

## HIGH-LATITUDE PASSERINE MIGRANTS OVERLAP ENERGETICALLY DEMANDING EVENTS IN AUTUMN

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**ABSTRACT.**—Temporal constraints on migratory birds to molt, store fat, and migrate in autumn are probably most severe in populations breeding at high latitudes. We examined whether high-latitude time constraints were related to the overlap of these energetically demanding events in migratory passerine species. We also examined how much overlap of molt and fattening occurs within individuals. Data were collected on molt intensity and subcutaneous fat during autumn migration from 1992 to 2004 in Fairbanks, Alaska, (64° 50' N 147° 50' W). Among 17 migrant species, we found a negative relationship between length of breeding ground occupancy (number of days between median spring and autumn passage, our measure of time constraints) and the amounts of molt-migration overlap. There was also a positive relationship between molt-fat overlap and distance to wintering range among these 17 species. No individual completely overlapped the peak levels of both molt intensity and fat storage observed within a species, but several individuals approached this theoretical maximum in four species. Molt-fat overlap was highest in an individual Yellow Warbler (*Setophaga petechia*) that achieved 70% of the maximum possible overlap of peak fat storage and peak molt intensity for that species. These findings indicate that high-latitude passerines can overlap energetically demanding events during the annual cycle but that there is considerable variation among species in how they juggle time and energy constraints. Our data provide strong support for a conceptual model that passerine migrants breeding at high latitudes use strategies that reduce the time required to complete breeding season activities. In doing so, many of these birds appear to push energetic limits by overlapping molt, migration, and fattening to a degree not previously documented. Received 10 March 2014. Accepted 24 April 2015.

Key words: fattening, migration, molt, passerines, time-energy tradeoffs.

At high latitudes, long-distance avian migrants occupy their breeding grounds for relatively brief periods. After reproductive activities are completed, most species undergo a complete prebasic molt (Dwight 1900, Jenni and Winkler 1994), which is energetically costly and in passerines requires a minimum of 28 to 45 days for completion (Morton et al. 1969, Payne 1972, Rimmer 1988, Vega Rivera et al. 1998, Flockhart 2010). Next, migrants must deposit fat, which also requires time and energy (Berthold 1975, Blem 1990). Finally, after molting and fattening, these birds must migrate to lower latitudes for the long nonbreeding season. Migration, fueled by stored fat, is also energetically costly (Berthold 1975, Blem 1990). Consequently, migration is usually temporally separated from molt (Payne 1972, Cannell et al. 1983, Ginn and Melville 1983, Vega Rivera et al. 1998). Separating energetically costly events such as molt and migration reduces immediate energetic demands on individuals and is thought to be an important strategy given limits to the amount of energy that an

animal can obtain from its environment each day (Kendeigh 1949, Kirkwood 1983).

Despite the advantages of temporally separating energetically costly events, time-limited species have less flexibility in scheduling prebasic molt and subsequent migration. For example, Lesser Whitethroats (*Sylvia curruca*) increase the speed of molt under constrained situations (Hall and Fransson 2000), while in other species the speed of molt among birds at high latitudes is likely to already be at a maximum given flight or thermoregulatory constraints, e.g., in Willow Warblers (*Phylloscopus trochilus*; Underhill et al. 1992) and Bluethroats (*Luscinia svecica*; Lindström et al. 1994). In North America, very few long-distance passerine migrants have been found to forego a breeding ground prebasic molt and do it instead on their wintering grounds after migration, e.g., Alder Flycatcher (*Empidonax alnorum*; Dwight 1900). If the speed of molt cannot compensate for time constraints, then time-constrained birds might overlap molt with other energetically demanding events, such as breeding or fattening for migration.

Bluethroats can overlap molt and fat deposition in extreme laboratory conditions, but under natural circumstances these events are temporally separated (Lindström et al. 1994). However, naturally occurring molt-breeding overlap has been found in some high-latitude populations. For example,

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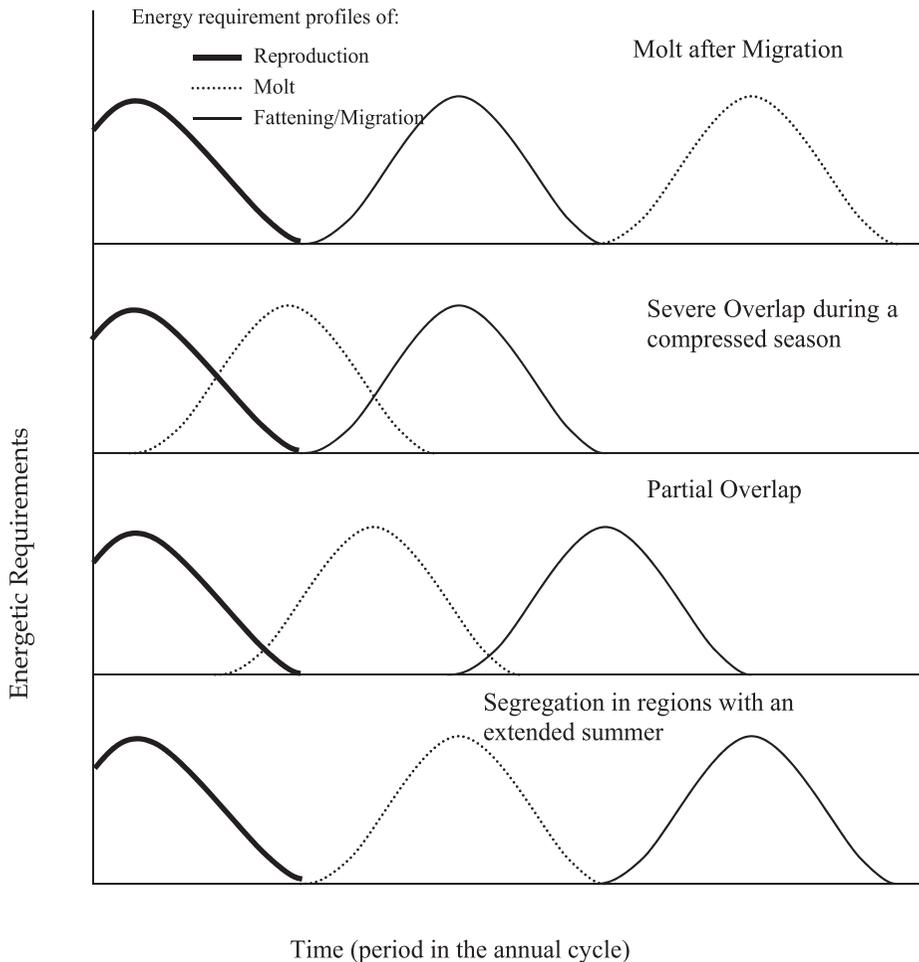


