Do migratory warblers carry excess fuel reserves during migration for insurance or for breeding purposes?

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RESEARCH ARTICLE

Do migratory warblers carry excess fuel reserves during migration for insurance or for breeding purposes?

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ABSTRACT

Migration is energetically costly, and many passerines prepare for and maintain migration with hyperphagia and increased fuel or fat reserves. During spring migration, as they approach their breeding grounds, passerines may deposit fat in excess of what is needed to complete migration. Individuals may carry excess fuel reserves as insurance against potentially poor environmental conditions in early spring (insurance hypothesis). If this is true, individuals arriving early at northern stopover locations or their breeding grounds should have greater energy reserves than later arrivals. Alternatively, passerines may arrive in spring with excess fat to help offset the demands of breeding (breeding performance hypothesis). Given the energetic requirements of egg production, females may arrive with greater reserves than males if excess fat directly or indirectly offsets breeding costs. We analyzed the energetic condition of 12 warbler species mist-netted during migration from 1999 to 2012 at Braddock Bay Bird Observatory, Monroe County, New York, USA. This northern stopover location is near the breeding range (in relation to total migratory distance) for most of the parulid species we examined and, therefore, is a likely location to show carryover effects between migration and breeding. In 11 of the 12 species, energetic condition was greater in the spring than in the fall for both sexes; and in all 12 species, condition was greater in females than in males in both seasons. Contrary to the insurance hypothesis, condition increased with arrival date for most species during spring migration. Although better condition in females supports the breeding performance hypothesis, the presence of this difference in both seasons suggests that additional factors influence energetic condition in parulids. Given that males arrive in better condition in the spring than when they depart in the fall, individuals of both sexes may carry excess energy reserves during spring migration to potentially use for reproductive efforts.

Keywords: breeding performance hypothesis, carryover effects, energetics, insurance hypothesis, migration, Parulidae, songbirds, stopover ecology

¿Los Parulidae migratorios cargan un exceso de reservas energéticas durante la migración como seguro o para fines reproductivos?

RESUMEN

La migración es costosa en términos energéticos, y muchos paserinos se preparan para la migración mediante hiperfagia y con un incremento de las reservas de energía o grasa. Durante la migración de primavera, a medida que se acercan a sus áreas de cría, los paserinos pueden generar reservas de grasa más allá de lo necesario para completar la migración. Los individuos pueden cargar un exceso de reservas como un seguro contra potenciales condiciones ambientales adversas al inicio de la primavera (hipótesis del seguro). Si esto es cierto, los individuos que llegan temprano a los sitios de parada del norte o a sus áreas reproductivas deberían tener mayores reservas energéticas que los que llegan tarde. Alternativamente, los paserinos pueden llegar en primavera con un exceso de grasa para ayudar a compensar las demandas reproductivas (hipótesis reproductiva). Debido a los requerimientos energéticos de la producción de huevos, las hembras pueden llegar con mayores reservas que los machos si los excesos de grasa compensan de modo directo o indirecto los costos reproductivos. Analizamos la condición energética de 12 especies de Parulidae atrapadas con redes de niebla durante la migración de 1999–2012 en el Observatorio de Aves de la Bahía Braddock, Rochester, NY. Este sitio de parada del norte está cerca del rango reproductivo (en relación a la distancia total de migración) de la mayoría de las especies de Parulidae que examinamos, y por lo tanto es un sitio que probablemente muestre los efectos de arrastre entre migración y reproducción. En 11 de las 12 especies, la condición energética fue mejor en la primavera que en el otoño para ambos sexos, y la condición fue mejor en las hembras que en los machos en ambas estaciones para las 12 especies. En contraposición a la hipótesis del seguro, la condición mejoró con la fecha de llegada para la mayoría de las especies durante la migración de primavera. Aunque una mejor condición de las hembras apoya la hipótesis reproductiva, la presencia de esta diferencia en ambas estaciones sugiere

que otros factores adicionales influencian la condición energética en los Parulidae. Debido a que los machos llegan en primavera en mejor condición de la que tienen cuando parten en otoño, los individuos de ambos sexos pueden cargar un exceso de reservas energéticas durante la migración de primavera para usarla potencialmente en los esfuerzos reproductivos.

Palabras clave: aves canoras, ecología de los sitios de parada, efectos de arrastre, energéticos, hipótesis del desempeño reproductivo, hipótesis del seguro, migración, Parulidae

INTRODUCTION

Migration is an energetically expensive behavior that is arguably the most vulnerable period of a bird's annual cycle (Moore et al. 1990, Sillett and Holmes 2002). There is evidence that basal metabolic rates increase considerably in migratory birds, particularly during spring migration (Swanson 2010). To compensate for these increased metabolic demands during migration, birds must acquire and deposit adequate energy reserves to reach distant breeding and wintering grounds successfully. Some species of Neotropical, intercontinental migratory passerines are capable of accumulating fat stores of up to 50% of their body mass in preparation for, or during, migration (Blem 1990). However, fat accumulation can also incur potential costs by negatively affecting maneuverability (i.e. predator avoidance) in songbirds (Kullberg et al. 1996, Lind et al. 1999, Gosler et al. 2002).

