Timing of events on the breeding grounds for five species of sympatric warblers

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ABSTRACT.   On the breeding grounds, migratory birds have limited time to breed and molt before autumn migration. However, few studies of long-distance migrants have examined the phenology of these events to determine what life-history trade-offs might result if these activities overlap. From 2000 to 2007, I used banding data to determine the timing of migration, breeding, and primary molt for Yellow Warblers (*Dendroica petechia*), Yellow-rumped Warblers (*D. coronata coronata*), American Redstarts (*Setophaga ruticilla*), Ovenbirds (*Seiurus aurocapilla*), and Canada Warblers (*Wilsonia canadensis*) at a study site in Alberta, Canada. Hatching date did not differ among species (*P* = 0.63), with means ranging from 27 June to 3 July. All species began primary molt between 12 July and 18 July, near the expected fledging date of offspring, and therefore all species exhibited overlap between postfledging parental care and molt. The duration of primary molt ranged from 28 d for Canada Warblers to 69 d for Yellow-rumped Warblers. Yellow Warblers, Yellow-rumped Warblers, and American Redstarts began autumn migration having completed about 50% of their primary molt. However, Ovenbirds departed when 21% of molt was complete, and Canada Warblers departed 2 d after completing molt. For all five species of warblers, molt did not overlap with nest-bound breeding activities. However, molt did overlap with both postfledging care and migration. This suggests that initiating migration as soon as possible is important, possibly because earlier arrival on the wintering grounds may improve access to high quality winter habitat. Overall, warblers may maximize individual fitness by combining life-history events that result in overlapping portions of the breeding cycle, molt, and migration.

RESUMEN.   **Fecha de elección de los eventos en las aéreas de reproducción para cinco especies de reinitas en simpatria**
En las aéreas de reproducción, las aves migratorias tienen un tiempo limitado para reproducirse y mudar antes del la migración otoñal. Sin embargo, pocos estudios en migrantes de largas distancias han examinado la fenología de estos eventos para determinar cuáles compromisos en las historias de vida resultarían si estas dos actividades se sobrelaparán. Desde el 2000 hasta el 2007 en Alberta, Canada, use datos de anillamientos para determiar la fecha de migración, anidación y muda primaria para *Dendroica petechia*, *D. coronata coronate*, *Setophaga ruticilla*, *Seiurus aurocapilla* y *Wilsonia canadensis*. Fechas de eclosion no fueron diferentes entre las especies (*P* = 0.63), con medias que variaron entre el 27 de Junio y el 3 de Julio. Todas las especies empezaron la muda primaria entre el 12 y 18 de Julio, cerca del día esperado de la salida de los polluelos y consecuentemente todas las especies presentaron sobrelapamiento entre el cuidado parental de los juveniles y la muda. La duración de la muda primaria tuvo un rango desde 28 días para *W. canadensis* hasta 69 días para *D. coronata coronata. D. petechia*, *D. coronata coronate* y *S. ruticilla* comenzaron la migración otoñal habiendo completado cerca del 50% de la muda primaria. Sin embargo, *S. aurocapilla* migró cuando completo el 21% de la muda y *W. canadensis* migró dos días después de completar la muda. Para las cinco especies de reinitas, la muda no se sobrelapó con actividades de anidación. Sin embargo, la muda se sobrelapó con el cuidado de los juveniles y la migración. Esto sugiere que iniciar la migración lo más pronto posible es importante, posiblemente porque llegar temprano a las aéreas invernales puede mejorar el acceso a hábitat invernales de alta calidad. En general, las reinitas pueden maximizar su aptitud a través de la combinación de los eventos de historias de vida que se sobreponen en porciones del ciclo reproductivo, muda y migración.

Key words: life history, migration, overlap, Parulidae, primary molt, time constraint

Migrant birds must successively complete several physiologically demanding activities on their breeding grounds (Hedenström 2006). Due to time constraints, these activities sometimes overlap. For example, among long-distance migrants, late breeders may begin molt while still caring for dependent offspring (Hemborg 1999), creating potential conflict between energy allocation for self-maintenance and care of offspring (Hemborg and Lundberg 1998). Alternatively, migrants may delay feather replacement until after initiating migration (Norris et al. 2004). If so, molt duration may be shortened, potentially reducing feather quality

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(Dawson 2004, Serra et al. 2007), flight efficiency (Swaddle and Witter 1997), the quality of sexual ornaments (Norris et al. 2004, Serra et al. 2007), and, ultimately, survival (Nilsson and Svensson 1996, Dawson et al. 2000).