FIG. 1. Strategies for juggling the major energetic demands (life history events) of summer and autumn among migratory birds under increasing time pressures. Curves are idealized, with energetic requirements being highest at the peaks of reproduction, molt, and migration (heights and widths made uniform just for illustrative purposes). The strategy of delaying molt until after migration is exhibited in some species.

some birds begin molting while still caring for fledglings (Rimmer 1988, Hemborg et al. 1998, Flockhart 2010), and overlap of molt and migration has been documented in several passerine migrants (Cannell et al. 1983, Rimmer 1988, Winker et al. 1992, Jenni and Winkler 1994, Yuri and Rohwer 1997, Norris et al. 2004, Flockhart 2010). The cost of molting during migration is not well documented, but in Barn Swallows (*Hirundo rustica*), there are reduced energy stores for birds molting compared with those that are not molting during migration (Rubolini et al. 2002). These observations are summarized in a conceptual model suggesting increasing levels of overlap with increasing time constraints (Fig. 1).

Seasonal time constraints are known to affect life histories of several taxa (e.g., Rowe and Ludwig 1991, Rowe et al. 1994, Johansson and Rowe 1999). In Fairbanks, Alaska, near the western and northern extreme of the continental landmass, the brief subarctic summer causes time constraints for individuals nesting near the northern limits of species' ranges. Therefore, autumn migration at high latitudes provides an opportunity for examining individual and species-level responses to some of the most extreme temporal pressures that migratory birds encounter. Extreme cold temperatures and early winter storms often occur in September, before all migrants have departed, providing, in theory, rather strong

evolutionary pressures for migrants to complete their breeding ground activities and depart without delay. If long-distance migrants respond to temporal constraints by overlapping energetically expensive events, as some evidence shows, then this overlap should be most visible among populations breeding at the highest latitudes of a species' breeding range, such as those breeding in and near Interior Alaska. Here, we examine the following questions: 1) Is there correlation between species-specific time constraints (number of days spent on the breeding grounds) and the amount of molt-fattening overlap or molt-migration overlap? We hypothesized that species with increased time constraints (shorter high-latitude breeding seasons) are more likely to overlap energetically demanding events than species that are less constrained by time. 2) Do molting individuals have lower fat scores than nonmolting individuals? We expected molting birds to pay a cost, in terms of lower fat scores, compared with nonmolting birds, because molt is energy demanding and may limit an individual's ability to fatten. 3) How frequently and to what extent do individuals at high latitudes overlap molt and fattening?

#### METHODS

*Data Collection.*—We operated mist nets at Creamer's Field Migration Station (CFMS), in Fairbanks, Alaska (64° 50' N, 147° 50' W). CFMS spans ~ 20 ha and includes the most common habitats locally available in this regional boreal forest (e.g., the station has mature spruce-birch forest, mid-successional aspen, and a mixed-shrub riparian areas; see Benson and Winker 2001 for more details). Our netting protocol used an array of 22–50 standard mist nets (30 mm mesh, 2.6 m × 12 m) operated daily beginning at sunrise and closing 7 hrs later from 1992–2000, and for 6 hrs from 2001–2004. Nets were operated daily from 15 July to 25 September and every other day from 26 to 30 September. These dates span the autumn migration of passerines in interior Alaska; after these dates, observations of migrant passerines are rare. For more details on our spring netting program, see Benson and Winker (2001).

For these analyses, we included only those species in which adults undergo a complete prebasic molt prior to autumn migration (Dwight 1900). Data on fat score, remex molt, and body molt were not always collected on each individual when large numbers of birds were captured

simultaneously and birds were processed quickly. Therefore, sample sizes of individuals included in each analysis vary. For example, many individuals were examined for the presence or absence of remex molt (used for comparing species-level overlap of molt and migration), but the intensity of remex molt was not recorded for all individuals and, therefore, an equal number of records could not be used for examining individual overlap of molt and fattening.

*Definition of Autumn Migrants.*—We examined species in which at least 30 adult individuals were captured (outside of local breeders; see below) during the 13 years of netting. We excluded hatch-year birds from these analyses because they do not undergo a prebasic molt (Dwight 1900); this paper thus considers only adults. All captured individuals were aged using degree of skull ossification. Birds that bred locally were excluded (e.g., females with incubation patches and birds banded during the breeding season). We also removed the first five percent of non-breeding captures to further exclude potential nonmigrants. Although we began autumn mist netting on 15 July (Julian date = 196 for most years), the first individual considered a migrant and included in these analyses is 4–6 weeks after this date for most species (Table 1). For example, Yellow-rumped Warblers (*Setophaga coronata*) bred at our study location and were frequently caught during the summer netting program. However, although netting began on 15 July (Julian date 196 in most years), the first Yellow-rumped Warbler included in these analyses was not captured until 30 days later (Fig. 2). The species is rarely observed in interior Alaska after 30 September. The number of birds captured during the breeding season is extremely small when compared with the vast numbers that move through CFMS during migratory period. After removal of known or suspected local breeders, we assumed that the vast majority of the birds in subsequent analyses were migrants.

*Molt.*—We consider molt in two ways in this study: its presence/absence and, if present, the intensity for each individual. We quantified molt intensity based on the number of remex feathers growing among individuals molting in a standard symmetrical sequence (Dwight 1900). Number of remex feathers growing was identified by a visual inspection of the feathers by spreading the wing and examining the underside. Feathers were considered growing if they had a sheath and appeared to be <100% of the full length. Body molt occurs

TABLE 1. First Julian day captured birds were included in analyses, and correlation between body molt and remex molt among adults captured during autumn migration in Fairbanks, Alaska (1992–2004).

