

TIMING OF THE DEFINITIVE PREBASIC MOLT IN YELLOW WARBLERS AT JAMES BAY, ONTARIO¹

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Abstract. The relationship between breeding, molt, and migration of Yellow Warblers (*Dendroica petechia*) was studied on the southwest coast of James Bay, Ontario from 1982 to 1984. Breeding chronology was similar in each year, with a mean fledging date of 11 to 12 July. Color-banded individuals regularly overlapped molt and care of fledglings. Known-breeding males began remigial molt 8.1 days after young fledged (range = 1-19 days), females 12.3 days (range = 9-15 days). The population mean date of molt onset was 17 July for males, and 22 July for females. Females molted significantly more rapidly than males, and both sexes completed molt on the mean date of 28 August. There were marked behavioral differences between the sexes during molt. Males typically remained on territories, advertising their presence with song. Females showed little site attachment, wandering over the study area or dispersing. Both sexes gained weight during the early and middle periods of molt, but lost weight prior to migration. Most birds began migrating during the final stages of remigial molt. Depletion of insect food and deteriorating weather in late summer appear to have selected for a rapid, intense molt of 35 to 45 days, during which some birds may become virtually flightless. The importance of maintaining thermoregulatory abilities and high rates of feeding may constrain further reduction in molt duration. The need for maintaining peak flight efficiency during fledgling care and migration may have partially determined the scheduling of molt in this population.

Key words: *James Bay; Yellow Warbler; Dendroica petechia; annual cycle; prebasic molt; breeding-molt overlap; molt-migration overlap; behavior during molt.*

INTRODUCTION

Migratory birds breeding in strongly seasonal environments typically partition the phases of reproduction, molt, and migration in their annual cycles. By separating these events in time, birds are thought to minimize conflicting demands on their energy resources (Kendeigh 1949, Farner 1964, Bancroft and Woolfenden 1982). At high latitudes, this segregation may be compromised by the constraints of an abbreviated summer, in which the interval between the end of breeding and the onset of migration is short. The abundant food resources and long photoperiods of the northern summer enable some species to overlap their breeding and molt schedules (Payne 1972). Overlap between molt and migration appears to be less common (King 1974), presumably because of the incompatible energetic and endocrine demands of both events and the need for full efficiency of flight feathers during migration.

Despite the documentation of molt-breeding

overlap in more than 100 species of birds, mostly from tropical climates (Payne 1972, Foster 1975), few studies have reported on the molt regimes of individuals of known breeding status (but see Nolan 1978, Orell and Ojanen 1980, Tiainen 1981, Bancroft and Woolfenden 1982). Since the breeding and migratory periods of a population may extend beyond those of its individual members, information on the precise scheduling of reproduction, molt, and migration can be obtained only from known-breeding individuals. Such data are important to an understanding of how birds integrate major activities in their annual cycle.

No published studies of molt exist for any discrete breeding population of a North American wood warbler (Parulinae) species from a high latitude. Only Foster (1967) and Nolan (1978) have reported on the timing of molt in species of this large, widespread subfamily. In this study I describe the patterns and timing of the definitive prebasic molt in a banded, breeding population of Yellow Warblers (*Dendroica petechia*) from northern Ontario, with emphasis on interactions between molt, breeding, and migration. Bancroft and Woolfenden's (1982) thorough study of molt in Florida Scrub Jays (*Aphelocoma*

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coerulescens) and Blue Jays (*Cyanocitta cristata*) serves as a model for this report.

During the brief boreal summer, adult Yellow Warblers breed and undergo a complete molt prior to migrating. They presumably face more severe time and energy constraints in scheduling these activities than juveniles, which have only a partial molt of body feathers and wing coverts prior to fall departure. My examination of the molt regime of Yellow Warblers therefore focuses on adults, since information on the adaptive patterns and timing of their molt seems likely to contribute more to the overall understanding of molt in migratory birds.

MATERIALS AND METHODS

Molt data were collected throughout the summers of 1982 to 1984, and during August of 1980 and 1981, at North Point, 27 km north-northeast of Moosonee, on the southwest coast of James Bay, Ontario (51°29'N, 80°27'W). The study site is about 650 km southeast of the northern breeding limit of Yellow Warblers on the Hudson Bay coastline, near Churchill, Manitoba (Godfrey 1986). This subspecies (*D. p. amnicola*) winters from southern Mexico to northern South America (AOU 1957).

The James Bay coast is extremely flat, low-lying, and poorly-drained, and is covered by snow and ice for 6 to 7 months of the year (see Martini et al. 1980). Breeding birds of the region face a relatively brief summer and a constant threat from severe northeast storms off the bay. Exposure of eggs and nestlings to adverse weather is by far the greatest cause of nesting failure in Yellow Warblers and other open-nesting passerines at North Point (Rimmer, unpubl.). Yellow Warblers breed primarily in wet thickets of willow (*Salix* spp.) and alder (*Alnus rugosa*), interspersed with cattails (*Typha latifolia*), immediately inland from the extensive supertidal marshes that characterize the James Bay coastline. Breeding density is high (up to 2.2 pairs per hectare) in suitable habitat, which forms a nearly continuous narrow band, broken only by scattered cattail marshes, along the coast.

Birds were captured in 6- and 12-m mist nets throughout the breeding, molting, and fall migration periods. I opened eight to 12 nets on most days and moved them frequently between sites to counteract the net familiarity of many individuals. I collected biometric data on all captured individuals, including weight to the nearest

0.1 g, extent of subcutaneous fat in the interclavicular fossa, and extent of development of cloacal protuberance or brood patch. During the mid-June to late July breeding season, all birds were uniquely color-banded, and nesting chronology was monitored. Thirty-three nests were followed through fledging in 1982 to 1984.