Overlap in the timing of migration, breeding, and molt could require trade-offs between adult body condition and reproductive success (Hemborg and Lundberg 1998, Norris et al. 2004), but few investigators have determined if and when such overlap occurs. This is primarily because few investigators have examined primary molt on the breeding grounds. Most estimates of molt timing and duration have been derived from museum specimens collected at multiple locations, potentially confounding molting schedule with differences in breeding phenology across latitude (Mewaldt and King 1978, Ryder and Rimmer 2003, Bonier et al. 2007). To better understand the possible effects of overlap between molt and other activities on the breeding grounds, molt schedules must be determined where breeding occurs.

I documented the timing of migration, primary molt, and breeding for five species of warblers at a single location in the boreal forest of Alberta, Canada. Warblers represent an excellent comparative model for the study of life-history trade-offs on the breeding grounds because they breed sympatrically and synchronously (Morse 1989), but may have different migration schedules that potentially result in different optimal life-history strategies. My objectives were to: (1) estimate the time spent on the breeding grounds by these warblers, (2) estimate hatching dates based on brood-patch development and determine the timing and duration of egg laying, incubation, fledging, and postfledging periods, (3) determine the timing of postnuptial molt, and (4) determine the extent of overlap between molt, breeding, and migration.

METHODS

Warblers were captured from 2000 to 2007 at the Lesser Slave Lake Bird Observatory (LSLBO; 55°20′N, 114°40′W) near the town of Slave Lake in northern Alberta, Canada. Banding occurred during spring (20 April to 10 June) and autumn (12 July to 30 September) as part of the Canadian Migration Monitoring Network (Crewe et al. 2008). Twelve mist nets (12 m × 3 m) were opened daily for 7 h beginning 30 min before sunrise. Vegetation at the migration monitoring station covers an area of 3 ha dominated by willows (*Salix*) and green alder (*Alnus viridis*). The station is bordered by Lesser Slave Lake on one side and mature boreal forest on the other.

During the breeding season, birds were captured adjacent to the migration monitoring station at four locations as part of the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante et al. 2008). Netting occurred from mid-June to early August. Each station was sampled once during a 10-d interval, with netting cycles repeated during each subsequent 10-d interval. A sampling period consisted of 10 mist nets (12 m × 3 m) opened for 6h beginning at sunrise (DeSante et al. 2008). MAPS stations were within 2 km of one another and were dominated by mature aspen (*Populus tremuloides*) mixedwood boreal forest.

Study species. I studied five species of wood warblers: Yellow Warblers (*Dendroica petechia*), Yellow-rumped Warblers (*D. coronata coronata*), American Redstarts (*Setophaga ruticilla*), Ovenbirds (*Seiurus aurocapilla*), and Canada Warblers (*Wilsonia canadensis*). Yellow and Yellow-rumped Warblers breed north of northern Alberta, whereas LSLBO is near the northern limit of the breeding range of the other three species. Individuals were not repeatedly recaptured either during the breeding season or migration so population estimates for migration timing and reproduction were used to determine the potential overlap of activities on the breeding grounds. Birds captured during migration represented individuals breeding an unknown distance north of the banding station (Wassenaar and Hobson 2001) and birds captured during the MAPS program were local breeders.

For each warbler captured, I noted age, sex, and, for birds in primary molt, their molt score. During 2007, I also measured the length of each primary feather on the right wing in a subsample of nonmolting warblers. I determined age based on skull ossification and feather features (Pyle 1997), but only adults were used in the analysis. Sex was determined by plumage and the presence of either a cloacal protuberance (males) or brood patch (females). Of my focal species, only Ovenbirds are monochromatic and, therefore, other than during the breeding season when females have brood patches and can be easily classified, all estimates for this species are for males and females combined (Table 1).

Table 1.   Samples sizes (males, females) used in the analyses of the timing of spring migration, breeding (females only, including Ovenbirds), primary molt, and autumn migration of five species of warblers from 2000 to 2007 at Slave Lake, Alberta. Spring and autumn migration timing data for Canada Warblers are from Flockhart (2007).