Species	First day	Body and remex molt	
		<i>n</i>	<i>r<sub>s</sub></i>
Hammond's Flycatcher ( <i>Empidonax hammondi</i> )	202	29	0.59 <sup>a</sup>
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	237	99	0.26 <sup>b</sup>
Gray-checked Thrush ( <i>Catharus minimus</i> )	230	56	0.49 <sup>a</sup>
Swainson's Thrush ( <i>Catharus ustulatus</i> )	226	100	0.42 <sup>a</sup>
American Robin ( <i>Turdus migratorius</i> )	236	94	0.39 <sup>a</sup>
Orange-crowned Warbler ( <i>Oreothlypis celata</i> )	230	530	0.36 <sup>a</sup>
Yellow-rumped Warbler ( <i>Setophaga coronata</i> )	228	360	0.43 <sup>a</sup>
Yellow Warbler ( <i>Setophaga petechia</i> )	203	86	0.58 <sup>a</sup>
Blackpoll Warbler ( <i>Setophaga striata</i> )	223	35	0.27
Northern Waterthrush ( <i>Parus noveboracensis</i> )	218	30	0.18
Wilson's Warbler ( <i>Cardellina pusilla</i> )	225	97	0.33 <sup>a</sup>
American Tree Sparrow ( <i>Spizella arborea</i> )	245	510	0.34 <sup>a</sup>
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	221	34	0.23
Fox Sparrow ( <i>Passerella iliaca</i> )	235	84	0.17
Lincoln's Sparrow ( <i>Melospiza lincolni</i> )	200	67	0.39 <sup>a</sup>
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	223	52	0.41 <sup>a</sup>
Dark-eyed Junco ( <i>Junco hyemalis</i> )	239	259	0.32 <sup>a</sup>

<sup>a</sup>  $P < 0.003$ .<sup>b</sup>  $P < 0.05$ .

simultaneously with remex molt; consequently, remex molt alone has been used as an index for the entire prebasic molt (e.g., Rimmer 1988). To validate the use of remex molt as a singular molt intensity index, we compared intensity of body molt with intensity of remex molt (based on the number of primaries or secondaries molting) using Spearman's rank correlation. Intensity of body molt was determined by examining the bases of the contour feathers on the bird's body and was classified based on a four-class scoring system: 0 (no body molt); 1 (light body molt; less than 1/3 of body contour feathers molting); 2 (medium body molt; from 1/3 to 2/3 of a bird's body contour feathers molting); and 3 (heavy body molt; more than 2/3 of the body contour feathers molting). When all species were combined, body molt and remex molt were correlated ( $r^2 = 0.451$ ,  $t = 26.05$ ,  $n = 2,654$ ,  $P < 0.001$ ). And there was a significant relationship between intensity of body molt and remex molt among adults in 13 of 17 species (Table 1). We found no significant correlation between body molt and remex molt for four species, but sample sizes of these species were less than the average of 148 individuals (Table 1) and these smaller sample sizes likely affected the power to detect a relationship. Additionally, a significant correlation between body and remex molt was difficult to detect because there were just

four body-molt categories and a maximum of 16 flight feathers growing. We considered flight-feather molt to be a better measure of molt stage because, unlike body molt, it is not estimated and it is easily quantified. Therefore, body molt data are not considered further.

*Fat.*—Observations of subcutaneous fat deposits, based on an eight-class scoring system modified from Helms and Drury (1960), were used as indicators of total body fat: 0) no fat observed in the furculum or on the abdomen; 1) trace of fat on the furculum and abdomen; 2) thin layer of fat on the furculum and abdomen; 3) one-half furculum fat filled, fat covering most of the abdomen; 4) fat in the furculum level with clavicles and slightly mounded on the abdomen; 5) slightly bulging in furculum, abdomen well mounded; 6) greatly bulging in furculum and mounded on abdomen; 7) large fat pads from the furculum and abdomen meet. Fat scores are independent of water and gut content, and provide a reliable index of lipid content that can be compared among species (Brown 1996). We did not use body condition indices (e.g., mass/wing) in these analyses, because body mass varies during molt in relation to the numbers of growing feathers (King et al. 1965, Holmes 1966, Newton 1968, Evans 1969, Myrcha and Pinowski 1970). Fat scores are not a measure of fattening rate, but rather a single

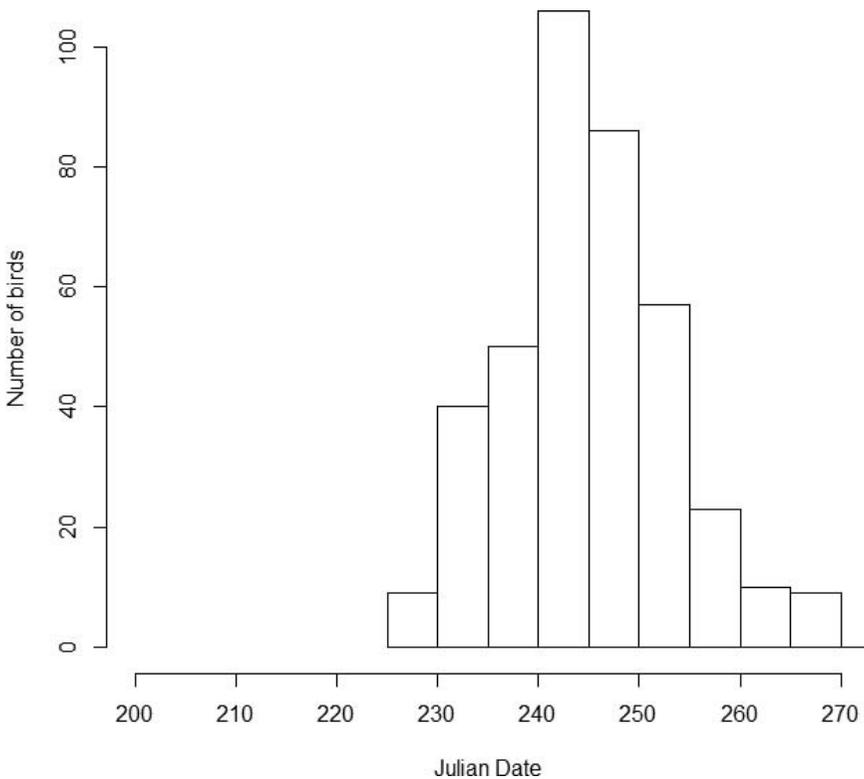


FIG. 2. Illustration of capture pattern of adult Yellow-rumped Warblers (*Setophaga coronata*,  $n = 392$ ) at CFMS. This species is a local breeder captured throughout the summer netting period, yet the first individual considered a migrant for these analyses was not captured until 30 days after the autumn netting period was initiated on Julian Date 196 (15 July in non-leap-years).

estimate of fat deposits; we use the shorthand term ‘fattening’ for evidence of fat deposition (total body fat score > 0) during migration.