Energy reserves are important for functions other than fueling migration. Energy reserves upon arrival at breeding grounds can affect the fitness of both males and females, if directed toward breeding activities (see Ojanen 1984, Sandberg and Moore 1996, Fransson and Jakobsson 1998, Bêty et al. 2003, Smith and Moore 2003, 2005). Therefore, one plausible hypothesis for depositing excess fuel reserves (i.e. in excess of minimum migration requirements) during spring migration is the breeding performance hypothesis: Reproductive success on northern breeding grounds is potentially influenced by stored fat that is accumulated en route at stopover sites and, subsequently, carried over to breeding sites (Gudmundsson et al. 1991, Sandberg and Moore 1996). Stored fat could either directly or indirectly influence reproductive success; for example, females arriving with fat reserves could produce larger clutches and/or begin breeding activities earlier than females that arrive with little or no reserves (Smith and Moore 2003). Because migratory passerines are income breeders (Langin et al. 2006), however, any potential benefits of arriving on breeding grounds with fat stores are likely indirect. Given the energy expense of egg production, which consumes up to 41% of a female's daily metabolic requirements (Carey 1996), carrying excess fuel reserves may benefit females more than males. Moreover, male parulids may utilize a time-minimization strategy during spring migration (Seewagen et al. 2013, Paxton and Moore 2015) and, consequently, may arrive with lower energy stores than

females (Sandberg and Moore 1996). Although several studies on breeding grounds have found that females were in better condition than males (Norment 1992, Sandberg 1996, Smith and Moore 2003, 2005), not all have found female-biased energetic condition (Yong et al. 1998, Morris et al. 2003).

A second plausible hypothesis for depositing excess fuel reserves during spring migration is the "insurance hypothesis": Birds breeding at high latitudes should benefit from arriving on breeding grounds, or northern stopover locations, with fat reserves because spring environmental conditions are often harsh, with unpredictable and scarce resources (Sandberg and Moore 1996). Spring food availability and weather conditions improve with time, so one prediction of this hypothesis is that earlier-arriving birds, in order to cope better with unpredictable conditions, should have greater fat reserves than individuals arriving later (Sandberg and Moore 1996). For example, Smith and Moore (2005) found that American Redstarts (*Setophaga ruticilla*) that arrived earlier on their Michigan breeding grounds had more fat than later-arriving individuals; they also found that birds were in better condition during years with poorer conditions.

Sandberg and Moore (1996) have suggested that both the breeding and insurance hypotheses imply that it is more beneficial for birds to have energy or fat reserves in the spring than when they depart in the fall—the spring fatter hypothesis. While there may also be advantages to energy reserves during fall migration, such as for the long migration ahead, several studies suggest that fall migration occurs at a slower rate and that many species may accumulate energy reserves as needed along their fall migratory route (e.g., Bauchinger and Klaassen 2005, Stutchbury et al. 2009). Some passerine species or populations, however, do not exhibit higher fat reserves in the spring than in the fall; Benson and Winker (2005) found that many passerines depart Alaska with greater fat reserves than when they arrive in the spring.

Whatever the reason, arriving on breeding grounds with an energetic surplus should be particularly beneficial for Arctic and subarctic (i.e. boreal) breeding birds, because of the temporal constraints associated with breeding at high latitudes (e.g., Smith and Moore 2003, 2005, Cooper et al. 2011). For long-distance migrants, given the high energetic requirements of migratory flights and the potential costs of carrying too much fat (Kullberg et al. 1996, Lind et al.

1999, Gosler et al. 2002), these reserves are likely acquired en route (Seewagen et al. 2013) and carried over to the breeding grounds (Sandberg 1996). Therefore, we would expect any energetic patterns predicted by the insurance and breeding hypotheses to likely be evident at stopover locations, particularly at northern latitudes relatively close to breeding grounds.

The main goal of our study was to determine whether variation in condition of parulid warblers at a northern stopover site in North America is consistent with the breeding performance or insurance hypotheses by examining how condition varies with season, sex, and arrival time. We examined 3 questions. First, do birds arrive in better condition in spring than in fall? Second, do females arrive in better condition than males in spring? Third, are birds that arrive earlier in spring in better condition than those that arrive later? We had no predilections for either the insurance or breeding performance hypothesis, and we assumed that insurance and breeding may provide complementary explanations for excess spring fuel reserves.