All individuals were aged and sexed. Based on examination of a series of known-age, banded individuals from previous years, I was able to classify 88% of adults as yearling (SY) or older (ASY) during the 1 June to 31 July breeding season. My aging criteria basically followed those in the *North American Bird Banding Manual* (1977; see Rimmer 1986). A few individuals did not fit clearly into either age category and were designated as after hatching-year (AHY). I excluded these individuals from age-specific aspects of the molt analysis. Males and females were distinguishable in all plumages and at all stages of molt (see Rimmer 1986).

I obtained 217 captures of 141 actively molting individuals between 1980 and 1984. Individuals captured in more than 1 year were counted separately for each year. Thirty birds were examined two or more times within a single year while in molt. Thirteen birds provided molt data in two different years, and four individuals were examined in 3 years.

The terminology used to describe the molts and plumages of Yellow Warblers follows that of Humphrey and Parkes (1959). The definitive prebasic molt is a complete, annual molt in this species. The primaries were numbered 1 to 10 distally from the carpal joint (the vestigial tenth primary was ignored). I distinguished secondaries from tertials (the innermost three secondaries), since the two sets molt independently. The secondaries were numbered 1 to 6 proximally from the carpal joint; the tertials were numbered 1 to 3 proximally from secondary 6. The six rectrix pairs were numbered 1 to 6 distally from the center of the tail.

I used a conventional molt scoring system (e.g., Ashmole 1962, Newton 1966) which assigns each remex and rectrix a score of 0 to 5 as follows: 0 = not dropped, 1 = missing or in pin, 2 = "brush" stage to one-third grown, 3 = one-third to two-thirds grown, 4 = two-thirds to full-grown but with waxy sheath remaining, 5 = completely regrown. I followed Bancroft and Woolfenden (1982) in obtaining a remex score summed from the individual scores of all 18 primaries and both

the left and right sixth secondary. Since remigial molt is virtually complete with renewal of the sixth secondary, this remex score results in a more linear relationship of molt score to date than by using primary score alone. The assumption of linearity between molt score and date is important if recapture data and regression analysis are used to estimate rate and duration of molt (Evans 1966, Newton 1966, Bancroft and Woolfenden 1982). A remex score of 0 indicates that remigial molt had not begun, while a score of 100 indicates complete remigial molt.

During the period of remex replacement in the definitive prebasic molt, all but a few body feathers are completely renewed. Therefore, the duration of remigial molt provides an accurate index of the period in which virtually the entire plumage is replaced. I estimated duration of the prebasic molt, based on the rates of remex molt, in two ways: (1) from individuals captured two or more times in the same molt cycle at least 5 days apart, and (2) by means of linear regression analysis of remex scores on date for all birds in active remigial molt. For recaptured birds rates of molt were calculated as the difference in remex score between captures divided by the number of days between captures. I used only birds whose initial remex score was less than 80, since molt rates slowed considerably late in the cycle. From regression, rate is the slope (m) of the fitted line $y = mx + b$. Both are expressed as points per day. Individual and population mean dates of molt onset and completion were calculated by extrapolation from rates of recaptured birds.

RESULTS

SEQUENCE OF THE DEFINITIVE PREBASIC MOLT

The sequence of remex and rectrix molt in Yellow Warblers followed that reported for other wood warblers (Stewart 1952, Foster 1967, Nolan 1978) and passerines in general (Dwight 1900, Stresemann and Stresemann 1966). The primaries were replaced in descendent order, proximal to distal, beginning with primary 1. The secondaries were molted in two groups, distal (1-6) and proximal (7-9, here called tertials). Secondary 1 usually dropped between the loss of primaries 6 and 7. Molt of the secondaries proceeded proximally and was generally complete shortly after primary molt. Tertial molt invariably began with the shedding of tertial 2, usually as primary 2 or

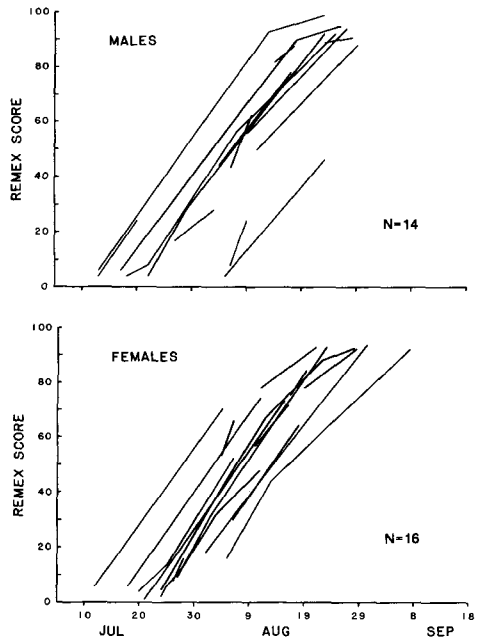


FIGURE 1. Remex scores of individual Yellow Warblers examined two or more times during one definitive prebasic molt.

3 was dropped, and finished with the growth of primary 6 or 7. Tail molt began with the central pair of rectrices, typically between the loss of primaries 3 and 4, and progressed centrifugally, ending at the same time primary 6 or 7 completed growth. The timing of body molt coincided closely with the period of remigial molt, beginning with the loss of primary 1 or 2 and finishing concurrently with, or shortly after, growth of secondary 6. Rimmer (1986) provided more detail on flight feather and body molt in this population.