Species	Spring	Breeding	Molt	Autumn
Yellow Warbler	177, 149	11	19, 17	36, 35
Yellow-rumped Warbler	588, 713	17	27, 75	46, 104
American Redstart	280, 326	44	97, 78	106, 134
Ovenbird[a]	157	16	84	116
Canada Warbler	126, 67	20	37, 17	25, 40

[a]Ovenbirds have one value because they are monochromatic.

Migration timing and time on the breeding grounds.   During spring, I used records of newly banded birds to avoid including birds using the area for multiple days as a stopover site. I also excluded birds that had begun to develop breeding characteristics that indicated they might breed locally. During autumn, I used new banding records to reduce the likelihood of including locally dispersing individuals. However, unlike spring, I included individuals if they still had breeding characteristics (cloacal protuberance or brood patch) because they can be retained during autumn migration. Most such individuals were females in the process of regrowing feathers on the breast (brood-patch score of 5, see below). I pooled samples over all years because capture rates of adults in autumn were low for some species (Table 1). For Canada Warblers, I used migration timing estimates from Flockhart (2007) that were based on larger sample sizes.

To assess time spent on the breeding grounds, I calculated the difference between the capture dates for spring and autumn migration (Benson and Winker 2001) for resamples drawn randomly from the migration capture records. This allowed me to determine a species-specific variance estimate for time spent on the breeding grounds, making comparisons between species possible. The number of samples for each species was determined by the samples size for each sex class from autumn migration (Table 1).

Timing of breeding.   For female warblers, brood patches were scored as none (0), smooth (1), vascularized (2), heavily vascularized (3), wrinkled (4), or breast feathers growing (5). Analyses were restricted to individuals with brood-patch scores of 3 (that develop during incubation and hatching; DeSante et al. 2008).

Local breeders were often captured repeatedly and, if individuals were captured twice in a single year with a brood-patch score of 3, the average of these two dates was calculated. I found no differences in timing of acquiring a brood-patch score of 3 between new bandings and recaptures among any focal species (all $P \geq 0.22$). I therefore considered all records because I was interested in the timing of breeding for the population. Although records were pooled across years due to small sample sizes (Table 1), the onset of breeding probably varies based on local weather conditions and food availability.

To delineate the dates over which a complete breeding cycle would occur, I calculated the mean date and 95% confidence interval (CI) of females captured with brood-patch scores of 3 and assumed this value corresponded with hatching date at the population level. I determined how accurate this assumption was by comparing hatch date estimates obtained from brood-patch development to known hatch dates for nests of Canada Warblers, the only species whose nests were monitored from 2004 to 2007 (see Results). Using brood-patch development to determine hatching date also assumes an equal probability of capture before and after hatch date and that the frequency distribution of a brood-patch score of 3 is equal for the periods before and after eggs hatch.

To derive species-specific estimates of clutch size, incubation length, age of fledging, and maximum length of postfledging care, I used the Birds of North America accounts (Van Horn and Donovan 1994, Sherry and Holmes 1997, Hunt and Flaspohler 1998, Conway 1999, Lowther et al. 1999). Specifically, I back-dated the incubation and egg-laying period and forward

counted to the date of fledging and the end of postfledging care. I assumed that females laid one egg per day and that incubation began after the last egg was laid.

The durations of various stages of the breeding cycle of warblers in my study were similar (Van Horn and Donovan 1994, Sherry and Holmes 1997, Hunt and Flaspohler 1998, Conway 1999, Lowther et al. 1999). Typical clutches consisted of four eggs, incubation periods were 11 or 12 d in duration, and fledging age ranged from eight (Yellow Warblers and Ovenbirds) to 12 d (Yellow-rumped Warblers). However, reported estimates of the duration of parental care after fledging varied from 7 d for Canada Warblers (Conway 1999) to 22 d for Ovenbirds (Van Horn and Donovan 1994; Fig. 1). None of the estimates for the duration of postfledging care were from populations in Alberta.

Scoring primary molt. Adult wood warblers in North America replace all body and flight feathers during their prebasic molt each autumn (Pyle 1997). Primary feather replacement begins with the first primary (P1) and proceeds distally to the last primary (P9). I assigned a score for each molting primary feather on the right wing for adult warblers: $0 =$ dropped feather, $1 =$ eruption of follicle to 33% fully grown, $2 =$ approximately 34–66% fully grown, $3 =$ approximately 67% grown to fully grown, but retaining the sheath, and $4 =$ fully grown (Ginn and Melville 1983, Dawson and Newton 2004).