We analyzed spring and fall banding data for 12 species of parulid warblers captured along the southern shore of Lake Ontario, during both fall and spring migration. Although not a breeding site for many of the species and individuals we studied, this location is relatively close to the breeding grounds for most of the species we examined; many parulids arriving at this northern stopover location are nearing the end of their spring migratory journey. The proximity of this stopover location to the boreal forest (estimated to be within ~500 km using shape files from Brandt 2009) arguably makes it a potential penultimate stopover for at least some parulids and increases the likelihood for potential carryover effects between migration and breeding. Additionally, stopover locations in close proximity to ecological barriers (e.g., deserts, bodies of water) are especially important for birds because they often need to refuel just before or just after crossing the barrier (e.g., Buler and Moore 2011). Although our field-site location, on the southern shore of Lake Ontario, could provide an additional reason why spring migrants might require higher energetic loads, we would not expect to find consistent differences in energetic condition between sexes at this stopover location if birds are using fuel reserves only to successfully cross Lake Ontario. Moreover, Deutschlander and Muheim (2009) showed that in some passerine species, the interaction between energetic condition and season at this location has no or little effect on forward migratory orientation and restlessness. Our field site, therefore, is an excellent location for the present study because seasonal and sexual differences in energetic condition could carry over to breeding grounds and be consistent with the breeding performance hypothesis, while a lack of sexual differences in condition would

suggest that any seasonal differences are due solely to migratory fueling.

METHODS

Data Collection

We used data collected from Braddock Bay Bird Observatory (BBBO) during spring and fall migration between 1999 and 2012. BBBO is located on the south shore of Lake Ontario near Rochester, Monroe County, New York, USA (43°19′N, 77°43′W). The most direct distance across Lake Ontario at this longitude is approximately 75–80 km. The vegetation surrounding BBBO is characterized as a mix of abandoned-field and early-successional land-cover types dominated by viburnum (*Viburnum* spp.), dogwood (*Cornus* spp.), honeysuckle (*Lonicera* spp.), ash (*Fraxinus* spp.), and alder (*Alnus* spp.) (Bonter et al. 2007). Much of the surrounding habitat is managed to maintain an early-successional vegetative state dominated by woody fruiting shrubs.

Songbirds were captured with mist nets (30 mm mesh) that were operated daily (weather permitting) as part of the constant-effort migration-monitoring protocol at BBBO. Across all years, birds were captured in the spring season from mid-April until late May and in the fall season from late August until mid-October. Nets were opened just before sunrise and operated for a minimum of 6 hr day^{-1}, with net checks at least every 30 min. The following data were recorded for each bird: date and time of capture, age, sex, unflattened wing chord or length (± 0.5 mm), mass (± 0.1 g), and fat score on a scale of 0–5 (Helms and Drury 1960).

We selected 12 sexually dimorphic warbler species for these analyses: Black-and-white Warbler (*Mniotilta varia*), Nashville Warbler (*Oreothlypis ruficapilla*), Mourning Warbler (*Geothlypis philadelphia*), Common Yellowthroat (*G. trichas*), American Redstart, Magnolia Warbler (*S. magnolia*), Blackpoll Warbler (*S. striata*), Black-throated Blue Warbler (*S. caerulescens*), Yellow-rumped Warbler (*S. coronata*), Black-throated Green Warbler (*S. virens*), Canada Warbler (*Cardellina canadensis*), and Wilson's Warbler (*C. pusilla*). Species were selected on the basis of adequate spring and fall sample sizes (≥ 14 individuals season^{-1} across all study years). Because we were not interested in analyzing yearly variation, we compiled seasonal data (fall and spring) for all years (1999–2012) for each species. All data were collected on the first day of capture, assumed to be the arrival day for individuals at the site if birds arrived at or before dawn (see Moore et al. 1995, Dunn 2000); data for recaptured individuals were not included in these analyses. We included only individuals that could be reliably sexed by plumage or, for hatch-year Blackpoll Warblers in the fall, wing chord (Pyle et al. 1997). Age ratios of known-age birds were similar in both seasons

for most species, with an average ratio of juveniles:adults of 2.4 for all species. Individuals with obvious errors in wing length or mass measurements were omitted; a conservative approach was used to omit only the most obviously erroneous measurements.

Data Analyses

Unlike some previous studies in which condition estimates were based on dividing body mass by wing chord (e.g., Dunn 2002, Benson and Winker 2005, Bonter et al. 2007), we used unflattened wing length and body mass to calculate a scaled mass index (SMI) of body condition for all individuals (following the methods of Peig and Green 2009). SMI adjusts the mass of all individuals to reflect what each individual's mass would be if its body size (i.e. unflattened wing length) was equal to the population mean. Therefore, the SMI is a size-corrected body mass (in grams) that enables comparison of the energetic condition of individuals within the population sample for each species. Although fat score was visually assessed for individuals, we did not use this as an additional estimate of condition because of the large number of banders at BBBO and the potential for observer variability in the assessment of fat.

