptation for a quicker migration and for confronting inclement weather on the breeding grounds. The arrival of female Pied Flycatchers (*Ficedula hypoleuca*) on breeding grounds in northern Finland with fat stores estimated at 14% body mass

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prompted Ojanen (1984) to suggest that “[A]rriving with plenty of reserves thus assists with energy requirements for competition over nest-holes and for a rapid onset of breeding activities.” Later, Sandberg (1996) reported that Pied Flycatchers, Bluethroats (*Luscinia svecica*), and Willow Warblers (*Phylloscopus trochilus*), three intercontinental landbird migrants, arrived on their breeding grounds in northern Sweden with varying amounts of fat (see also Fransson and Jakobsson 1998). Møller (1994) reported that male Barn Swallows (*Hirundo rustica*) with larger energy stores were better able to capture food or sustain periods of food shortage during times of adverse weather in early spring. Romero et al. (1997) found that both male and female Redpolls (*Carduelis flammea*) arrived at their northerly breeding grounds in Alaska with fat stores, which may have allowed for rapid onset of breeding.

We report on reproductive performance of male and female American Redstarts (*Setophaga ruticilla*) that arrive to breed along the north shore of Lake Huron in Michigan’s eastern Upper Peninsula with varying fat loads, and test predictions advanced by Sandberg and Moore (1996), who proposed reproductive advantages for those individuals arriving at the breeding grounds with fat stores: (1) females will arrive at our study site with more fat, because of sex-related differences in reproductive costs (e.g. Raveling 1979), (2) females with more fat on arrival will initiate clutches sooner as evidenced by decreasing the interval between arrival date and clutch initiation, and (3) females arriving with endogenous fat stores will experience enhanced reproductive success, as evidenced by increases in clutch size, egg size and nestling mass.

Materials and methods

We chose Redstarts as a focal species for this study for several reasons. First, aspects of Redstart biology facilitate capture, as well as finding and monitoring nests (e.g., very active, highly territorial, low nest heights). Secondly, this species is present in relatively high densities in shoreline habitats throughout the eastern Upper Peninsula of Michigan (Sherry and Holmes 1997; R.J. Smith personal observation), and this relative abundance allowed us to maximize sample sizes. Finally, the arrival window for breeding individuals is compressed, and birds commence breeding activities almost immediately after arrival; males are territorial within hours of arrival and females typically pair within hours (up to 1 day) (Sherry and Holmes 1997; R.J. Smith personal observation). The average time between female arrival at our study site and clutch initiation day was 16 days. Compressed arrival and settlement might increase intraspecific competition, adding to the significance of fat stores on arrival if fat confers advantages in territory acquisition and mate or territory choice.

Field research was conducted during 1997, 1998 and 1999 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 at this site is a mixture of conifers including balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), white pine (*Pinus strobus*), and deciduous species including paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and red maple (*Acer rubrum*). 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 and 30 April through 23 July in 1999. For the purposes of this paper, we have restricted analyses to birds captured prior to the median arrival date (6 June) to ensure that first captures accurately reflect day of arrival at the site. Inclusion of birds captured after that date increases the chance that an individual has been at the site more than 5 days. We used a combination of passive and active mist-netting to maximize the probability of capturing birds on the day they arrived. Within our 5 ha study plot we ran 26 permanently positioned mist-nets. During the arrival period we augmented this netting by intensively searching the study area, capturing new arrivals (both males and females) not caught in the permanent nets by placing temporary nets in the new arrival’s territory and broadcasting song-chip playbacks.

Nets were opened shortly before sunrise, and remained open through early afternoon. We reopened in early evening, and closed nets at dusk. Nets were closed in the event of low temperatures, high wind or rain. Standard measurements taken from birds 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 reproducible method of indexing fat stores, especially when comparisons are made within species (Krementz and Pendleton 1990). All measurements were performed by trained individuals who were periodically tested by R.J.S. to ensure validity and reproducibility of measurements. Each bird was aged and sexed according to characteristics outlined in Pyle (1997), fitted with a United States Fish and Wildlife Service aluminum band and uniquely color-banded. All recaptures were measured without reference to previous records.