Scoring feathers in this manner makes the data nonlinear because each flight feather is assumed to be the same length and weight and thus could bias estimates of molt timing (Dawson 2003). To reduce this potential bias, I scaled the proportion of regrown feathers using measurements of primary feather length for each species (Yuri and Rohwer 1997, Dawson and Newton 2004, Butler et al. 2006). I found no evidence that feather proportions differed among age and sex classes (Flockhart, unpubl. data), so I calculated proportions using all measured individuals for each species. I then divided the categorical molt score of each primary feather by four and multiplied this value against the proportion that each primary contributed to the total length of all primaries. The summed scores of all primaries determined the progression of molt and ranged from 0 to 1 (0 = dropped

one or more feathers and no regrowth; $1 =$ fully regrown). Individuals with a score of 0 were retained in the analysis because they had just initiated molt, but I excluded records of individuals with scores of 1 because they could bias molt-timing estimates if they had completed molt long before they were captured. Molting records were pooled across years due to small sample sizes (Table 1).

Statistical analyses. Using dates of capture (Julian dates), I compared the timing of spring and autumn migration of males and females using Mann–Whitney tests. Inter- (where appropriate) and intraspecific differences in time spent on the breeding grounds were assessed using Mann–Whitney tests. Using hatch dates, I examined differences in the timing of breeding among species with a Kruskal–Wallis test. I used Pimm's (1976) linear regression method using Julian date as the dependent variable and molt score as the independent variable to estimate start date and duration of primary molt. I tested for differences in the slope of the regression between males and females using analysis of covariance (ANCOVA) with Julian date as the dependent variable and sex and molt score as independent variables. A significant sex × molt score interaction suggests a dependence of molt score on sex (Butler et al. 2006). I used Pearson correlation tests to examine relationships among species for migration timing and between molt start date and duration. Tests were considered significant at $\alpha = 0.05$ and all tests were conducted using SPSS 16.0 (SPSS 2007). Values are presented as means $\pm$ SE.

RESULTS

Migration timing and time on breeding grounds. For the four species where I could determine sex, spring arrival dates of males and females were correlated ($r = 0.99$, $P = 0.01$) and males arrived on the breeding grounds before females (range = 2–5 d, all $P \leq 0.001$; Fig. 1). Female American Redstarts ($U = 5882$, $P = 0.022$) and Canada Warblers ($U = 273$, $P = 0.002$) initiated autumn migration earlier than males (Fig. 1), but I found no difference between the sexes for either Yellow ($U = 530$, $P = 0.25$) or Yellow-rumped ($U = 2122$, $P = 0.27$; Fig. 1) warblers.

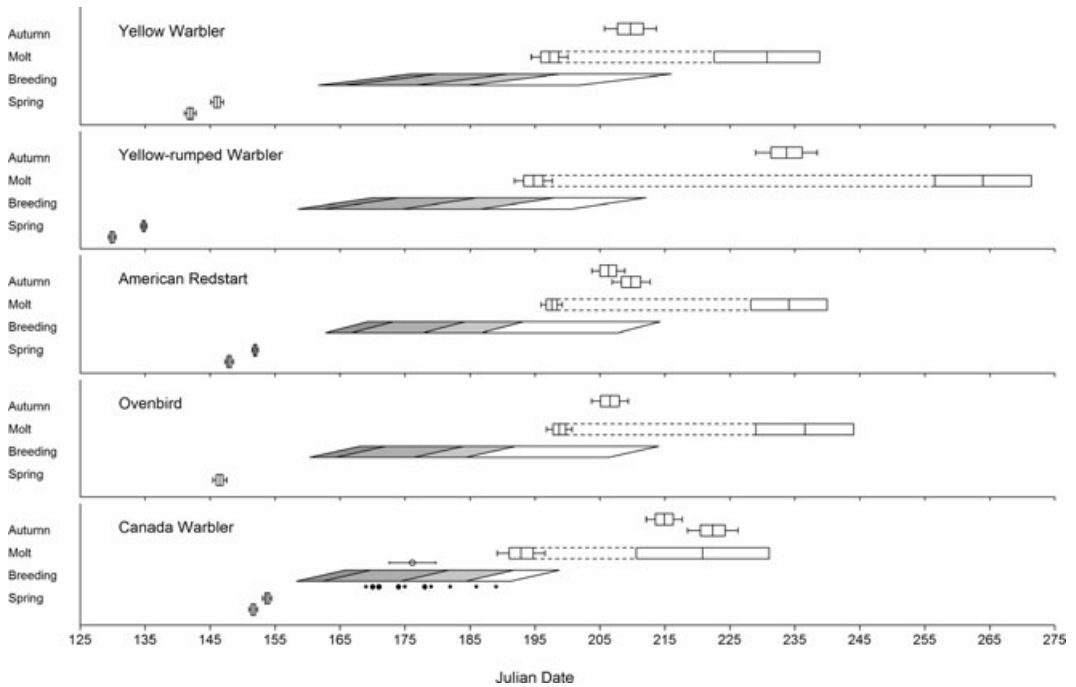Time on the breeding grounds differed between the sexes for Canada Warblers (females =