A general linear model (GLM) was used to determine whether there were differences in energetic condition between seasons and sexes for each species; we created interaction plots for energetic condition (i.e. SMI) to show specific details (and effect magnitudes) for males and females in spring and fall. Because arrival dates during migration can vary between males and females in warblers (Francis and Cooke 1986, Yong et al. 1998, Morris et al. 2003, Smith and Moore 2005, Benson et al. 2006), we graphed arrival-date distributions (using ordinal dates) for each species by sex and season to determine whether there were intraspecific differences in arrival time between sexes in our study population (Supplemental Material Figure S1). Some species exhibited sexual differences in arrival date in the fall, but not consistently among species. However, for all 12 species, males tended to arrive at BBBO earlier than females during spring migration. Therefore, each of our GLMs used analysis of covariance (ANCOVA) to investigate whether arrival date was a significant covariant for energetic condition across seasons and sexes, and to control for arrival-date differences between sexes and seasons when comparing condition of the sexes. We standardized arrival dates to compare both spring and fall arrival for the ANCOVAs. Median arrival date was calculated for each season by year, and the differences between individual arrival date and median date (median arrival date was equal to zero) were used for the analyses.

We used linear regression analyses to investigate the nature of the relationship between energetic condition (SMI) and arrival date for all species; season and sex were regressed separately for each species (Supplemental Material Figure S2). For each species, the linear regression slopes (g day^{-1}) and average SMI (g) of all birds with a fat score of 0 were used to calculate the change in SMI by day across the season. A daily percent change across the season (from lean mass) was determined on the basis of these regressions; but note that this analysis is different from using hourly (i.e. time-of-capture) mass regressions to determine a daily change in mass during daily stopover (as in, e.g., Dunn 2002, Bonter et al. 2007). Although calculating percent change in SMI by day across the season was not critical to any of our questions, determining the magnitude of change as a percentage allowed for comparisons among species and between sexes and seasons within our data. All data met test-appropriate assumptions before analyses were conducted. SPSS 21 (SPSS IBM, Armonk, New York, USA) and Minitab 16 (Minitab, State College, Pennsylvania, USA) were used to perform the statistical analyses. A sequential Bonferroni procedure was used to adjust P values for multiple comparisons (in Tables 1 and 2).

RESULTS

Season

Results of ANCOVA showed a significant effect of season on the energetic condition of 11 species (8 when corrected for multiple comparisons; Table 1). In 11 species, energetic condition was higher in the spring than in the fall (Figure 1). The overall SMI increase between fall and spring for these 11 species, regardless of sex, was 4.3%. The greatest seasonal increase occurred in the Blackpoll Warbler, which had, on average, a 16.3% greater mean SMI in the spring than in the fall. The Black-and-white Warbler showed the opposite seasonal pattern from the 11 other species, with a mean SMI difference of −2.1% between spring and fall (Table 1).

Sex

ANCOVA results also showed significant condition differences between males and females for all species except the Mourning Warbler (Table 1). Interaction plots show that females of all species were in better energetic condition than males when they arrived at BBBO (Figure 1). Across all 12 species and both seasons, mean SMI was 5.5% greater for females than for males. The largest mean SMI difference between sexes was found in Blackpoll Warblers, with females averaging 17.9% heavier than males. The smallest difference was among American Redstarts, with females weighing 2.1% more than males (Table 1).

Interactions between Sex and Season

Although the overall trends for sex and season among all species are stated above, 3 species (Magnolia Warbler,

TABLE 1. ANCOVA results (*F* and *P* values) for 12 warbler species captured at Braddock Bay Bird Observatory, Monroe County, New York, USA, 1999–2012, showing effect(s) of sex and season on energetic condition with arrival (or capture) date as a significant covariate. Also shown are the overall percent differences in mean energetic condition (i.e. scaled mass index [SMI]) between sexes and seasons. To characterize the overall difference in SMI between the sexes for each species, we calculated the percent increase in female SMI for both seasons combined, compared to male SMI. To show the overall difference in SMI between seasons for each species, we calculated the percent increase (or decrease, in Black-and-white Warblers) in spring SMI for both sexes combined, compared to fall SMI. Actual mean SMI values for each sex and each season are shown in Figure 1. (Regression analyses detailing the effects of arrival date on SMI are presented in Table 2 and Supplemental Material Figure S2.)

| Species | n | Sex | | Season | | |
		F	Energetic condition difference	F	Energetic condition difference	Arrival date
Black-and-white Warbler	571	17.19**[†]	6.6%	4.03*	−2.1%	31.19**[†]
Nashville Warbler	1,041	81.86**[†]	4.9	73.92**[†]	4.3	28.78**[†]
Mourning Warbler	551	1.41	2.9	5.47*	3.9	39.54**[†]
Common Yellowthroat	2,650	40.56**[†]	4.0	4.15*	1.3	118.8**[†]
American Redstart	3,129	23.55**[†]	2.1	40.09**[†]	1.6	109.29**[†]
Magnolia Warbler[‡]	4,604	123.91**[†]	3.2	157.44**[†]	4.0	250.86**[†]
Blackpoll Warbler[‡]	1,189	375.31**[†]	17.9	196.74**[†]	16.3	83.41**[†]
Black-throated Blue Warbler	2,160	268.75**[†]	6.7	17.22**[†]	1.8	31.66**[†]
Yellow-rumped Warbler[‡]	2,493	95.18**[†]	6.9	117.00**[†]	5.0	87.37**[†]
Black-throated Green Warbler	560	15.28**[†]	3.3	19.49**[†]	3.5	20.24**[†]
Canada Warbler	936	25.65**[†]	5.1	1.75	1.0	19.79**[†]
Wilson's Warbler	1,890	48.91**[†]	3.0	129.82**[†]	4.7	52.79**[†]

Notes: Uncorrected significance values: $*P \leq 0.05$, $**P \leq 0.005$. [†]Table-wide significance assessed with a sequential Bonferroni procedure. [‡]Significant interaction effect between sex and season ($P < 0.005$).