Birds remaining on the study site were relocated during the breeding season to determine beginning of nest building, date of laying the first egg, clutch size, egg and nestling mass at day 5 (hatch day = day 0). Mean egg and nestling mass was computed for each clutch, these averages are used in subsequent analyses. We used several types of evidence to identify individuals as local breeders: capture or observation during the breeding season, morphological evidence of breeding (i.e., brood patch or obvious cloacal protuberance), and evidence of nest attendance. Comparisons of males to females and examination of relationships between arrival date and fat encompass all individuals classified as local breeders based on these criteria. Relationships between arrival fat and reproductive performance were necessarily limited to first captures of marked individuals whose nests we located, hence the smaller sample sizes.

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

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

where FMR is in kJ/day and m is body mass in grams. FMR represents the total daily energy cost of a wild animal and includes basal metabolism, 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 g 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 h.

Data were analyzed using SPSS (1999) and SYSTAT (1997). Distributions of relevant variables were examined for departures from normality and the appropriate non-parametric statistics used when necessary (Siegel and Castellan 1988; Zar 1996). We performed Median tests to compare male and female arrival within year. As fat score did not meet normality assumptions, we performed a general linear model (GLM) on ranks (Zar 1996), then used the SPECIFY option in SYSTAT to generate individual F tests in order to compare male to female arrival fat score within each year. We used GLM and paired t -tests to investigate the relationship between female mass and female mass change between arrival at the breeding grounds and clutch initiation date, and used

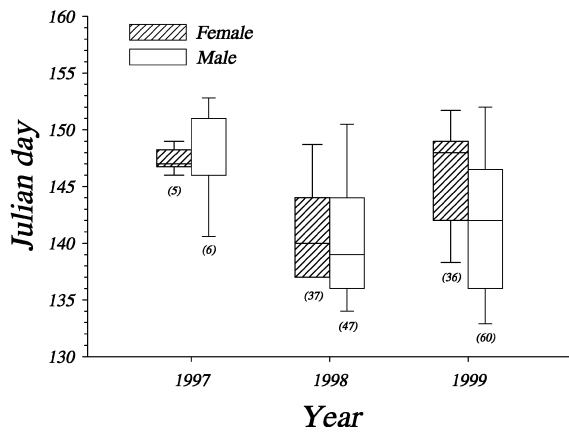


Fig. 1 Median arrival day for male and female breeding American Redstarts in the Upper Peninsula of Michigan during 1997–1999. Sample sizes in brackets, upper and lower box boundaries indicate 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles. Males preceded females in 1999 ($\chi^2=10.401$, $df=1$, $P=0.001$) though not in 1997 ($\chi^2=0.004$, $df=1$, $P=0.95$) or 1998 ($\chi^2=0.225$, $df=1$, $P=0.636$)

non-parametric correlations to explore relationships between arrival fat and reproductive performance. When necessary, we calculated Kendall partial rank-order correlations, a nonparametric method that eliminates the effect of a third variable on the relationship between variables of interest (Siegel and Castellan 1988). Tests are one-tailed when we made a priori predictions, and are so indicated.

Results

Arrival timing and fat load

Breeding males preceded females in arrival at our study site in only 1 of the 3 years of this study (Fig. 1). Both sexes, on average, arrived with fat (Fig. 2). Estimates of FMR suggested that females arrived with enough fat stores to sustain normal activity without foraging for 24–35 h, and males for 25–30 h (Table 1). Females arrived at the breeding grounds with more fat than males (sex effect: $F=18.77$; $df=1$, 188; $P=0.006$) in 1997 and 1999 but not in