RATE AND DURATION OF MOLT

The rate of increase of remex score against date was plotted for all Yellow Warblers examined more than once during molt (Fig. 1). Each line connects remex scores of one individual on successive capture dates. Changes in the slope indicate changes in the rate of remex molt in points per day. Due to small sample sizes, both age classes were grouped for each sex.

I calculated the rate of remex molt for 23 actively molting individuals captured two or more times in the same molt cycle, based on the change in remex score between first and last captures. From these a mean rate of molt was determined

TABLE 1. Mean molt rate of Yellow Warblers based on recapture data and regression analysis.

Class	Recapture			Regression		
	<i>n</i>	Rate ^a	SD	<i>n</i>	Rate ^a	SD
SY males	5	2.348	0.509	29	2.157	0.202
ASY males	5	2.279	0.209	47	2.219	0.148
SY females	1	2.514	0.000	27	2.547	0.185
ASY females	10	2.746	0.292	51	2.080	0.155
All males ^b	10	2.313	0.368	94	2.178	0.093
All females ^b	13	2.704	0.260	123	2.384	0.097
All SY birds ^b	6	2.375	0.460	56	2.276	0.134
All ASY birds ^b	15	2.590	0.346	98	2.213	0.103

^a Change in remex score per day.

^b Includes AHY individuals.

for each of the four age-sex classes (Table 1). Because the means for SY and ASY males did not differ significantly ($t = 0.281$, $df = 8$, $P > 0.5$), and because only one SY female provided appropriate recapture data, I calculated pooled estimates of mean rates for the two sex and the two age classes (Table 1). The mean remex molt rate of females (including AHY individuals) was significantly higher than the mean rate of males ($t = 3.11$, $df = 22$, $P < 0.01$). The mean molt rate of ASY birds did not differ significantly from that of SY individuals ($t = 1.14$, $df = 20$, $P > 0.2$).

Based on these calculations, females completed remigial molt on average in 37 days, and males in 43 days. Individuals of both sexes varied considerably around the mean rates. Remex molt rates of females ranged from 2.30 to 3.11 points per day (estimated durations of 32 to 42 days), while males molted at rates between 1.57 and 2.86 points per day (estimated durations of 35 to 64 days). The greatest deviations from the mean molt rates were exhibited by individuals that were examined only late in the molt cycle or in which the interval between captures was short (Fig. 1). Although rates were slowest at the beginning and end of molt, when fewer remiges than average were growing simultaneously, the longest lines in Figure 1 are nearly parallel, indicating that the overall rate of remex molt was similar among individuals of each sex, regardless of starting date.

Ten birds were examined from two to seven times in both early and late stages of remex molt. All had increased their remex score between initial and final captures by more than 65 points. Four males averaged 2.38 points per day (SD = 0.25, range = 2.24–2.75), while six females averaged 2.68 points per day (SD = 0.29, range =

2.30–3.11). These estimates are consistent with those calculated from the total sample in Table 1.

Fluctuations in the rate of remex molt were examined for 10 individuals handled three or more times at least 5 days apart in the same molt cycle. Three birds with rates calculated from both early to middle and late stages of molt showed the greatest fluctuations, their fastest rates being between 3.9 and 4.2 times their slowest. The rates were highest between early and middle stages of molt, dropping markedly in late stages. Two ASY females showed nearly constant rates of molt up to remex scores of 70 and 74, respectively. One SY female also maintained a relatively constant rate up to remex score 67, then slowed between each of two successive captures.

Linear regression analysis of remex score against date for all actively molting birds (Table 1) gives consistently lower estimates of molt rate than do calculations from recapture data. SY females are the only class for which regression analysis gives a higher estimate than recapture data, suggesting that the calculation of molt rate from the one recaptured SY female underestimates the mean rate for that class. For ASY females a disproportionate difference is evident between the estimates from recapture data and regression analysis. The timing of molt in a population must be relatively synchronized in order for regression analysis to accurately estimate the rate and duration of molt (Newton 1966, Pimm 1976, Bancroft and Woolfenden 1982). Since the onset of remex molt in each age-sex class was asynchronous (see below), the values for mean molt rates from regression analysis are probably underestimates.

Based on the estimates from regression analysis, female Yellow Warblers completed remigial molt on average in 42 days, males in 46 days.

However, four males and six females captured both early and late in molt replaced their remiges on average in 37 and 42 days, respectively. These estimates are nearly identical to those calculated from the total sample of recaptured males and females. Therefore, it seems reasonable to consider values obtained from recapture data as more accurate estimates of the rate and duration of remigial molt in this population.

CHRONOLOGY OF MOLT

Molting Yellow Warblers were captured during a 2-month span between early July and early September. Plots of remex score against date (Fig. 2) illustrate the progression and timing of pre-basic molt in the population. The onset of molt was spread over a 3- to 4-week period between early July and early August in each year. The earliest record of a molting individual was of an ASY male captured on 9 July with a remex score of 2, indicating molt had just begun. An SY male with a remex score of 6 on 10 July may have started molt a day or two before this bird. Only three individuals, all females, that had not begun molt were examined after 1 August, the latest being an AHY female captured on 7 August. The earliest individuals completed remigial molt in mid-August. Only one bird, an ASY female, captured after 1 September was still in remex molt.

SY males began molt earlier than other classes, while SY females were the last class to initiate molt. However, molt onset for any one class was spread over a 3-week period, and there is considerable overlap in remex scores between classes on any given date (Fig. 2). Based on rates calculated from individuals captured two or more times during molt, males began remex molt on 17 July, significantly earlier than the 22 July mean starting date of females ($t = 2.12$, $df = 22$, $P < 0.05$). However, both sexes completed molt on the mean date of 28 August, suggesting that the more rapid molt of females compensates for their later start. SY birds tended to begin molting earlier than ASY birds, but the difference was not significant ($t = 1.66$, $df = 19$, $P > 0.1$).