Yellow-rumped Warbler, and Blackpoll Warbler) showed a significant interaction between sex and season. In Magnolia Warbler and Blackpoll Warbler, males showed a greater difference in condition between seasons than did females. Male Magnolia Warblers had a 5.5% greater mean SMI in the spring than in the fall, compared with 1.9% for did females. Male Blackpoll Warblers had a 21.1% greater mean SMI in the spring than in the fall, compared with 5.3% for females. In contrast to Magnolia and Blackpoll warblers, female Yellow-rumped Warblers showed a greater seasonal difference in mean SMI between spring and fall than males (8.3% and 3.6%, respectively).

Arrival Date

ANCOVA results for all species showed significant relationships between arrival date and condition, regardless of season (Table 1). Regression analyses for spring migrants revealed a significant and consistent trend for all 12 species: Energetic condition increased with spring arrival date at BBBO for both males and females (Table 2 and Supplemental Material Figure S2). Estimates of the daily change in SMI across the spring season ranged from 0.1% (in Magnolia Warbler) to 1.2% (in Blackpoll Warbler) in females and from 0.2% (in Magnolia Warbler and American Redstart) to 1.2% (in Blackpoll Warbler) in males (Table 2). For fall migrants, regression analyses showed much less significant and less consistent trends with arrival date (Table 2 and Supplemental Material Figure S2). Four

species in the fall (Blackpoll Warbler, American Redstart, Common Yellowthroat, and Wilson's Warbler) showed patterns similar to those in spring (i.e. energetic condition increased with arrival date at BBBO). The mean daily change in SMI across the fall season for these 4 species ranged from 0.2% (in American Redstart, Common Yellowthroat, and Wilson's Warbler) to 0.6% (in Blackpoll Warbler) for females and from 0.2% (in American Redstart, Common Yellowthroat, and Wilson's Warbler) to 0.5% (in Blackpoll Warbler) for males. Four other species (Nashville Warbler, Black-throated Green Warbler, Black-and-white Warbler, and Canada Warbler) showed no significant relationship between arrival date in the fall and condition. In the remaining 4 species (Magnolia Warbler, Black-throated Blue Warbler, Yellow-rumped Warbler, and Mourning Warbler), one sex had a significant regression between condition and the other did not (for a summary of intraspecific fall differences, see Table 2).

DISCUSSION

Most Parulids Arrive in Better Condition in Spring Than in Fall

In 11 of 12 species, we found that males and females had greater energy reserves in spring than in fall. This suggests that individuals of both sexes deposit and carry more energy reserves en route in the spring, which could potentially be directed toward survival en route or

TABLE 2. Regression results (*F* and *P* values) for 12 warbler species captured at Braddock Bay Bird Observatory, Monroe County, New York, USA, 1999–2012, showing the effect(s) of arrival (or capture) date on energetic condition (i.e. scaled mass index [SMI]) for each sex during both spring and fall migration. For each species, the linear regression slopes (in SMI g day^{-1}; shown in Supplemental Material Figure S2) and average SMI (g) of all birds with a fat score of zero were used to calculate a percent change in condition (SMI) across the season (percent change in SMI from lean mass day^{-1}, or ΔSMI day^{-1}). (Regression plots for each sex for all 12 species are shown in Supplemental Material Figure S2.)