Fig. 1. Timing of activities on the breeding grounds for five species of warblers at Slave Lake, Alberta. All box plots are mean ± SE and whiskers are the 95% mean CI. Separate box plots for males (bottom) and females (top) indicate significant differences in timing of spring or autumn migration. Sexes are pooled where no statistical difference exists between males and females or if sex is indeterminable. Parallelograms (left to right) represent the days required for each species for the egg laying (darkest), incubation, nestling, and postfledging (lightest) periods (based on female brood-patch development; see text). The vertical angle of the parallelogram depicts the 95% CI dates encompassing that event; the horizontal plane represents duration. Box plots for molt represent the starting date, dashed lines indicate duration, and the final box is the estimate of the earliest (lowest 95% CI of starting date with lowest 95% CI of duration) mean (mean start date plus mean duration) and latest completion date (latest 95% CI of starting date with latest 95% CI of duration). For Canada Warblers, the error bar above the parallelogram represents the mean and 95% CI of hatching date for 14 monitored nests and dots below represent the raw data. Large dots represent two nests.

61 ± 1.6. d, males $= 70 \pm 2.0$ d; $U = 265$, $P = 0.002$), American Redstarts (females $= 54 \pm 1.3$ d, males $= 60 \pm 1.4$ d, $U = 5004$, $P < 0.001$), and Yellow-rumped Warblers (females $= 97 \pm 3.0$ d; males $= 108 \pm 4.3$ d, $U = 1835$, $P = 0.023$), but not for Yellow Warblers (68 ± 2.2 d; $U = 592.5$, $P = 0.67$). For Yellow-rumped Warblers, time on the breeding grounds exhibited a bimodal distribution (Fig. 2), precluding comparison with other species. Among species, time on the breeding grounds differed between Ovenbirds and Canada Warblers ($U = 2555$, $P < 0.001$), but not between American Redstarts and Ovenbirds ($U = 12764$, $P = 0.20$) or between Yellow and Canada Warblers ($U = 2250$, $P = 0.80$; Fig. 2).

Breeding. For all species, mean population hatching dates were between 27 June and 3 July and did not vary among species ($\chi_4^2 = 2.6$, $P = 0.63$). The mean population hatching date for Canada Warblers was 27 June, whereas known hatching dates for 14 Canada Warbler nests monitored from 2004 to 2007 ranged from 18 June to 8 July and averaged 25 June (Flockhart, unpubl. data; Fig. 1); this difference was not significant ($U = 120$, $P = 0.48$). Overall, the portion of the breeding cycle that included laying eggs, incubating eggs, and caring for nestlings required approximately 23–28 d and, for most species, ended near 12 July (Fig. 1).