#### Data Analysis

*Species-Level Comparisons.*—We fit general linear models to our data to evaluate factors influencing molt-fat overlap and molt-migration overlap among species. For both responses, molt-migration overlap and molt-fat overlap, we constructed a plausible model set, comprised of the following models:

$$\begin{aligned} \text{Overlap}_i &= b_0 + e_i \\ \text{Overlap}_i &= b_0 + b_1 \text{Duration}_i + e_i \\ \text{Overlap}_i &= b_0 + b_2 \text{Diet}_i + e_i \\ \text{Overlap}_i &= b_0 + b_3 \text{Distance}_i + e_i \\ \text{Overlap}_i &= b_0 + b_4 \text{Genus}_i + e_i \\ \text{Overlap}_i &= b_0 + b_5 \text{Species}_i + e_i \\ \text{Overlap}_i &= b_0 + b_1 \text{Duration}_i + b_2 \text{Diet}_i + e_i \\ \text{Overlap}_i &= b_0 + b_2 \text{Diet}_i + b_3 \text{Distance}_i + e_i \end{aligned}$$

In these models,  $\text{Overlap}_i$ , our response, was the percent of birds molting during migration (molt-migration overlap) or the percent of birds fattening during molt (molt-fat overlap) for the  $i^{\text{th}}$  species. We used an angular transformation of the response variable, i.e.,  $\sin^{-1} \sqrt{\text{percent overlap}}$ , which is commonly used when modeling proportions to ensure that the data distribution was approximately normal (Zar 2010).  $\text{Duration}_i$  was the estimated breeding season duration (Benson and Winker 2001) for the  $i^{\text{th}}$  species.  $\text{Diet}_i$  was a categorical variable (plant, animal, mixed), for the  $i^{\text{th}}$  species (using data from del Hoyo et al. 2004–2011).  $\text{Distance}_i$  (km) was estimated migration distance from the center of the wintering range to CFMS (using del Hoyo et al. 2004–2011; Poole and Gill 2005; and Google Earth, Google Inc., Mountain View, CA, USA),  $b_0$  is the intercept,  $e_i$  is random error. We also ran models including family and genus to examine phylogenetic effects. We did not include distance and duration in the same model

TABLE 2. Differences in median fat scores between molting and nonmolting adults, and percent of individuals overlapping molt and migration and molt and fattening during autumn migration in Fairbanks, Alaska (1992–2004).

Species	Fat scores					Overlap			
	Molting		Nonmolting		$Z^a$	Molt and migration		Molt and fat	
	<i>n</i>	Median	<i>n</i>	Median		<i>n</i>	% <sup>b</sup>	<i>n</i>	% <sup>c</sup>
Hammond's Flycatcher	26	0	9	0	-0.54	35	71.4	35	31.0
Ruby-crowned Kinglet	13	1	92	1	-0.18	105	12.4	105	10.5
Gray-cheeked Thrush	24	2	36	2	-0.02	60	40.0	60	33.3
Swainson's Thrush	36	2	69	2	-0.15	105	34.3	105	30.5
American Robin	15	1	84	3	-3.81*	99	15.2	99	9.1
Orange-crowned Warbler	88	1	459	1	-1.10	550	16.4	547	10.8
Yellow-rumped Warbler	160	1	229	1	-1.83	392	41.6	389	23.4
Yellow Warbler	36	0	56	2	-2.46*	93	38.7	92	18.5
Blackpoll Warbler	11	1	28	2	-0.61	39	28.2	39	20.5
Northern Waterthrush	11	0	22	1	-1.64	34	32.4	33	12.1
Wilson's Warbler	12	2	89	2	-0.39	101	11.9	101	8.9
American Tree Sparrow	40	1	473	2	-2.78*	513	7.8	513	5.6
Savannah Sparrow	8	0	27	1	-2.19*	36	22.2	35	2.8
Fox Sparrow	8	1	75	1	-0.49	83	9.6	83	7.2
Lincoln's Sparrow	35	1	40	2	-2.37*	76	47.4	75	22.7
White-crowned Sparrow	21	1	34	2	-1.31	55	38.2	55	27.3
Dark-eyed Junco	50	1	216	1	-1.66	266	18.8	266	10.9

<sup>a</sup>  $Z$ -values from Mann-Whitney  $U$ -test comparing fat scores between molting and nonmolting birds, \*  $P < 0.05$ , \*\*  $P < 0.003$ .

<sup>b</sup> Percentage of captured birds molting during migration.

<sup>c</sup> Percentage of captured birds showing any fattening during molt.

because these variables are negatively correlated ( $r^2 = -0.616$ ,  $P = 0.008$ ). Samples were pooled across the entire study period, rather than compared among years, because small sample sizes prevented a more refined grouping.

**Model Selection.**—We used an information theoretic approach wherein the “best” model had the smallest AIC score (Akaike's Information Criterion corrected for small sample sizes, Burnham and Anderson 2002). The best models were evaluated with standard diagnostics, and we did not find evidence of departure from a normal error distribution, nonconstant variance, and no data points were overly influential in our models.

**Overlap of Molt and Fattening within Individuals.**—We used the following heuristic approach to make comparisons of individuals within species. For each species, we determined a theoretical maximum model: an individual exhibiting complete overlap of molt and fattening (i.e., simultaneously exhibiting the highest fat score and the highest remex growth score recorded for that species at our study site). Each individual in the data set was given an overlap score of 0–100% by multiplying its fat percentage (its fat score divided by the highest fat score recorded for that species at our study site) by its molt percentage (its remex growth intensity score divided

by the highest remex growth intensity score recorded for that species at our study site). For example, an individual exhibiting 80% of the maximum fat level exhibited in the species while at the same time exhibiting 50% of the highest remex growth score for the species would have an overlap of 40% ( $80\% \times 50\%$ ) of the theoretical maximum (complete overlap, or 100% using this index). We recognize that this is a local solution dependent on our sampled populations and this comparison is not without limitations. However, it is a useful means of assessing individuals in these populations and also of making among-species heuristic comparisons, too. More details are given in the Appendix, and the distribution of fat scores and number of molting feathers is illustrated in Supplemental Material Figs. A2 and A3. For species with large enough sample sizes (evaluated by whether the data resembled a normal distribution and diagnostics indicated model fit), we also conducted linear regression analysis to examine whether Julian date influenced the amount of overlap within an individual.

## RESULTS

**Species-Level Comparisons.**—All 17 species examined had individuals that overlapped molt and migration and/or molt and fattening. Proportions

TABLE 3. Results from eight models used to evaluate factors influencing the amount of molt-migration overlap (proportion of birds molting during migration).