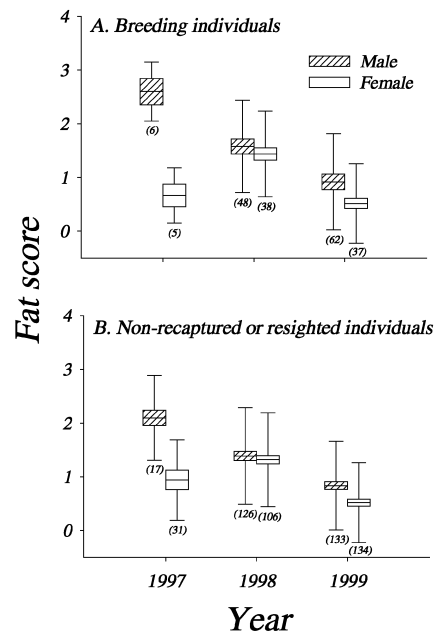


Fig. 2A, B Mean arrival fat score for male and female American Redstarts in Michigan's eastern Upper Peninsula during 1997–1999. **A** Breeding females and **B** females not recaptured or resighted during the breeding season arrived with significantly more fat than males in 1997 and 1999. Sample sizes in brackets; whiskers = ± 1 SD, box = \pm SE

1998 (year effect: $F=22.34$; $df=2$, 188; $P<0.001$; sex \times year effect $F=5.29$; $df=2$, 188; $P=0.006$) (Fig. 2A). We performed the same analyses on birds not recaptured or resighted during the breeding season and found a similar pattern. Females again arrived at the breeding grounds with more fat than males (sex effect: $F=9.51$; $df=1$, 334; $P=0.002$) in 1997 and 1999 but not in 1998 (year effect: $F=26.99$; $df=2$, 334; $P<0.001$; sex \times year effect $F=2.80$; $df=2$, 334; $P=0.062$) (Fig. 2B). Birds arriving earlier in 1998 had more fat than later arrivals regardless of sex (males: Spearman's $r=-0.491$, two-tailed $P<0.001$, $n=119$; females: Spearman's $r=-0.321$, two-tailed $P=0.001$, $n=102$), whereas there was no relationship

Table 1 Summary of field metabolic rate (FMR) calculations based on first captures for female and male American Redstarts known to have bred in northern Lake Huron shoreline habitat 1997–1999

Fat score	<i>n</i>	Average body mass (g) \pm SE	Estimated arrival fat (g)	FMR (kJ/day)	Estimated energy from fat (kJ)	Estimated fast time (h)
Female						
0	8	7.38 \pm 0.01	0.99	37.94	37.68	23.84
1	27	7.42 \pm 0.01	1.03	38.08	38.81	24.46
2	25	7.74 \pm 0.01	1.35	39.21	50.87	31.14
3	10	7.93 \pm 0.01	1.54	39.87	58.03	34.93
Overall	70	7.62 \pm 0.01	1.23	38.79	46.26	28.62
Male						
0	47	7.71 \pm 0.01	1.09	39.10	41.08	25.21
1	36	7.81 \pm 0.01	1.19	39.45	44.84	27.28
2	30	7.91 \pm 0.10	1.29	39.80	48.61	29.31
3	3	7.93 \pm 0.26	1.31	39.83	49.37	29.75
Overall	118	7.81 \pm 0.04	1.19	39.45	44.84	27.28

between date of arrival and fat score for either sex in 1997 and 1999 (1997 male, Spearman's $r=0.078$, two-tailed $P=0.773$, $n=16$; 1997 female, Spearman's $r=-0.164$, two-tailed $P=0.386$, $n=30$; 1999 male Spearman's $r=0.005$, two-tailed $P=0.956$, $n=125$; 1999 female, Spearman's $r=-0.052$, two-tailed $P=0.571$, $n=120$).

We recaptured a number of breeding females and males between 1 and 5 days after initial capture. Examination of the distribution of days from capture to recapture suggests that our fat and mass comparisons were not biased by a preponderance of recaptures within 1 or 2 days of initial capture (female $\bar{x}(\pm\text{SE}) = 3.20 \pm 0.40$ days; male $\bar{x}=3.40 \pm 0.40$ days).

Within 5 days of initial capture, neither sex significantly changed fat score (female initial $\bar{x}=1.46 \pm 0.20$, female recapture $\bar{x}=1.04 \pm 0.14$, $Z=-1.740$, $n=24$, $P=0.082$; male initial $\bar{x}=0.97 \pm 0.14$, male recapture $\bar{x}=0.77 \pm 0.12$, $Z=1.269$, $n=39$, $P=0.205$) or body mass (female initial $\bar{x}=7.41 \pm 0.08$, female recapture $\bar{x}=7.50 \pm 0.10$, $t=-0.992$, $n=23$, $P=0.437$; male initial $\bar{x}=7.90 \pm 0.07$, male recapture $\bar{x}=7.81 \pm 0.07$, $t=1.214$, $n=39$, $P=0.232$).