Chronology of molt did not appear to influence its rate. Among recaptured individuals, the two earliest-molting males (neither a known breeder) increased 85 points in 31 days (2.74 points per day) and 84 points in 32 days (2.62 points per day), respectively, before tapering off in the late stages of remex molt. The latest-molting male, who fledged young on 19 July, increased his re-

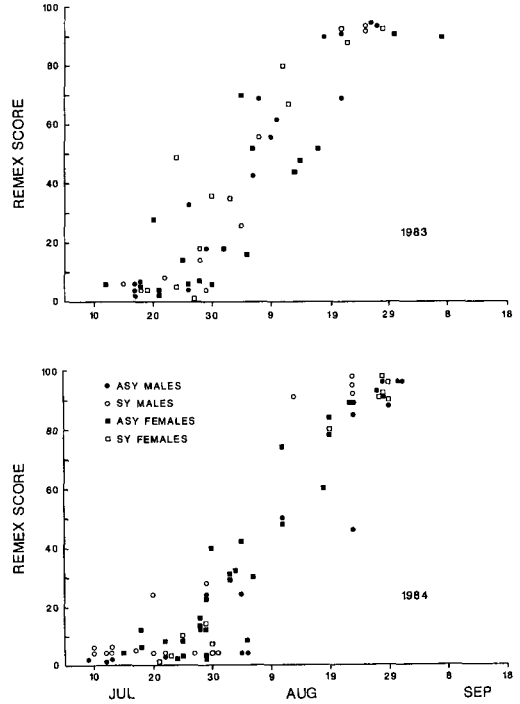


FIGURE 2. Remex scores of Yellow Warblers examined during the definitive prebasic molt in 1983 and 1984.

mex score from 4 to 46 points between 5 and 23 August, at a rate of 2.33 points per day. None of the early- and late-molting females captured two or more times during molt were known breeders. The earliest two females to begin molt increased 64 points in 23 days (2.78 points per day) and 68 points in 24 days (2.83 points per day). The latest female to start remex molt increased at the rapid rate of 3.50 points per day between 5 and 13 August, but then slowed in the next 25 days until her final capture on 7 September, for an overall rate of 2.30 points per day. Another late-molting female increased 2.52 points per day between 1 and 30 August.

Timing of molt for the population was similar in 1983 and 1984, based both on recapture data and regression analysis (Table 2). The mean remex molt rates, calculated from recaptures, were not significantly different ($t = 1.28$, $df = 18$, $P > 0.2$). Estimates of timing for 1982, based on small sample sizes with relatively high variances, are probably not accurate. They indicate a higher mean rate than for the other 2 years from regression analysis and a lower mean rate from recap-

TABLE 2. Differences in population timing of the prebasic molt among years, based on recapture data and regression analysis.

	Recapture ($\bar{x} \pm SD$)			Regression ($\bar{x} \pm SD$)		
	1982 ($n = 3$)	1983 ($n = 9$)	1984 ($n = 11$)	1982 ($n = 18$)	1983 ($n = 83$)	1984 ($n = 92$)
Molt rate ^a	2.26 \pm 0.60	2.50 \pm 0.30	2.68 \pm 0.32	2.67 \pm 0.31	2.20 \pm 0.11	2.26 \pm 0.09
Start of molt	18 July \pm 1.5 days	19 July \pm 6.0 days	21 July \pm 6.6 days	23 July	17 July	18 July
End of molt	2 September \pm 13.6 days	29 August \pm 7.6 days	28 August \pm 8.1 days	29 August	31 August	1 September
Molt duration (days)	46.67 \pm 15.01	40.78 \pm 4.79	38.18 \pm 4.96	37.39	45.43	44.26

^a Change in remex score per day.

tures of molting individuals. The mean dates of molt onset and completion in 1983 and 1984 were very similar. This suggests that while individuals vary in the scheduling of their prebasic molt from year to year, the population molting period is constrained within fairly narrow time limits, presumably because of the abbreviated northern summer.

Fourteen individuals provided molt data in 2 or more years between 1982 and 1984. I calculated a date of molt onset for each individual in each year, based on the mean rate from recaptures for its class. In general, females showed closer synchrony between years than males, beginning molt on average 4.2 days apart in different years (range = 0–10 days), while males started molt on average 6.1 days apart (range = 0–20 days). This difference was not significant ($t = 0.67$, $df = 14$, $P > 0.5$). These patterns appear to have resulted from variations in the timing of breeding among individuals in different years.

INTEGRATION OF MOLT AND BREEDING

Nesting chronology was similar among years (Table 3). The incubation period (date of last egg laid to last egg hatched) of 12 nests was invariably 11.0 days. Using this value, I calculated a date of clutch completion for all other nests whose

dates of hatching I knew. I combined known and estimated dates to determine a mean date of clutch completion for the population in each year (Table 3), and found that chronology of first nesting attempts is synchronized within 2 weeks in a given year. Only three pairs re-nested following failures in the egg or early nestling stages, and only one of their replacement clutches produced fledglings. There appears to be little flexibility in this population for adjustment of the breeding schedule during the brief summer.