	Female			Male		
Species	*n*	*F*	ΔSMI day^{-1}	*n*	*F*	ΔSMI day^{-1}
Spring migration						
Black-and-white Warbler	258	18.09**[†]	0.3%	222	30.81**[†]	0.5%
Nashville Warbler	253	13.37**[†]	0.3	495	51.20**[†]	0.4
Mourning Warbler	274	16.95**[†]	0.5	246	26.97**[†]	0.5
Common Yellowthroat	901	41.49**[†]	0.4	1,163	95.22**[†]	0.3
American Redstart	1,333	28.70**[†]	0.2	1,393	45.76**[†]	0.2
Magnolia Warbler	947	6.48*[†]	0.1	1,752	17.56**[†]	0.2
Blackpoll Warbler	373	53.35**[†]	1.2	342	52.57**[†]	1.2
Black-throated Blue Warbler	702	22.12**[†]	0.3	493	52.48**[†]	0.4
Yellow-rumped Warbler	800	81.40**[†]	0.5	1,258	68.53**[†]	0.4
Black-throated Green Warbler	100	4.35*[†]	0.2	182	27.70**[†]	0.3
Canada Warbler	452	13.15**[†]	0.3	418	13.24**[†]	0.3
Wilson's Warbler	292	10.83**[†]	0.4	1,088	57.11**[†]	0.4
Fall migration						
Black-and-white Warbler	49	2.91	0.2%	42	0.12	0.1%
Nashville Warbler	164	0.11	0.0	129	3.72	0.2
Mourning Warbler	14	7.19*	0.5	17	1.94	0.5
Common Yellowthroat	129	4.59*	0.2	456	8.12**	0.2
American Redstart	214	17.23**[†]	0.2	189	9.02**	0.2
Magnolia Warbler	429	1.72	−0.1	1,403	16.82**[†]	0.1
Blackpoll Warbler	171	18.87**[†]	0.6	303	26.31**[†]	0.5
Black-throated Blue Warbler	506	26.06**[†]	0.2	459	1.29	0.0
Yellow-rumped Warbler	226	0.1	0.0	209	7.11*	0.2
Black-throated Green Warbler	55	0.46	0.1	96	3.07	0.1
Canada Warbler	33	0.51	0.2	33	0.33	0.1
Wilson's Warbler	191	5.25*	0.2	319	13.61**[†]	0.2

Notes: Uncorrected significance values: *$P \leq 0.05$, **$P \leq 0.005$. [†]Table-wide significance assessed with a sequential Bonferroni procedure.

toward reproductive efforts at the breeding grounds, if these reserves carry over. Reproduction is costly for females because of energetic investment(s) in egg production, and for males because of investments in singing and in acquisition and defense of territory. Both sexes, therefore, have energetic demands related to breeding and to surviving unpredictable and potentially harsh spring conditions and thus could benefit from excess fat reserves during spring migration, whether en route or upon arrival at breeding grounds (Gudmundsson et al. 1991, Sandberg and Moore 1996). In studies on the breeding grounds of some species, both males and females arrived in the spring with relatively high fat reserves (Norment 1992, Sandberg 1996, Fransson and Jakobsson 1998).

Likewise, both sexes may have similar constraints or pressures during fall migration that may lead to relatively lower condition. The lower fall condition of both sexes may reflect differences in the location of our study site in relation to the goal area for migration (i.e. near the beginning of migration in fall, near the end of migration in spring); birds of both sexes have likely incurred significant energy costs during breeding and are likely recuperating and/or adding fuel reserves at stopover sites during fall migration (Bonter et al. 2007; see below). Moreover, the location of our field site in relation to Lake Ontario may influence or accentuate seasonal differences in condition; migrants that had recently crossed Lake Ontario in the fall may have experienced depleted energy reserves compared to spring migrants, which had not yet crossed the lake. However, Lake Ontario is a relatively small barrier (which would incur a relatively minimal energetic cost to cross). It is also unlikely that our spring birds had the time to fatten upon arrival in preparation for crossing the lake—most of the birds were captured within 6 hr after sunrise, likely after an overnight
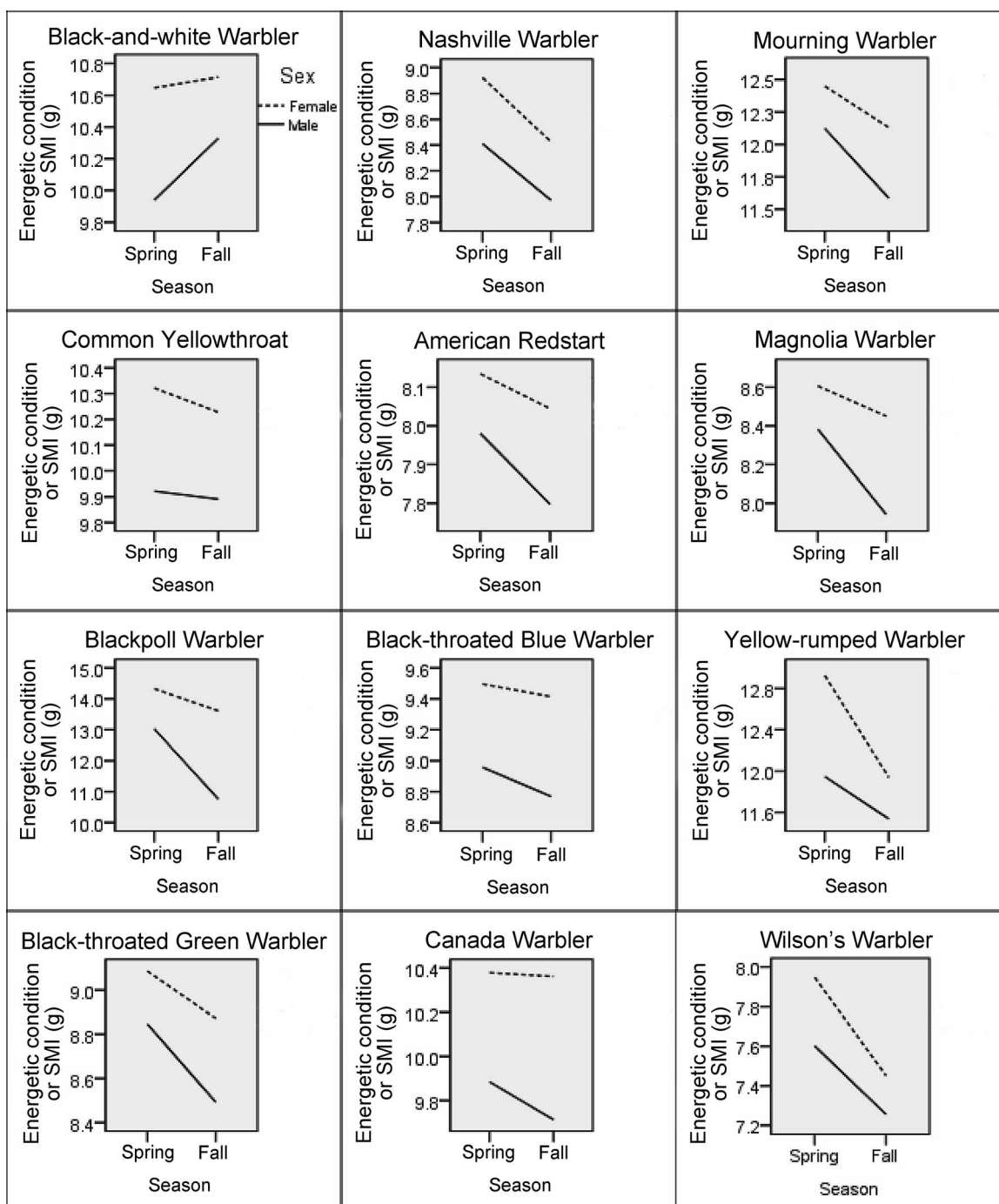
FIGURE 1. Interaction line plots for 12 warbler species captured at Braddock Bay Bird Observatory, Monroe County, New York, USA, showing the effect(s) of season and sex on energetic condition. Scaled mass index (SMI) is reported in grams; mean female SMI values for fall and spring are connected with a dashed line, and mean male SMI values for fall and spring are connected with a solid line.