	Parameters	Deviance	AICc	ΔAICc	AICc weight
Duration	3	-24.32	-16.48	0	0.93
Null	2	-14.04	-9.18	7.3	0.02
Diet duration	5	-24.44	-8.99	7.49	0.02
Distance	3	-16.48	-8.63	7.84	0.02
Diet	4	-15.68	-4.36	12.12	0.00
Family	6	-23.22	-2.82	13.65	0.00
Diet distance	5	-16.82	-1.37	15.11	0.00
Genus	14	-56.64	181.35	197.83	0.00

ranged from 71% of Hammond’s Flycatchers (*Empidonax hammondi*) to 8% of American Tree Sparrows (*Spizella arborea*) molting during migration (Table 2). The percentage of individuals fattening during molt ranged from 31% of Hammond’s Flycatchers to just 3% of Savannah Sparrows (*Passerculus sandwichensis*; Table 2).

The best model for estimating molt-migration overlap for 17 species contained only estimated duration on the breeding grounds as an explanatory variable (Table 3). This model had 93% of the weight of the model set (Table 3). Among the 17 species there was a significant negative relationship between length of breeding range occupancy

and the amount of molt-migration overlap ( $r^2 = -0.42$ ,  $F = 10.66$ ,  $P = 0.005$ ,  $n = 17$ ; Fig. 3). Taxonomy (family or genus) was not a useful predictor of molt-migration overlap.

The best model for estimating molt-fattening overlap among 17 species contained only estimated distance to the center of the wintering range (Table 4). This model had 61% of the weight of the model set (Table 4). There was a positive relationship between distance to wintering range and the amount of molt-fattening overlap among species ( $r^2 = 0.299$ ,  $F = 6.41$ ,  $P = 0.023$ ,  $n = 17$ ; Fig. 4). Taxonomy was not a useful predictor of molt-fattening overlap.

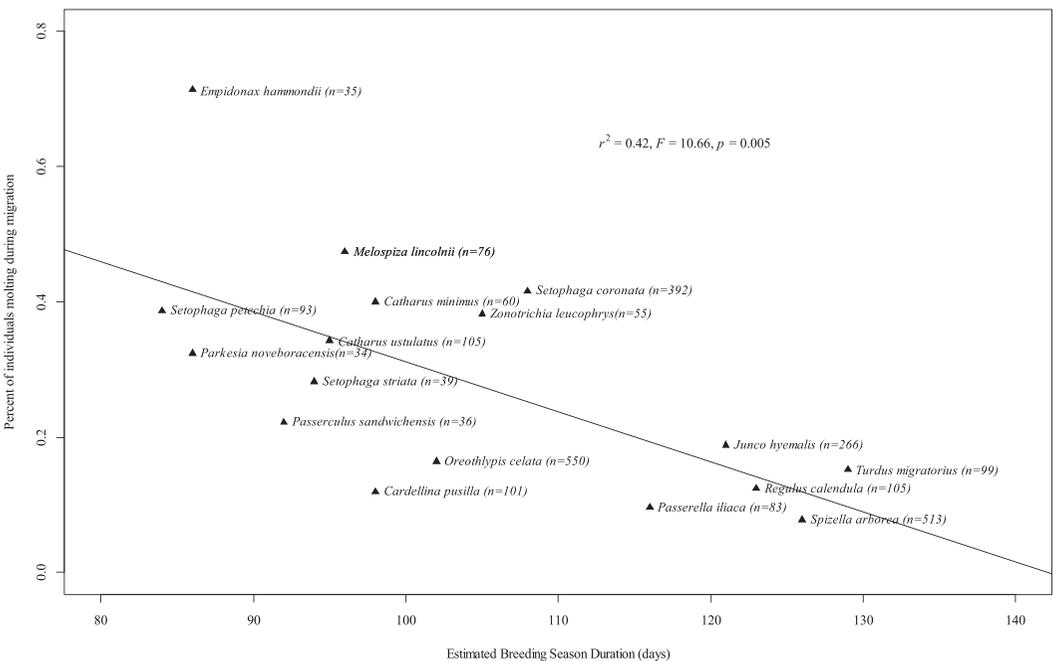


FIG. 3. The relationship between duration of breeding ground occupancy and overlap of molt and migration among species in Fairbanks, Alaska (1992–2004).

TABLE 4. Results from eight models used to evaluate factors influencing the amount of molt-fat overlap (proportion of birds storing body fat during the molt).

	Parameters	Deviance	AICc	$\Delta$ AICc	AICc weight
Distance	3	-29.12	-21.28	0.00	0.61
Duration	3	-26.76	-18.91	2.37	0.19
Null	2	-23.30	-18.44	2.84	0.15
Diet	4	-26.14	-14.81	6.47	0.02
Diet distance	5	-29.68	-14.23	7.05	0.02
Diet duration	5	-28.06	-12.61	8.67	0.01
Family	6	-29.52	-9.13	12.16	0.00
Genus	14	-98.08	139.92	161.20	0.00

We compared fat scores between molting and nonmolting birds (Table 2). Only American Robins (*Turdus migratorius*) showed clearly higher fat scores among nonmolting individuals, although four more species showed this trend before Bonferroni correction (Table 2).

*Overlap of Molt and Fattening within Individuals.*—Within species, no individual reached the theoretical maximum of the highest fat level possible coupled with peak molt. However, some individuals approached this theoretical peak of 100% overlap (Fig. 4). Individuals of four species had more than 50% overlap of molt and fattening: Gray-cheeked Thrush (*Catharus minimus*), Swainson's Thrush (*Catharus ustulatus*), Yellow

Warbler (*Setophaga petechia*), and White-crowned Sparrow (*Zonotrichia leucophrys*). Seven more species had individuals showing 30-50% molt-fat-fattening overlap: American Robin, Orange-crowned Warbler (*Oreothlypis celata*), Yellow-rumped Warbler (*Setophaga coronata*), Wilson's Warbler (*Cardellina pusilla*), American Tree Sparrow, Lincoln's Sparrow (*Melospiza lincolni*), and Dark-eyed Junco (*Junco hyemalis*). Hammond's Flycatcher, Ruby-crowned Kinglet (*Regulus calendula*), Blackpoll Warbler (*Setophaga striata*), Northern Waterthrush (*Parkesia noveboracensis*), Savannah Sparrow, and Fox Sparrow (*Passerella iliaca*), had no individuals with >30% overlap, and none of these latter six species had more than