I collected both breeding and molt data on 30 individuals. While molt-breeding overlap does exist for the population as a whole (Fig. 3), no birds of known breeding status that were examined during the nesting cycle had initiated remex molt (Fig. 4). The extrapolated dates of molt onset for adults handled during the post-fledging period further indicate that no remex molt was initiated while young were in the nest. Based on rates of molt calculated from recapture data, known-breeding males ($n = 16$) began remigial molt on average 8.1 days after young fledged ($SD = 2.65$, range = 1–19), while known-breeding females ($n = 6$) started molt on average 12.3 days after fledging young ($SD = 2.65$, range = 9–15). This difference is significant ($t = 2.073$, $df = 20$, $P = 0.051$). Fledglings reach independence 2 to 3 weeks after leaving the nest (pers.

TABLE 3. Breeding chronology of Yellow Warblers in different years.

	1982			1983			1984		
	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range
Date of clutch completion ^a	6	23 June \pm 5.0 days	18 June– 2 July	12	23 June \pm 3.1 days	19 June– 30 June	14	21 June \pm 4.6 days	15 June– 30 June
Date of fledging	6	12 July \pm 6.2 days	5 July– 23 July	11	12 July \pm 3.3 days	9 July– 19 July	16	11 July \pm 5.4 days	6 July– 27 July

^a Includes known and calculated dates.

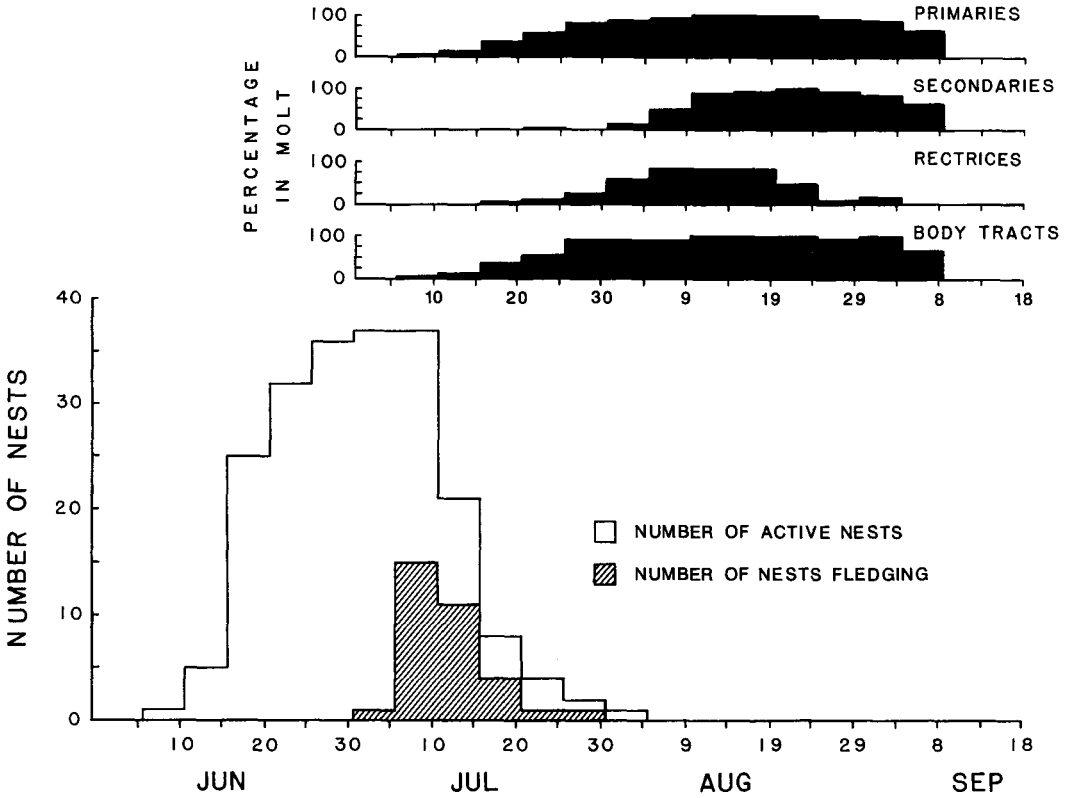


FIGURE 3. The timing of breeding and prebasic molt in adult Yellow Warblers. Four regions of the plumage are distinguished.

observ.), so it appears that nearly all breeding Yellow Warblers initiate remex molt during the period of fledging care.

Molt of both members of five known-breeding pairs was examined during the same year. Of the four pairs whose young fledged close to the population mean date of fledging, the males started molt on average 7.5 days after their young fledged ($SD = 2.38$, range = 6–10), while the females began on average 14.0 days after fledging young ($SD = 0.82$, range = 13–15). The fifth pair fledged young on the late date of 19 July (a probable second attempt). The male was captured on 5 August with a remex score of 4, suggesting that he had initiated molt 1 or 2 days earlier. His mate was examined on 29 July with a remex score of 2, almost certainly having dropped primary 1 on each wing the previous day. This male's relatively delayed start may have resulted from his apparently having assumed full care of the pair's four fledglings. Typically, both members

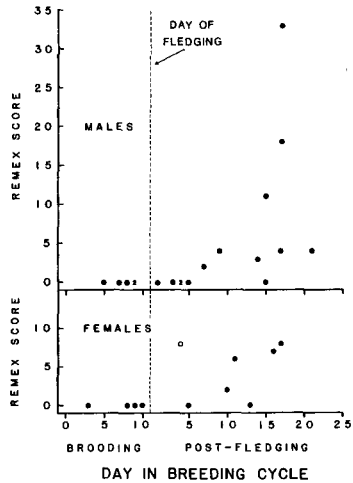


FIGURE 4. Remex scores for Yellow Warblers of known breeding status relative to day in their breeding cycle. The open circle indicates a female whose nest failed (see text).