migratory flight, and their energy reserves were likely carried over from a previous stopover at a North American site to the south. Consistent with our results, Seewagen (2008) found that male and female parulids stopping over near New York City, a site with no obvious

water barrier, had greater fat reserves in the spring than in the fall. Finally, we found consistent differences in energetic condition between sexes at BBBO, which suggests that parulids are not overloading solely to cross Lake Ontario during spring; if increased condition were

due only to the cost of crossing Lake Ontario, we would expect little difference between males and females.

In contrast to the other 11 species, Black-and-white Warblers at our field site showed an inverse seasonal pattern (i.e. both males and females were in better condition in the fall). Reasons for this pattern are unclear, although interspecific differences in migratory behavior and foraging ecology (Sandberg 1996) or intraspecific differences carried over from previous life stages (Paxton and Moore 2015) may influence energetic condition during migration.

Female Parulids Arrive in Better Condition Than Males

Females of all 12 species were in better energetic condition than males upon arrival at our study site during spring migration. This finding is congruent with one prediction of the breeding performance hypothesis: that, given the high energy demands of egg production, females en route to breeding grounds should deposit and carry more fat and arrive with more energy reserves than males (Sandberg and Moore 1996). Females begin reproductive activities shortly after arriving on breeding grounds (Ojanen 1984), which may lend additional value to any fat reserves accumulated en route. However, parulids are income breeders (Langin et al. 2006), so any benefit incurred from arriving on breeding grounds with energy reserves would likely be indirect (e.g., beginning reproductive activities earlier) rather than direct (e.g., energy directed toward egg production).

Support for the breeding performance hypothesis is partially complicated by the finding that females are in better energetic condition than males at our study site during both spring and fall migration; therefore, this sex difference may not be fully attributable to breeding activities. Excess energy reserves are likely not just incidental of birds accumulating calories and mass for growth. Energy reserves are beneficial for songbirds during migration (McWilliams et al. 2004) and upon arrival at breeding grounds (Sandberg and Moore 1996); however, reserves can negatively affect maneuverability (e.g., Kullberg et al. 1996). This trade-off suggests that a migrant's energy reserves are advantageous rather than incidental.

Birds Arriving Earlier in Spring Are in Lower Energetic Condition Than Birds Arriving Later

We found that the energetic condition of all species increased with capture (assumed arrival) date during spring; therefore, for all species, the earliest spring birds to arrive at our site were in lower energetic condition than later arrivals. Our findings for this study site contradict the prediction of the insurance hypothesis that earlier arrivals should carry excess fat en route to northern breeding grounds as insurance against inclement or unpredictable weather earlier in the season (Sandberg and Moore 1996).