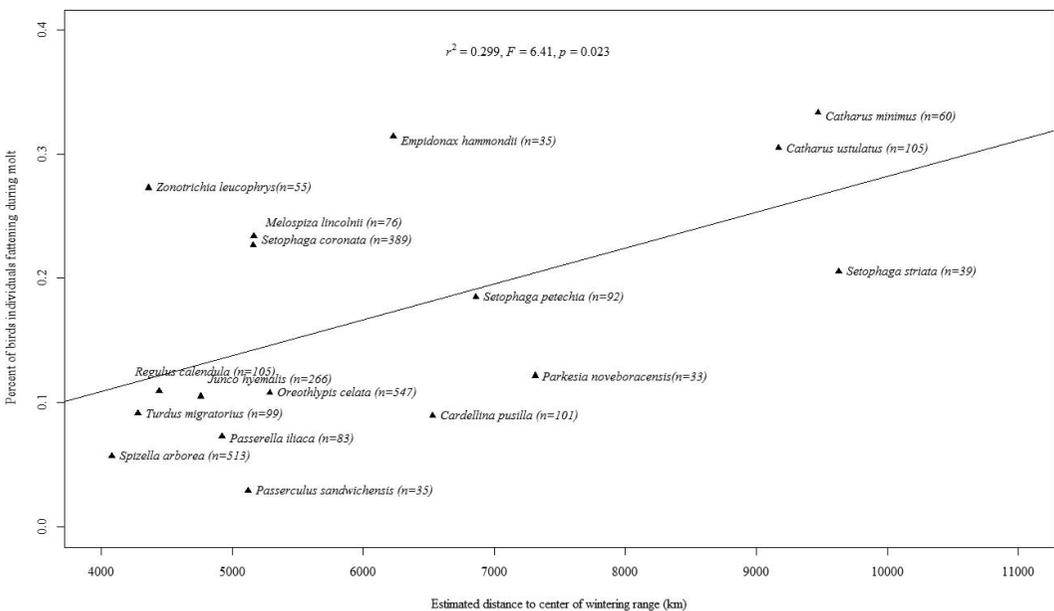


FIG. 4. The relationship between distance to wintering area and overlap of molt and fattening among species in Fairbanks, Alaska (1992–2004).

7 individuals that showed any fattening while molting (Fig. 4).

We evaluated whether Julian date was related to the amount of overlap. Only three species had adequate sample sizes to fit linear models to the data (i.e., data were normally distributed for the linear regression analysis). For these three species there was no evidence of departure from a normal error distribution, nonconstant variance, and no data points were overly influential in our models. Of these three species, Yellow-rumped Warbler was the only species with a positive relationship between Julian date and the amount of molt-fat overlap (i.e., molt-fat overlap increased later in the season).

## DISCUSSION

Some individuals of all 17 species in this study overlapped energetically demanding events in interior Alaska. Indeed, the frequency and intensity of overlaps occurring among individuals at our study site has not been found in previous studies documenting molt-fattening or molt-migration overlaps in passerines (Cannell et al. 1983, Rimmer 1988, Winker et al. 1992, Jenni and Winkler 1994, Lindström et al. 1994, Yuri and Rohwer 1997). Only Flockhart (2010), in a study of five species of wood warblers (Parulidae) in northern Alberta, Canada (55° 22') has shown high levels of molt-migration overlap. Despite the commonly held assumption that passerine birds usually segregate energetically demanding events during the annual cycle (Payne 1972, Cannell et al. 1983, Vega Rivera et al. 1998), our results indicate that migrant individuals at high latitudes can overlap energetically demanding events. These types of overlaps are more commonly documented among large birds, which take longer to molt and breed (Newton 2011). For individual passerines, overlap of fattening during the completion of the prebasic molt may be a necessary strategy to complete these energetically demanding events within the brief subarctic summer. It is important to note that most individuals captured at this study site were in the mid- to late stages of molt (Supplemental Material).

*Costs of Overlap.*—In the short seasonal timeframe of our study, we observed little evidence of costs to overlapping molt and autumnal migration, as measured by the ability to maintain fat deposits compared to non-molting migrants. There was only one case, the American Robin, in which there was a significant difference in fat levels between

birds that were molting remiges and those that were not (though four other species showed this trend; Table 2). Similar results have been found in Blue Tits (*Parus caeruleus*) at high latitudes (Svensson and Merilä 1996). The longer-term consequences of overlapping molt and fattening are unknown. The overlap of molt and breeding can impose more observable fitness costs (e.g., fewer fledged young, Hemborg et al. 1998), and Flockhart (2010) found less overlap of molt with breeding and more with migration. In our study it is noteworthy that relatively high proportions of these adult animals exhibited considerable molt-fattening overlap (e.g., 31% of Hammond's Flycatchers), and among most of these populations short-term migratory investment did not seem to be compromised by a simultaneous completion of molt.

How are these costs paid? Reznick et al. (2000) suggested that superior phenotypes are often restricted to situations where resources are abundant. Whether the results of our study represent a late-season product of abundant high-latitude resources (correlated with long summer days), as suggested by superflea theory (Spitze et al. 1991, Reznick et al. 2000), remains to be determined. There also may be long-term costs not visible in our study, such as lower-quality feathers being grown during competing energetic demands (Norris et al. 2004, Griggio et al. 2009), higher metabolic loads resulting in long-term costs in terms of oxidative stress, and decreased survival during migration.

*Time Constraints and Their Among-Species Variation.*—Our results show that energetic juggling acts among migratory passerines during the breeding season are impressive at high latitudes, where time pressures are at an extreme. Further, there are strong relationships among species between energetic overlaps and length of breeding ground occupancy and distance to wintering grounds. Just as important, however, is the indication that species-specific responses to these time constraints are quite variable, and that at least some of this variation probably stems from heterogeneities in the nature of the time constraints themselves.

We consider that brevity of breeding ground occupancy is ultimately responsible for the energetic overlaps observed, but at the same time we find it perfectly plausible that "time constraints" vary within the season of high-latitude occupancy and among the species exposed to these pressures.