TABLE 4. Movements of known-breeding Yellow Warblers during the prebasic molt, 1984 ($n = 15$ males, 13 females).

	Males	Females
Remained on breeding territories	9 (60%)	2 (15%)
Wandered over study area	2 (13%)	1 (7%)
Not encountered, probably dispersed	4 (27%)	10 (67%)

of Yellow Warbler pairs cared for fledglings, either by splitting the brood or by keeping the brood together and sharing feeding duties. This male was frequently observed flying between his breeding territory, where he continued to advertise his presence by singing, and areas up to 100 m distant, where he tended all four fledglings. His delayed molt onset may have been due to energetic or endocrine incompatibility of parental care, territoriality, and molt.

Suppression of molt by breeding is further indicated by one female (Fig. 4, open circle). She lost a replacement brood 10 days after it hatched, on 1 August, and was captured later that day not yet in molt. However, 4 days later she was examined with her innermost four primaries on each wing in pin, suggesting that termination of breeding had acted as an immediate release on the beginning of molt.

A comparison of extrapolated starting dates for males of known and unknown breeding status gives further evidence of incompatibility between breeding and molt in this population. The earliest-molting known breeders were eight males that began remex molt on the mean date of 15 July (SD = 2.4 days, range = 12–18 July), an average of 4.9 days after their young fledged (SD = 2.80, range = 1–9). Eight males of unknown breeding status captured during the first half of July had started molt on the mean date of 9 July (SD = 1.6 days, range = 7–11 July). Six of these were SY birds. I believe these earliest-molting males were either failed breeders or nonbreeding individuals, i.e., the “floaters” of Brown (1969), Smith (1978), and others. During the nesting period in each year, I captured up to 57 unbanded, nonlocal males that were not subsequently encountered. More than 68% of these were SY birds. Of 24 known-age breeding males in 1982 to 1984, only two were SY individuals, suggesting a very low recruitment into the breeding population by this age class. I do not believe these floating males

TABLE 5. Numbers of adult Yellow Warblers of unknown breeding status captured during molt, 1983–1984 ($n = 39$ males, 57 females).

		Males	Females
Initial remex score < 90	Captured once	18	29
	Captured > once	5	10
Initial remex score > 90	Captured once	16	18
	Captured > once	0	0

were extraterritorial birds, as documented in a Minnesota breeding population by Ford (1983). Known-breeding males at North Point were rarely captured off their territories, and regular searching up to 1 km away from the study site failed to locate any males color-banded at North Point. The apparent adult sex ratio, based on banding totals, is highly skewed towards males, and I never examined a female during the breeding season that did not show a well-developed brood patch. It thus appears that a transient subpopulation of nonbreeding males does exist along the James Bay coast and that these birds, free from the constraints of breeding, are the first to begin prebasic molt.

BEHAVIOR AND MOVEMENTS DURING MOLT

Observations on the activities and movements of postbreeding adults in 1984 showed pronounced differences between the sexes during the period after young reached independence (Table 4). Seven males remained on or within 100 m of breeding territories throughout molt, advertising their presence with intermittent secondary song, through the day of their presumed southward departure. I searched for four of these males during the first morning on which I detected no singing and failed to locate them. I believe that they had migrated the previous night. Two males were captured on their breeding territories late in the molt cycle and may have temporarily moved off the site after reproduction ended. Two molting males were observed or captured at considerable distances from their breeding territories. They may have either wandered over the study area during molt or regularly ventured off the territory base. Apart from the subdued singing behavior of some males, molting birds of both sexes tended to be very inconspicuous. It is possible that I failed to detect or capture some individuals that did remain on territories.

Females showed comparatively little site at-

tachment. Most apparently dispersed from North Point either while tending fledglings or after terminating parental care. I found no evidence of postreproductive association of any mated pairs, nor of any mate fidelity in subsequent breeding seasons despite high levels of philopatry by both sexes (64% in males, 75% in females, 1984 data). Banding data from 1983 and 1984 indicate a molt dispersal, rather than a true molt-migration overlap, of females (Table 5). In addition to the departure of most breeding females, there was a substantial influx of unbanded females in early and middle stages of molt. Some of these remained at North Point through most or all of their molt. Since approximately equal numbers of unbanded males and females were captured in the late stages of remex molt (Table 5), it seems unlikely that females initiated actual migration before or during the peak molt period.

MOLT AND MIGRATION

James Bay Yellow Warblers regularly began migration during the late stages of remex molt. Despite intensive mist-netting through early- to mid-September in 1982 to 1984, I handled only six adults in completely new basic plumage, between 25 August and 8 September. None was a known breeder. All were previously unbanded, presumably nonlocal birds. Of the 34 individuals of unknown breeding status that I first examined late in their molt cycle, none was recaptured (Table 5); they were probably moving through the area. Banding results indicate that adult migration peaked in late August and early September (Fig. 5). Immatures, without the constraints of a flight

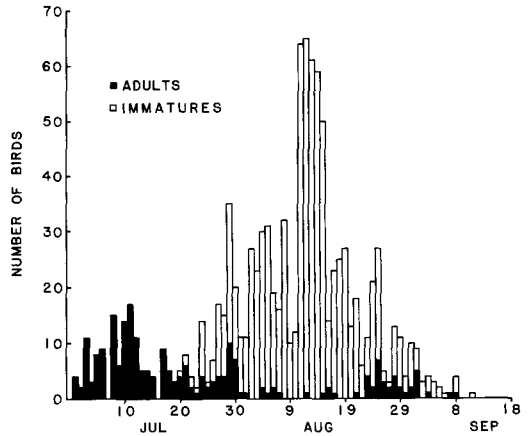


FIGURE 5. Numbers of unbanded adult and immature Yellow Warblers captured at North Point, 1982 to 1984.

feather molt, peaked in numbers during mid-August, when heavily-molting adults were extremely sedentary. The numbers of adults banded in July do not represent true migrants, but were resident breeders, early dispersers, and the presumed floating males. Of the 35 unbanded adults captured between 23 August and 8 September, the six (17%) that had completed remex molt had a lower mean weight than individuals at any stage of molt, further evidence that they were migrating.