A possible explanation for a direct relationship between condition and arrival date is that as environmental conditions (i.e. weather, temperature, resources) become more favorable later in the spring, birds are better able to gain and maintain mass en route (Dunn 2000, Bonter et al. 2007). Earlier in the spring, some migrants actually lose mass at northern stopover sites, likely because of poor resource levels and/or thermoregulatory challenges (Dunn 2000).

The implications of excess fuel reserves (and sexual disparity of condition) in the spring need to be interpreted in light of arrival-time differences among individuals. The earliest-arriving individuals in the spring were consistently male (Supplemental Material Figure S1), which is indicative of the differential timing of spring migration that is widespread in parulids across North America (Francis and Cooke 1986, Yong et al. 1998, Morris et al. 2003, Smith and Moore 2005, Benson et al. 2006). Males of some species depart from wintering grounds before females (Marra et al. 1998), and males may opt for a time-minimization strategy to arrive earlier (Paxton and Moore 2015). Males that arrive early might be more likely to secure high-quality territory and, hence, increase fitness (see Sandberg and Moore 1996, Kokko 1999). Moreover, there is evidence, for both sexes, that high-quality individuals arrive on breeding grounds earlier (e.g., Cooper et al. 2011) and that arriving early confers increased reproductive success (Smith and Moore 2003, 2005, Cooper et al. 2011). Therefore, it should be beneficial for both sexes to arrive early on breeding grounds and with excess energy reserves to offset the energetic demands of reproductive activities (e.g., Sandberg and Moore 1996). However, we found that the earliest-arriving birds of either sex were in poorer condition than those that arrived later, which suggests that there may be a trade-off between arriving early and arriving in good condition.

Stopover Ecology and Translating Energetic Condition Patterns to Breeding Grounds

The Braddock Bay region is not a likely breeding site for most of the individuals and species we examined. Of the 12 species, 10 are unlikely breeders or do not breed in this area, and only 2 (Common Yellowthroat and American Redstart) are common breeders in the region (McGowan and Corwin 2008). Even for those species that breed locally, we anticipate—on the basis of species range and the number of birds banded and locally recaptured (data not shown) during migration at BBBO—that most individuals were not local residents. The precise breeding location (i.e. remaining migratory distance) of the parulids that stop over at Braddock Bay is unknown and likely variable. For instance, Blackpoll Warblers could breed anywhere from ~500 km to ~6,500 km from BBBO. However, when considering the scale of total migration

distance for most parulids, the Braddock Bay area is relatively close to breeding grounds and is clearly a stopover site near the end and beginning of migration during the spring and fall, respectively. The south shore of Lake Ontario could arguably be a penultimate stopover location during spring for at least some of the individuals and populations banded at BBBO, with a high likelihood of carryover effects between stopover and breeding.

Braddock Bay should provide adequate resources for most migrating songbirds, but habitat quality is likely better in the fall for warblers because of the delayed spring phenology caused by proximity to Lake Ontario (Bonter et al. 2007, Smith 2013). Bonter et al. (2007) demonstrated that energetic condition varies with time of day and, like others (e.g., Dunn 2002), used hourly regression analyses to show that many species of migrants can gain mass even in one day while stopping over near Braddock Bay. In the spring, Bonter et al. (2007) found that mean hourly mass change ranged from 0.33% to 1.13% of lean mass, with an average of 0.69% for 10 warbler species included in our study. In the fall, mean hourly mass change was higher overall than in the spring, and ranged from 0.79% to 1.58%, with an average of 1.03% for 7 warbler species in our study. Interestingly, our results show that these warblers arrived at Braddock Bay in poorer condition in the fall than in the spring; and at this stopover site, fall migrants in poorer condition have the opportunity to gain more mass prior to continuing migration than they would in the spring. Therefore, in the fall, these birds potentially carry less fat upon leaving their breeding grounds because they can acquire adequate fuel reserves en route, even at relatively northern stopover locations. Likewise, the lower hourly mass gains upon arrival in the spring at BBBO (and other northern sites; Dunn 2002) suggest that the differences in energetic condition between males and females will probably not be offset by additional mass gain at this stopover site or en route to the breeding grounds. Although the lower hourly mass gains in spring could be offset if individuals stay longer, the fast pace of spring migration and urgency to reach breeding grounds, particularly for males (Dierschke et al. 2005), likely minimize stopover length for most individuals; hence, patterns in energetic condition between our stopover study site and arrival on breeding grounds would likely be small.

Conclusion

Our results elucidate seasonal and sexual differences in the energetic condition of 12 warbler species that used stopover habitat near BBBO. In general, our findings lend support to the breeding performance hypothesis, but not the insurance hypothesis. However, we cannot make conclusive statements about how the energetic condition of birds at our study site affected their subsequent reproductive performance. Given our finding that both males and females are consistently heavier during spring migration when resources are scarcer than during fall (Bonter et al. 2007), we can cautiously conclude that there is a possible reproductive advantage to carrying excess fat reserves en route to breeding grounds during spring migration. Females are in better condition than males (even when we controlled for arrival-time differences), which suggests there may be a sexually asymmetrical advantage of carrying excess fuel reserves during spring migration.

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