Influence of arrival timing and fat load on female reproductive performance

Whereas a female's arrival date significantly influenced when she initiated a clutch (Fig. 3), there was no relationship between female arrival date and average clutch size (Pearson's $r=-0.292$, two-tailed $P=0.157$, $n=25$), nor was there a relationship between arrival fat and the interval between arrival and clutch initiation date (Spearman's $r=0.083$, one-tailed $P=0.172$, $n=26$). Females arriving with more fat did not appear to breed sooner than females in poor condition. We did find a relationship between female arrival fat and average egg mass. Fatter females on arrival laid clutches with larger eggs (Spearman's $r=0.711$, one-tailed $P=0.005$, $n=12$; Fig. 4). After controlling for clutch initiation date (clutch size was related to clutch initiation date: Spearman's $r=-0.377$, one-tailed $P=0.035$, $n=24$), we found that fatter females on arrival also laid more eggs (Kendall's partial $T=0.3152$, $n=24$, one-tailed $P=0.026$). Finally, the correlation between female arrival fat and nestling mass at day 5 approached significance (Spearman's $r=0.528$, one-tailed $P=0.059$, $n=10$), and subsequent power analysis suggests that the lack of statistical significance for this analysis might be attributed to the small sample size ($\beta=0.420$).

Influence of arrival timing and fat load on male reproductive performance

We found no relationship between a male's arrival date and when the female with which he was paired initiated her clutch (Pearson's $r=0.192$, two-tailed $P=0.391$, $n=22$). As with females, there was no relationship between male arrival day and the interval between his arrival at the study site and clutch initiation date (Spearman's

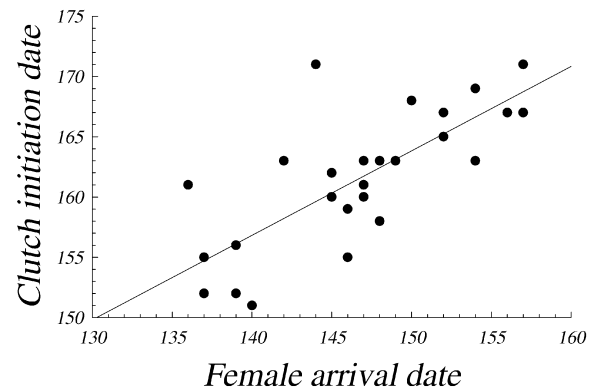


Fig. 3 Relationship between female first capture date and clutch initiation date, eastern Upper Peninsula of Michigan, 1997–1999. Dates are Julian (1 May=Julian Day 121). Pearson's correlation for these data: $r=0.741$, one-tailed $P < 0.001$

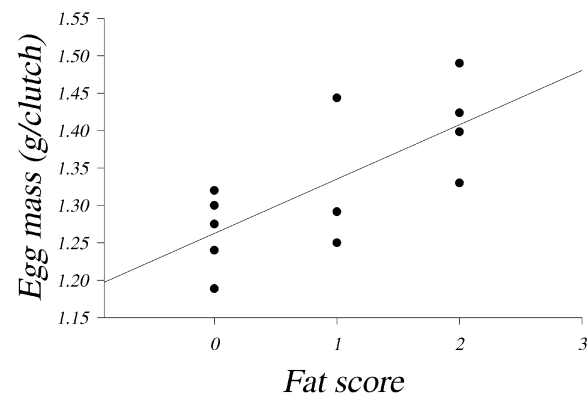


Fig. 4 Relationship between female fat at first capture and average egg mass per clutch, eastern Upper Peninsula of Michigan, 1997–1999. Spearman's rank correlation for these data: $r=0.715$, one-tailed $P=0.004$

$r=-0.081$, two-tailed $P=0.720$, $n=22$). There was, however, a positive relationship between average egg mass and male arrival fat (Spearman's $r=0.756$, two-tailed $P=0.030$, $n=8$). Partial correlation analysis examining the relationship between male arrival fat and clutch size and controlling for clutch initiation date, revealed no relationship (Kendall's $T=-0.234$, $df=16$, two-tailed $P=0.186$, $n=16$). We found no relationship between average nestling mass at day 5 and male arrival fat (Spearman's $r=-0.504$, one-tailed $P=0.101$, $n=8$).