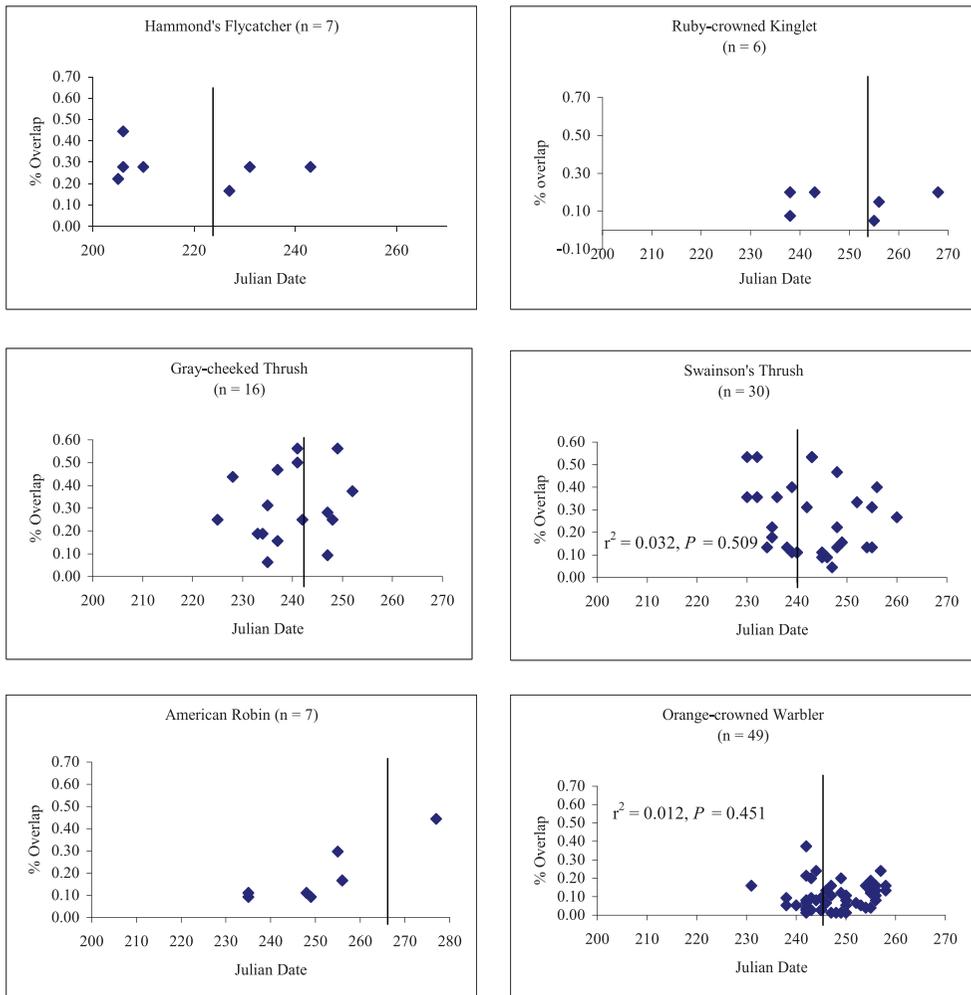


FIG. 5. Molt-fattening overlap among individuals during autumn migration in Fairbanks, Alaska (1992–2004). Each dot represents a single individual. For species with adequate sample sizes, linear regression analysis was used to determine whether date influenced the amount of overlap. Vertical lines show the median date of passage for each species (Benson and Winker 2001).

An overarching concept of length-of-season as being the sole measure or indicator of time constraints may be too simplistic. For example, post-breeding habitat suitability will undergo autumn declines that differ among species; at high latitudes, insectivores will experience a steeper drop-off of autumn food availability than will omnivores or frugivores. Thus, temporal pressures are probably heterogeneously distributed within the period of high-latitude occupancy, with compression or constraint more likely at the end of the season among some species than others. We did not, however, find evidence of diet affecting overlaps (Tables 3 and 4).

There remains a substantial amount of unexplained variation, suggesting additional differences in species-specific molt-migration and molt-fat overlaps. For example, other factors must affect the amount of overlap in Wilson's Warblers. Few individuals of this species overlapped molt and migration, despite their short breeding ground occupancy and relatively early departure date (Fig. 2). To segregate molt and migration, Wilson's Warblers may overlap molt and breeding, which has been observed in some species (Rimmer 1988, Hemborg et al. 1998, Norris et al. 2004). Alternatively, Wilson's Warblers may take less time to molt or breed than the other species we

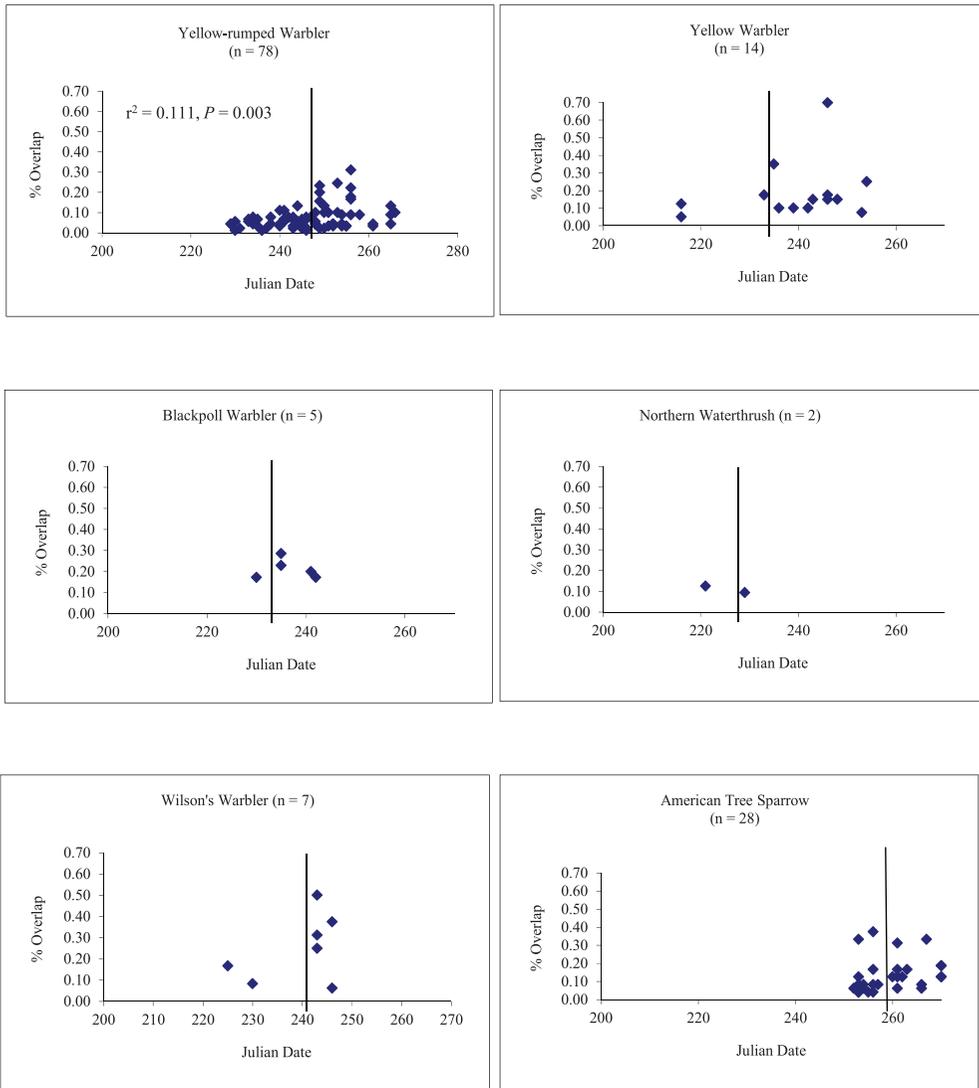


FIG. 5. Continued.