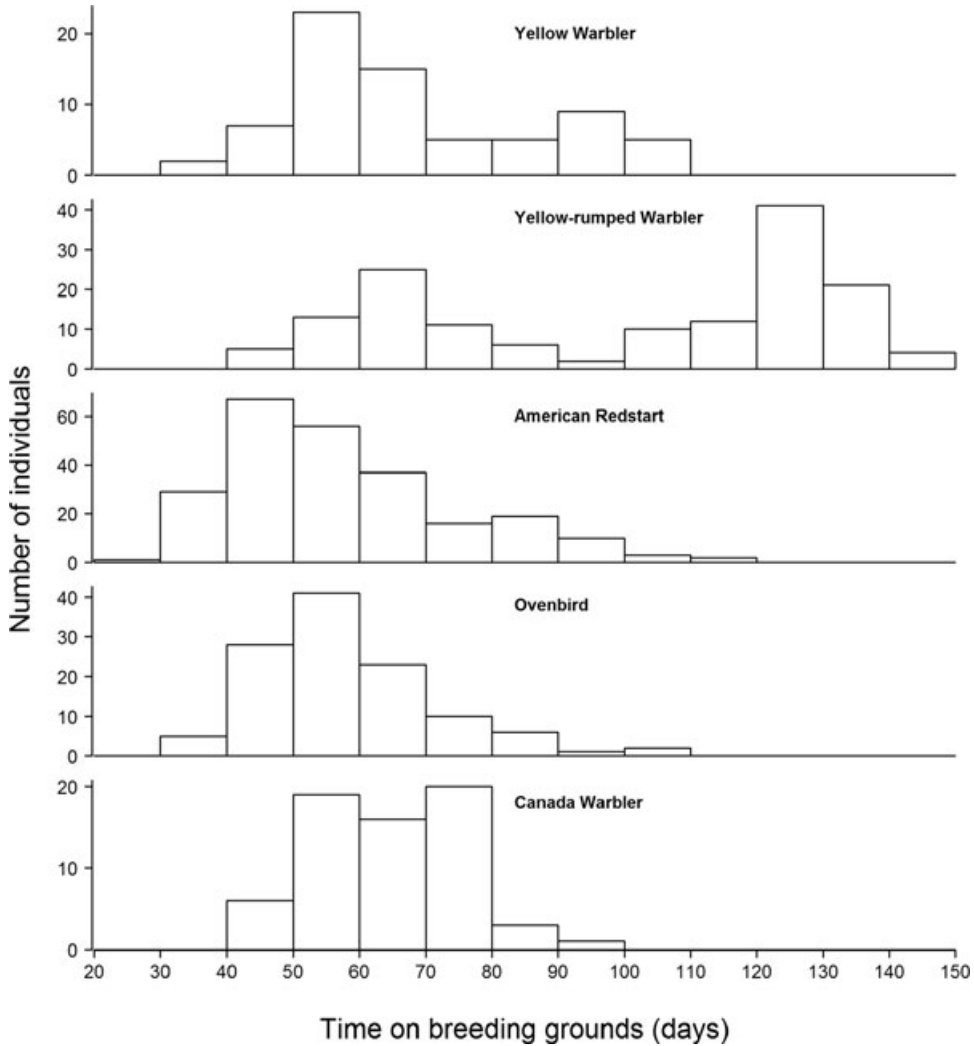**Molt.** The duration of primary molt was more than twice as long for Yellow-rumped

Fig. 2. Estimated time on the breeding grounds for five species of warblers breeding near Slave Lake, Alberta, obtained by resampling the observed spring and autumn datasets and subtracting the departure date from the arrival date. Sample sizes for each species correspond to the total number of individuals captured and used to determine the timing of autumn migration (Table 1).

Warblers (69 d) than Canada Warblers (28 d), and ranged from 30 to 40 d for the other three species (Fig. 3). I found no significant interaction between sex and molt score for Yellow Warblers ($F_{1,35} = 0.01$, $P = 0.97$), Yellow-rumped Warblers ($F_{1,101} = 2.2$, $P = 0.14$), American Redstarts ($F_{1,174} = 2.4$, $P = 0.13$), and Canada Warblers ($F_{1,53} = 2.8$, $P = 0.10$). All species initiated primary molt within a 6-d period. Canada Warblers initiated molt the earliest (12 July), whereas Ovenbirds initiated molt the latest