The few individuals examined during the peak molt period, when maximum numbers of remiges and rectrices were growing simultaneously, typically showed large gaps in the wings, with the

TABLE 6. Mean weights of adult Yellow Warblers before molt and at different stages of the prebasic molt, 1982 to 1984.

		Males		Females	
		n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$
Molt not started	June 1-15 ^a	35	9.87 ± 0.58	16	9.07 ± 0.43
	June 15-30	54	9.70 ± 0.43	17	10.11 ± 0.82
	July 1-15	68	9.77 ± 0.43	67	9.75 ± 0.70
	July 16-31	15	9.43 ± 0.42	29	9.55 ± 0.56
Remex score ^b	1-10	29	9.76 ± 0.42	34	9.68 ± 0.64
	11-30	11	10.00 ± 0.60	18	9.90 ± 0.61
	31-50	5	10.42 ± 0.72	11	10.33 ± 0.78
	51-70	5	10.44 ± 0.66	8	10.03 ± 0.75
	71-90	6	10.35 ± 0.29	15	9.71 ± 0.72
	91-99	28	9.81 ± 0.47	23	9.35 ± 0.56
	100	4	9.68 ± 0.58	2	9.10 ± 0.00

^a Data from 1982 only.
^b See text for explanation.

unmolted remiges badly abraded or broken, and often had all tail feathers in early growth stages. There is no doubt that these birds were aerodynamically, and perhaps physiologically, incapable of sustained flight. However, individuals nearing the completion of remigial molt, with only the distal one or two primaries and proximal three or four secondaries in final growth stages, were likely capable of beginning migration. I therefore conclude that most, if not all, of the unbanded adults captured late in molt were actively migrating.

WEIGHTS OF BREEDING AND MOLTING ADULTS

Both sexes steadily gained weight between the end of breeding and the middle of remex molt (Table 6). Peak mean body weights coincided with the periods of greatest intensity of flight feather and body molt. Eighteen known breeders (11 males, seven females) were weighed at least once during the nesting cycle and again during molt in the same year. Only two of these lost weight between the two periods. The mean weights of known male and female breeders dropped during the interval between the end of nesting and the onset of remex molt, but increased through mid-molt. This suggests that the first 1 to 2 weeks of fledgling care are an especially energy-demanding period. Mean weights from the sample of all molting adults indicate a progressive decline during the late stages of remex molt (Table 6). There was no indication that James Bay Yellow Warblers deposited subcutaneous fat prior to southward migration.

DISCUSSION

TIMING OF THE PREBASIC MOLT

Most Yellow Warblers at James Bay completed remigial molt in 35 to 45 days. This is a considerably shorter duration than that reported for three other wood warbler species, although precise data on individuals are lacking from those studies. Foster (1967) reported that adult Orange-crowned Warblers (*Vermivora celata*) complete prebasic molt in about 2 months, but she was not able to examine subspecific variation in her sample, which was collected from a wide geographic range. In Indiana (ca. 39°N), Nolan (1978) found that Prairie Warblers (*Dendroica discolor*) without dependent offspring were in "noticeable molt" for 39 to 42 days. He concluded that an additional 10 to 15 days were

required to complete the process, so that a realistic estimate of remex molt duration would be 50 to 60 days for an individual. Stewart's (1952) estimate that Common Yellowthroats (*Geothlypis trichas*) in southern Michigan complete molt in considerably less than 30 days is based on only nine birds collected between 9 August and 4 September and is undoubtedly a gross underestimate. In the absence of strictly comparable molt data among the Parulinae, there is little basis for evaluating prebasic molt patterns in James Bay Yellow Warblers with respect to other members of the subfamily.

Several migratory passerine species that breed at north-temperate and higher latitudes undergo a more rapid molt than sympatric, nonmigratory populations and species, or those breeding further south (Evans 1966, Dolnik and Blyumenthal 1967, Evans et al. 1967, Morton et al. 1969, Snow 1969, Baggott 1970, Haukioja 1971a, Mewaldt and King 1978). Six migratory passerine species studied in Scandinavia have short and intense molts of 30 to 40 days (Stresemann and Stresemann 1966, Berger 1967, Haukioja 1971a), similar to that of James Bay Yellow Warblers. In the strongly seasonal alpine zone of Wyoming, Verbeek (1970) found that Water Pipits (*Anthus spinoletta*) complete molt in slightly more than a month, prior to migrating.

In contrast, sedentary passerines at high latitudes may undergo a relatively protracted molt of up to 3 months' duration (Pitelka 1958, Newton 1966, Dhondt 1973, Orell and Ojanen 1980). At James Bay, Common Redpolls (*Carduelis flammea*), which may be permanent residents in some years, molt much more slowly than Yellow Warblers. They require 2 to 3 months to complete remigial molt (Rimmer, unpubl.). This species is primarily granivorous and does not face the pressures of a diminishing late summer insect food supply and an impending long-distance migration. A protracted molt would seem to be the optimal pattern for a bird facing few constraints on its time and energy. This option does not exist for insectivorous migrant passerines of north-temperate and higher latitudes.