examined, as has been documented in the laboratory for Lesser Whitethroats (Hall and Fransson 2000). We could not quantify interspecific differences in the duration of molt, and we did not have data on nesting chronology to explore these possibilities. However, the time required for breeding and molt varies among species, and Flockhart (2010) also observed interspecific variation among five species of wood warblers. It is also possible that species vary in how they move between the end of reproduction and the initiation of migration, causing among-species variation in the detectability of molt and fattening overlap.

It seems plausible that species will respond to the time constraints of a brief breeding season differently. Overlaps between reproduction and migration, which we could not measure, may be greater among some individuals and species than others, perhaps representing a less risky strategy than late-season overlaps in molt and migration. In this regard, it is important to remember that we have only examined one of three potential areas of energetic overlaps during breeding ground occupancy (the other two being gonadal development in spring migration and breeding-molt overlap; Fig. 1). Strategies of time-energy juggling at these other

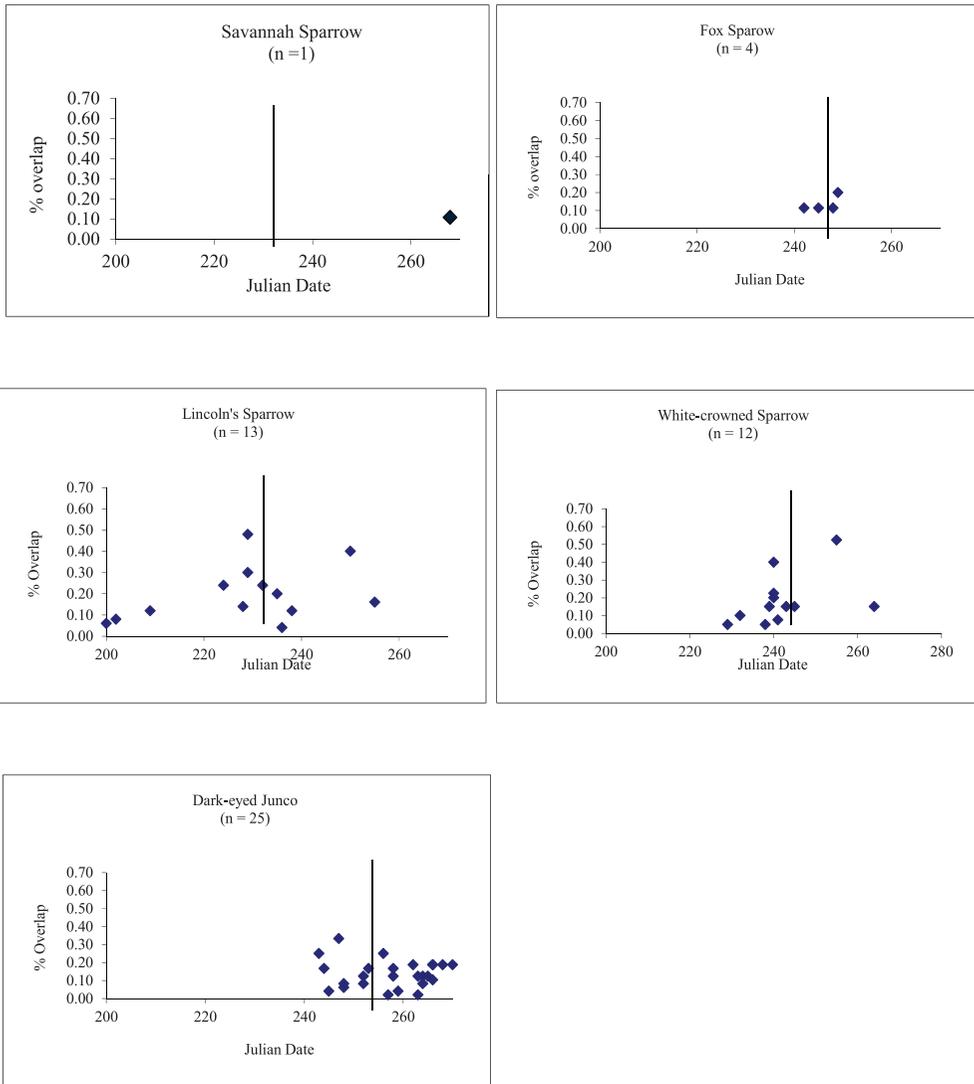


FIG. 5. Continued.

points in the annual cycle may also show species-specific variation, and may in part help to explain variation in the late-season overlaps we observed.

Finally, the relationship that we found in molt-fattening overlap and distance to wintering range indicates that this distance to be traveled (south and east) represents an additional significant factor affecting breeding range energetics at this high latitude. However, because this variable is negatively correlated with breeding season duration, it is difficult to separate these two pressures and understand how each affects the evolution of migratory strategies at this latitude.

*Overlap within Individuals.*—There is no ready explanation for this among-species variation, either in levels of extreme molt-fattening overlap or in the timing that individuals overlap in relation to species-specific departure dates (Fig. 4). Many factors could play a role in the variation exhibited among these migratory bird species in the production and timing of high levels of overlap. In non-molting birds at this latitude, body condition indices were influenced by day length and overnight temperature in several species (Benson and Winker 2005). Some other factors could be things such as diet, food availability, endogenous control

of migration, and the species-specific nature of "time pressure." Determining the cause(s) of this variation is likely to be a multivariate problem, and we have not yet measured enough variables to effectively tease out those most important in dictating individual strategies. Yet who would have thought that among small landbird passerines there could be such variation exhibited at the species level in accomplishing such a seemingly simple task as departing the breeding grounds in autumn migration?

Among these high-latitude, time-constrained populations, we find substantial frequencies and levels of overlap among molt, fattening, and migration. These overlaps are correlated with important variables of time constraint and with the distance to be traveled. But the manner in which these overlaps in energy demands are juggled at this high latitude shows remarkable variation.

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