(18 July; Fig. 3). For all focal species combined, I found no correlation between molt initiation date and molt duration ($r = -0.1$, $P = 0.87$) and, for all five species, molt overlapped with the initiation of migration (Fig. 1). Further, all species began molt after fledging young, but probably while still caring for fledglings (Fig. 1). Most species began migration having completed about 50% of their molt, with Canada Warblers and Ovenbirds being the exceptions. Based on mean population estimates, Canada Warblers
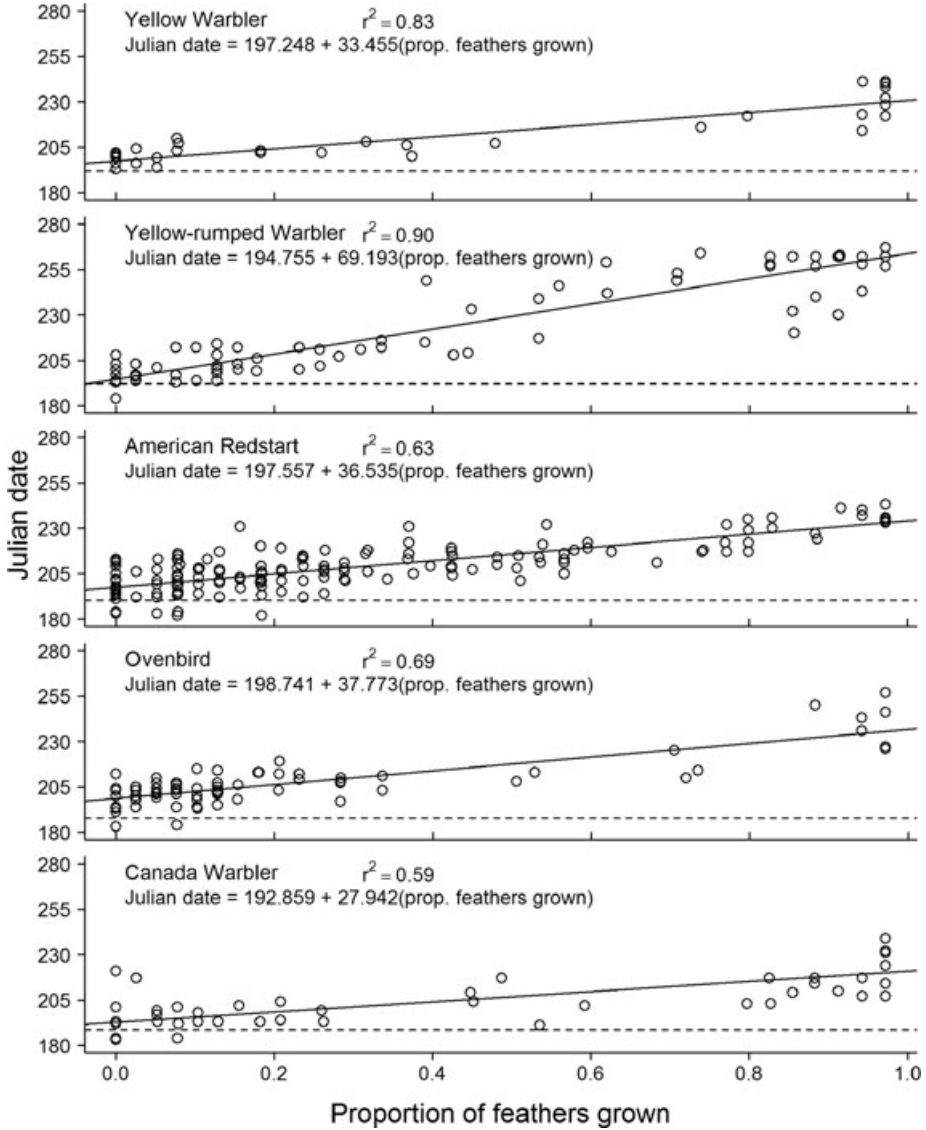
Fig. 3. Scatterplots of Julian date regressed on primary molt score for five species of warblers at Slave Lake, Alberta. The linear regression equation below each species name is predicted Julian date as the proportion of feathers grown ranges between 0 and 1 and is represented by the diagonal line; a steeper slope indicates longer primary molt duration. The horizontal dashed line is the estimated mean fledging date for each species. Julian date 205 = 24 July.

departed 2 d after finishing molt and Ovenbirds when 21% of molt was complete (Fig. 1). I found no relationship between molt initiation date and autumn migration date ($r = -0.7$, $P = 0.18$, $N = 5$) and species that took longer to replace feathers did not initiate migration later ($r = 0.79$, $P = 0.11$).

DISCUSSION

For all five species of warblers in my study, flight feather molt started within days of the expected fledging date of nestlings. I found no sex differences in the timing of molt, and molt duration was shortest for Canada Warblers and

longest for Yellow-rumped Warblers. The timing of autumn migration varied among species, but I found intersexual differences for only Canada Warblers and American Redstarts. All species were molting when migration commenced.