Discussion

Our results support the hypothesis that arriving with fat at the breeding grounds contributes to seasonal reproductive performance. We do not argue that American Redstarts are capital breeders in the sense that they prepare a complete clutch of eggs from body stores (see Perrins

Table 2 Comparison of female mass between first and last capture prior to clutch initiation along the northern Lake Huron shoreline, Michigan, 1997–1999. Means±SE are reported. Females arriving in all fat classes gained mass as they moved into the breeding season.

Fat score at first capture	Mean number of days between first and last capture	Mean number of days between last capture and clutch initiation	Mean body mass at first capture (g)	Mean body mass at last capture (g)	Difference between last and first capture (g)	df	Paired <i>t</i>	P
0	6.80±1.05	9.50±2.33	7.46±0.10	7.80±0.21	0.34	8	2.56	0.034
1	6.50±0.97	11.33±2.54	7.36±0.10	7.87±0.17	0.51	10	3.30	0.008
2	6.08±1.37	9.00±1.68	7.57±0.12	7.68±0.18	0.11	10	0.70	0.507
3	3.50±0.87	12.67±1.20	7.50±0.21	7.73±0.23	0.23	3	0.98	0.398
Overall	6.08±0.61	10.42±1.16	7.47±0.06	7.77±0.09	0.31	34	3.712	0.001

To reduce the possibility that observed mass change was biased by follicular development, we limited our analyses to recaptures prior to 8 June and excluded all females with mass greater than 8.2 g

1970; Klaasen et al. 2001), rather that the availability of resources in the form of endogenous fat stores provide indirect benefits that influence reproductive success among songbird migrants (Sandberg and Moore 1996). Although our results do not allow us to draw inferences regarding a causal relation between fat stores and reproductive performance, they do reveal interesting correlations consistent with expectations. Understanding causal relations and underlying mechanisms will necessarily depend on manipulative field experiments.

An important assumption of this study is that fat load at first capture is representative of actual arrival fat. There are a number of reasons why we believe this to be valid. First, our use of passive and active netting was designed to maximize the probability of capturing birds on the day of arrival. Second, field observations, especially of singing males, support this assumption. The study site and surrounding area was under intense daily observation because we were looking for newly arrived, unbanded individuals and recording foraging behavior as part of another study. Newly arrived males and, to a lesser extent, females were typically confirmed as captured (observed with bands) within a few hours of the original observation. Finally, our recapture data for both breeding males and females indicate no significant changes in mass or fat score between first capture and recapture within 5 days. This finding suggests that even if we were unable to catch individuals on the day of arrival, our fat estimates are valid as mass and fat score did not change significantly within 5 days after first capture.

Fat and early arrival

Perhaps the most obvious benefit of arriving with fat stores is as insurance against predictably variable environmental conditions encountered upon early arrival on the breeding grounds. Landbird migrants outpace phenological development of vegetation and terrestrial invertebrates as they move north during spring migration (Slagsvold 1976; Ewert and Hamas 1995; R.J. Smith and F.R. Moore, unpublished data). Consequently, many birds may arrive at northerly breeding grounds when food

abundance is low. Early arrival may increase the potential for exposure to poor weather conditions such as late season snowstorms, low temperatures or extended periods of rain. Food limitation and/or poor environmental conditions may lead to substantial mortality (Dence 1946; Zumeta and Holmes 1978; Brown and Brown 2000), reverse migration (Alerstam 1978; Terrill and Ohmart 1984; Akesson et al. 1996), or to shifts in foraging behavior as birds attempt to overcome food limitation and offset increased thermoregulatory requirements (Zumeta and Holmes 1978; Martin and Karr 1990). As migrants encounter unfavorable circumstances during this early transition period, fat stores accumulated during passage would serve to overcome unpredictable foraging situations (see Møller 1994), sustaining an individual until the environment becomes more suitable. Our results suggest that Redstarts arrived with fat stores sufficient to allow fasting while maintaining normal levels of activity for more than 24 h.

