Arrival Timing and Seasonal Reproductive Performance in a Long-distance Migratory Landbird

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Introduction

The date when a landbird migrant arrives on its breeding grounds may have reproductive consequences. Generally, early arriving individuals acquire higher quality territories (Bensch and Hasselquist 1991) and mates (Møller 1994), begin breeding earlier (Cristol 1995), and consequently experience greater seasonal reproductive performance (Rowe et al. 1994; Hasselquist 1998) . Relationships between arrival date, territory quality and seasonal reproductive performance highlight the importance of settlement tactics for both male and female migratory birds that hold breeding territories.

Objectives

This study examined the relationship between arrival timing and seasonal reproductive performance in a long-distance landbird migrant, the American redstart (*Setophaga ruticilla*), arriving at northerly breeding grounds in Michigan's eastern Upper Peninsula. Specifically, we evaluated the influence of arrival day on (1) territory quality, as reflected by territory vegetation, (2) timing of breeding, and (3) seasonal reproductive performance by testing the following predictions:.

Prediction 1: Given redstarts' preference for young, second-growth forest with abundant shrubs (Sherry and Holmes 1997), we expected early arriving males to settle on territories encompassing more second-growth vegetation than later arrivals. Variation in forest age allowed evaluation of this prediction. The study area was characterized by a gradient of differentially aged patches ranging from < 20 years to > 75 years since clearing. The youngest areas contained dense stands of young balsam fir (*Abies balsamea*), with no canopy, whereas the oldest patches were dominated by older northern white cedar (*Thuja occidentalis*), and contained little to no shrubby vegetation.

Prediction 2: Breeding date is positively affected by arrival date. This prediction reflects the increased probability of offspring successfully entering the breeding population if fledged early (Klomp 1970; Perrins and McCleery 1989).

Prediction 3: Arrival timing influences reproductive performance; early arriving individuals produce larger clutches with heavier eggs and nestlings than later arrivals. Egg and nestling size relate positively to recruitment probability (Magrath 1992).

Methods

This work was conducted during the spring migratory and breeding periods at a five ha site on the shoreline of northern Lake Huron in Michigan's eastern Upper Peninsula (Figure 1; 46º2'N, 84º35'W). Forest vegetation was a mixture of conifers including northern white cedar (*Thuja occidentalis*) = 61%, balsam fir (*Abies balsamea*) = 10%, quaking aspen (*Populus tremuloides*) = 7%, white spruce (*Picea glauca*) = 5%, paper birch (*Betula papyrifera*) = 2%, white pine (*Pinus strobus*) = 1%, red pine (*Pinus resinosa*) < 1%, and balsam poplar (*Populus balsamifera*) < 1%.

Birds

We combined a permanent netting array with target netting to maximize the likelihood of capturing birds on the day they arrived. We restricted analyses to first captures of birds before 12 June to ensure capture data accurately reflected arrival day. Standard measurements included body mass, tarsus length and unflattened wing chord. Visible, subcutaneous fat deposits were quantified using a six-point ordinal scale (Helms and Drury 1960). Each bird was aged and sexed according to characteristics outlined in Pyle (1997), fitted with a USFWS aluminum band and individually color-banded.

Nests

After finding a nest, the color-band combination of each adult was verified and the nest monitored to determine clutch initiation date, clutch size, egg mass and nestling mass at Day 5 (hatch day = Day 0). Nests were only included in analyses when we were confident of clutch initiation date. Where necessary, we estimated hatch and fledge dates based on averages calculated from nests for which these dates were known. We calculated mean egg and nestling mass for each clutch; these averages are used in subsequent analyses.

Territory Vegetation

We estimated vegetation composition using a modification of methodology proposed by James and Shugart (1970). We used two vegetation sampling points to characterize each territory. We located one point at the nest and one at a random direction and distance from the nest, yet remaining within the attending male's territory. Territory boundaries were delineated by noting locations of singing males and aggressive interactions with other males. We included for analysis only those males for which we were confident of territory boundaries.

Results

• The arrival period was more compressed for females than males, with 75% of males arriving over a 23-day period and 75% of females arriving over a 16-day period (Figure 2). Pooled across years, median arrival day for breeding males was 24 May (Julian Day 144) and for females 26 May (Julian Day 146). This two-day difference was not significant (χ^2 = 1.007, *df* = 1, *n* = 431, *P* = 0.366).

• In all years, older males preceded younger males (Table 1).

Arrival Timing and Territory Vegetation

•Arrival day was related to shrub density within a male's territory (Figure 3).

Arrival Timing and Reproduction

• Female arrival day was related to clutch initiation date (Figure 4).

• Early females laid more eggs ($r_{P=}$ -0.524, *n* = 39, *P* = 0.001). There were no relationships between clutch initiation day and average egg mass ($r_{P=}$ 0.132, *n* = 33, *P* = 0.463), or average nestling mass at Day 5 ($r_{P=}$ 0.088, *n* = 24, *P* = 0.681).

• Female arrival day correlated with average nestling mass at day five (Figure 5). We found no relationship between female arrival day and egg mass (r_s = -0.004, *n* = 41, one-tailed *P* = 0.490).

• Male arrival day was not related to when his mate initiated her clutch (ASY $r_{P=}$ -0.038, *n* = 17, one-tailed *P* = 0.442; SY $r_{P=}$ 0.021, *n* = 21, one-tailed *P* = 0.464). After controlling for clutch initiation day, male arrival day was related to hatch day (ASY: Partial $r_{P=}$ 0.474, *n* = 14, one-tailed *P* = 0.016, adjusted *P* = 0.017; SY Partial $r_{P=}$ 0.391, *n* = 18, one-tailed *P* = 0.023, adjusted *P* = 0.025).