Timing of events on the breeding grounds. Yellow-rumped Warblers were on the breeding grounds longer (100 d) than the other warblers in my study (55–70 d). This may be a function of differences in migration distances, with Yellow-rumped Warblers wintering primarily in the southern United States and Mexico (Hunt and Flaspohler 1998) and the other species wintering primarily from central Mexico to northern South America (Morse 1989, Van Horn and Donovan 1994, Sherry and Holmes 1997, Conway 1999, Lowther et al. 1999). Conversely, similarities in the timing and duration of breeding may be best explained by the peak of food availability during the breeding season (Lack 1954) and phylogenetic relatedness (Morse 1989, Martin 1995). Yellow-rumped Warblers were also the only species in my study to exhibit a bimodal distribution in time spent on the breeding grounds. The two peaks might represent breeding populations near and distant to the study area moving past the migration station at different times, earlier migration of failed breeders compared to successful breeders (Kjellén et al. 2001), or differences between single- and double-brooded individuals (Evans Ogden and Stutchbury 1996).

The time of molt initiation was similar for all five species, but the duration of molt was longer for Yellow-rumped Warblers than the other species. One possible explanation for this difference is that molting may be protracted because Yellow-rumped Warblers do not defend winter territories (Hunt and Flaspohler 1998) and, therefore, migrating immediately after breeding may be less critical. In contrast, Yellow Warblers (Lowther et al. 1999), American Redstarts (Sherry and Holmes 1997), Ovenbirds (Brown and Sherry 2008), and Canada Warblers (Rohwer et al. 2005) defend winter territories so selection may favor earlier autumn migration or a more rapid molt. Alternatively, molting by Yellow-rumped Warblers may be protracted because they have more time to complete their prebasic molt and do not have to migrate as far to reach their wintering grounds (Morse 1989).

Overlap of events on the breeding grounds. As illustrated by the warblers in my study, adults may minimize negative effects on their young by beginning molt near the time when young fledge. Similar observations have been reported for Louisiana Waterthrushes (*Seiurus motacilla*; Mulvihill et al. 2009) and Wood Thrushes (*Hylocichla mustellina*; Vega Rivera et al. 1998). Such observations suggest that molting while provisioning nestlings is maladaptive, potentially decreasing foraging efficiency and making offspring more susceptible to predation by lengthening the nestling period (Martin 1995, Evans Ogden and Stutchbury 1996). Furthermore, overlap of breeding and molt may decrease adult survival (Hemborg and Lundberg 1998) if, for example, molt affects flying ability (Swaddle and Witter 1997) that potentially increases the likelihood of predation (Slagsvold and Dale 1996).

Fledging and initiation of molt by warblers in my study were synchronous, suggesting that life-history trade-offs between breeding and molt may be greater than those between molt and migration. Thus, adults may be less likely to overlap breeding and molt because it reduces their survival and the likelihood of recruitment of their offspring (Hemborg and Lundberg 1998). In contrast, molting after young fledge may minimize the risks to nestlings associated with nest-bound activities (Martin 1995). In addition, fledglings may seek areas of dense vegetation that improve their chances of survival (King et al. 2006) and molting adults with reduced flying ability may also prefer such areas because they provide more protection from predators (Swaddle and Witter 1997, Vega Rivera et al. 1998).

All species in my study began migration after completing about half of their primary molt, indicating molt was completed away from their breeding areas. Similar results have been reported for Swainson's Thrushes (*Catharus ustulatus*; Wassenaar and Hobson 2001), Yellow Warblers (Rimmer 1988), and American Redstarts (Norris et al. 2004). In the short-term, individuals that molt during migration may have slower movement rates and increased energy demands due to reduced flight performance (Swaddle and Witter 1997). Overlapping molt and migration could result in lower quality feathers with reduced ornamentation (Norris et al. 2004, Serra et al. 2007) that, in the long-term, can influence subsequent reproductive success (Norris et al. 2004). However, overlap

of molt and migration may be beneficial by allowing earlier arrival on the wintering grounds, improving access to high quality winter habitat that would have repercussions for survival and reproductive output (Marra and Holmes 2001). If the costs to feather quality caused by molting south of breeding territories are small relative to the benefits that promote individuals to combine these activities, then adult warblers should depart on migration as soon as offspring are independent.

In sum, I found that both the start of breeding and molt was synchronous among five species of warblers, likely to match food availability during the nestling period and avoid molting while provisioning nestlings. However, molt overlapped both the late stages of breeding and the beginning of autumn migration as a way of combining life-history events that presumably maximizing individual fitness. Overall, breeding, molt, and migration were not mutually exclusive events, suggesting that life-history trade-offs exist among small-bodied passerines breeding at northern latitudes.

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