Sex differences in arrival fat

Differential migration with males preceding females is a commonly observed pattern among many passerines during spring migration (Ketterson and Nolan 1983; Francis and Cooke 1986). If significant temporal differences exist within a species, the later sex may arrive at the breeding grounds with more fat simply because they encounter better food and climatic conditions en route. Yet, the arrival of female American Redstarts coincided with male arrival in 2 of the 3 years of this study. We also found no consistent relationship between female arrival date and fat load. Females arrived with more fat when median arrival dates were coincident between the sexes (1997) as well as when they differed (1999).

Evidence of reproductive benefits from arrival timing and arrival fat

Seasonal declines in clutch size, along with an associated reduction in the probability of recruitment, are well

documented in passerines (Perrins 1970; Nilsson 1994; Rowe et al. 1994; van Noordwijk et al. 1995). Individual delays in the onset of breeding of just a few days can have important fitness consequences (Nilsson 1994; van Noordwijk et al. 1995). Early nesting individuals typically lay more and larger eggs and have heavier nestlings and fledglings than delayed nesters (see Carey 1996). Our results indicate that arrival schedules significantly influence breeding schedules such that earlier arriving birds commence breeding activities sooner. Further, birds at our study site appear to experience reduced fitness if clutches are delayed. Early nesters have more and larger eggs, as well as more and heavier nestlings than later clutches (R.J. Smith and F.R. Moore, unpublished data).

The significant relationships between arrival fat and reproductive performance in both females and males suggest reproductive advantages in arriving on the breeding grounds with fat. Egg production is energetically expensive, costing up to 41% of a female's daily basal metabolic rate (Walsberg 1983; Carey 1996). American Redstart females arriving with higher fat loads laid more eggs, produced larger eggs and possibly produced heavier nestlings at day 5. The positive relationship between male arrival fat and egg size suggests that females paired with fatter males also laid larger eggs. Egg number, egg mass and nestling mass have all been shown to enhance the number of young recruiting into the breeding population (see Martin 1987; Magrath 1991, 1992; Carey 1996; Smith and Bruun 1998).

Our results do not permit us to evaluate how arriving with surplus fat stores confers reproductive advantages. Sorting out the mechanism(s) warrants further work. Although it is unlikely that female Redstarts utilize some of the added energy as a direct aid in forming eggs or increasing egg size (see Perrins 1970; Meijer and Drent 1999; Klaassen et al. 2001), we cannot rule out the possibility. It is more likely, however, that arrival fat may allow females to (1) devote more time to territory or mate assessment or both during the compressed arrival period, or (2) acquire specific nutrients in preparation for breeding (see Sandberg and Moore 1996). Females may also discriminate against males in poor condition during mate choice (Møller 1994). Fatter males may gain a competitive advantage during the short, but energetically expensive period of territory acquisition, allowing them to procure a higher quality territory. Song is an important component of both territory establishment and maintenance for males as well as mate choice in females (Wasserman and Cigliano 1991). However, increased foraging entails a trade-off between singing and foraging activity (Reid 1987; R.J. Smith and F.R. Moore, unpublished data); the more time spent foraging the less time a male can afford to sing. Fatter males may be able to allocate more time to song. Arrival fat might also be a consequence of individual quality, reflecting numerous factors such as an individual's ability to offset the energetic costs of migration or the ability to compete for and maintain a quality wintering territory.

Our findings are consistent with the fact that breeding season consequences arise not only from timing of arrival on the breeding grounds but also from the bird's energetic condition upon arrival. Moreover, the results of our study emphasize the connection among events of the annual cycle. A migrant's energetic status is subject to circumstances encountered during migration (Moore et al. 1995) as well as the wintering grounds (Marra et al. 1998), and energetic status influences reproductive performance. Whereas a bird's annual cycle is typically synchronized to segregate the major energy-demanding functions of molt, migration and reproduction (Helms 1968; King 1972), synchronization of different functions does not preclude the possibility that events in one phase of the annual cycle influence survival and reproductive success in a subsequent phase.

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