Significance

Whereas a bird's annual cycle is synchronized to segregate the major energy-demanding functions of molt, migration and reproduction (e.g., Helms 1968), 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 (Marra et al. 1998). Migratory delays likely influence arrival timing, and the findings of this study point to fitness consequences arising from when a bird arrives at its breeding grounds.

Figure 1. Pontchartrain Shores study site in Michigan's eastern Upper Peninsula. The asterisk marks the approximate location of the 5 ha study area.

Typical Breeding Habitat

Nestling at Day 5

Redstart Nestlings in Balsam Fir

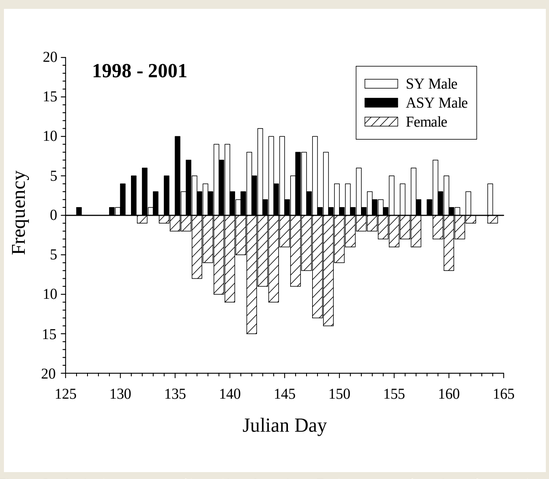

Figure 2. Arrival sequence of breeding American Redstarts as a function of sex and male age, Pontchartrain Shores, Michigan 1998 - 2001

Table 1.
Arrival dates by sex and male age for breeding American redstarts at Pontchartrain Shores, Michigan. Male age comparisons were made using Mann-Whitney tests.

	Mean	Median	S.E.	C.V.	Min	Max	n	Z	P
1998 - 2001									
SY Male	147.58	147	0.60	5.08	130	164	158		
ASY Male	140.42	139	0.81	5.77	126	160	101	-6.865	**< 0.001**
Female	146.19	146	0.53	4.74	132	164	171		
1998									
SY Male	145.11	145	0.91	4.67	136	162	55		
ASY Male	136.82	135	1.26	3.79	130	146	17	-4.370	**< 0.001**
Female	144.46	143.5	1.08	5.29	134	162	50		
1999									
SY Male	148.76	148	1.18	5.32	137	162	45		
ASY Male	140.00	137	1.50	6.15	126	159	33	-4.471	**< 0.001**
Female	147.07	148.5	0.89	4.02	136	160	44		
2000									
SY Male	147.91	147	0.87	2.69	142	157	21		
ASY Male	141.14	140	1.41	5.20	130	160	27	-3.438	**0.001**
Female	144.27	143	0.89	3.60	132	160	34		
2001									
SY Male	149.65	149	1.43	5.83	130	164	37		
ASY Male	139.06	138.5	2.18	6.27	129	159	16	-3.737	**< 0.001**
Female	149.03	148	1.28	5.28	138	164	38		

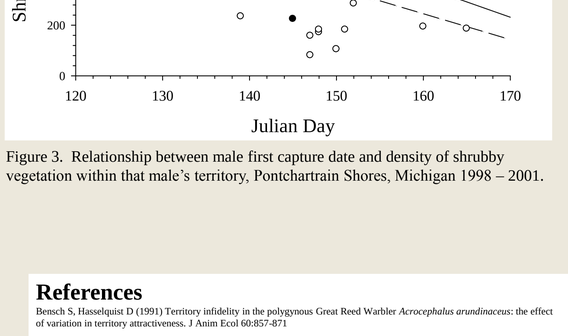

Figure 3. Relationship between male first capture date and density of shrubby vegetation within that male's territory, Pontchartrain Shores, Michigan 1998 – 2001.

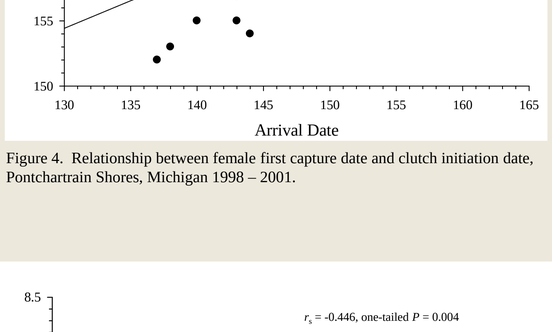

Figure 4. Relationship between female first capture date and clutch initiation date, Pontchartrain Shores, Michigan 1998 – 2001.

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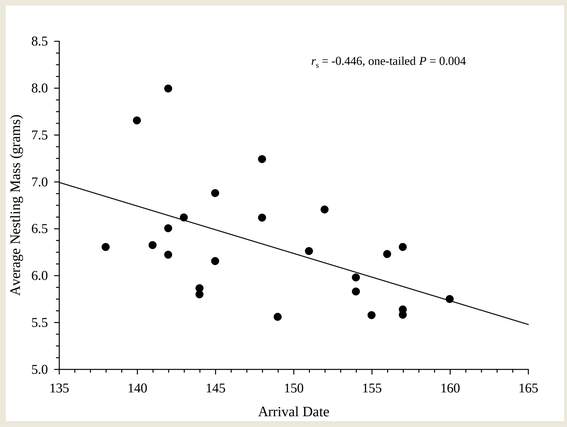

Figure 5. Relationship between female first capture date and average nestling mass at Day 5 (hatch day = 0), Pontchartrain Shores, Michigan 1998 – 2001.

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