A rapid molt may seriously impair flight efficiency and has been shown to cause flightlessness in individuals of some passerine species (Stresemann and Stresemann 1966, Berger 1967, Haukioja 1971a). Haukioja (1971a) noted that the skulking behavior adopted by many heavily-molting birds may result from extreme reluc-

tance, rather than physical inability, to fly. A decrease in flying activity may be important in decreasing vulnerability to avian predators and in conserving energy for feather synthesis and thermogenesis. Several factors suggest that Yellow Warblers become essentially flightless during the middle stages of their rapid molt. Individuals were very secretive and difficult to observe during this time, and many fewer were captured in mist nets than during early and late stages of molt. Singing males occupied well-concealed songposts and sang subdued songs only intermittently. Birds examined in mid-molt typically had high "raggedness values" (e.g., Haukioja 1971a), with as many as eight primaries and all twelve rectrices growing concurrently. The extreme reduction in flight feather surface and the severe abrasion of unmolted remiges observed in several heavily-molting Yellow Warblers suggest that sustained flight and quick changes of direction may be aerodynamically impossible at this time.

The first Yellow Warblers to begin molting were SY males. Yearlings of several other passerine species are known to start molting earlier than older birds (e.g., Pitelka 1958, Newton 1966, Snow 1969, Samson 1976, Sealy 1979, Bancroft and Woolfenden 1982). The usual explanation is that many yearling birds do not breed successfully and that nonbreeders can channel energy into an earlier molt (Bancroft and Woolfenden 1982). It appears that few SY male Yellow Warblers obtain breeding opportunities at James Bay. Without the energetic demands of breeding and the accompanying inhibition of molt by gonadal hormones (Payne 1972), SY males began to molt before older, breeding birds. However, SY females, which do regularly breed at North Point, were the last class to start molting. Samson (1976) found that nonbreeding SY male Cassin's Finches (*Carpodacus cassinii*) molt earlier than ASY breeders, but they also molt more slowly, which is not the case in Yellow Warblers. He assumed that the total energy demands for unmated males are less than for breeders, permitting a more relaxed molt schedule. SY female Cassin's Finches do breed, and their molt schedule is the same as that of ASY breeders. In Northern Orioles (*Icterus galbula*), some SY males breed successfully, but others apparently do not (Sealy 1979). The latter individuals are thought to account for the earlier molt of SY males in this species.

In many passerine species, as in Yellow Warblers at James Bay, males initiate molt before females (e.g., Verbeek 1970, Orell and Ojanen 1980, Tiainen 1981). However, sexual differences in timing may be less pronounced at lower latitudes. Nolan (1978) found no significant differences in the onset or duration of molt in male and female Prairie Warblers in Indiana. Breeding Eurasian Bullfinches (*Pyrrhula pyrrhula*) of both sexes in England begin molt on similar dates and molt at similar rates (Newton 1966), as do Eurasian Blackbirds (*Turdus merula*; Snow 1969).

BODY WEIGHT DURING MOLT

In many passerines, body weight increases during molt, often most rapidly in the beginning and middle stages (King et al. 1965; Evans 1966, 1969; Newton 1966, 1968a; Nisbet 1967; Bell 1970; Morton and Welton 1973; Nolan 1978; Orell and Ojanen 1980). In some species, deposition of body fat is at least partly responsible for weight increases during molt (Evans 1966, 1969; Newton 1968a; Payne 1972; Morton and Welton 1973). Fat deposition is known to be essential in fueling the long-distance migrations of many species (e.g., Odum et al. 1961, Nisbet et al. 1963, King and Farner 1965). However, most studies of migratory fattening in wild passerines have sampled transient birds. Few reports have documented premigratory fat deposition on the breeding grounds. King et al. (1965) and DeWolfe (1967) found that breeding White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in Alaska significantly increase their premigratory lipid reserves in late summer. However, total body weight does not reflect this increase, because of a concurrent decrease in lean body weight. These authors concluded that body weight is not necessarily a reliable index of migratory fat deposition in this species. White-crowned Sparrows breeding at high altitudes in California increase their body weight by 25% between the end of reproduction and migration, due mostly to fat accumulation (Morton and Welton 1973). About half of this weight gain occurs during molt and half immediately following molt, suggesting that hyperphagia begins early in the molt period. Dolnik and Blyumenthal (1967) found that Common Chaffinches (*Fringilla coelebs*) steadily increase their body fat content prior to migrating from the Baltic coast, but that northern populations depart their breeding grounds without significant fat reserves and migrate south with "low inten-

sity," sometimes completing prebasic molt en route. On staging areas to the south, these and other northern migrants accumulate large fat reserves before beginning true migration.

Despite their weight losses prior to migration, it is possible that, during late molt, James Bay Yellow Warblers did store some metabolizable fat, which I failed to detect. Even a small net deposition might enable a relatively short flight to a stopover area with more favorable feeding conditions than the James Bay coast. Sufficient fat to fuel the bulk of the long-distance migration could be accumulated. No other breeding passerines at North Point deposited detectable pre-migratory fat, evidence that late summer conditions at the site may not be suitable for fat accumulation (Rimmer, unpubl.).

Hormonal conflicts may suppress hyperphagia and fat deposition during the late molt-premigratory period. Prolactin, which inhibits molting in some birds, induces fat deposition and nocturnal restlessness in some migratory passerines (e.g., White-crowned Sparrow; Payne 1972). Species that overlap molt and migration may have evolved mechanisms for inhibiting prolactin secretion, at the expense of hyperphagia and fat accumulation. The interplay among the endocrine controls on the accelerated and partially overlapping breeding, molt and migration schedules in northern passerines is probably complex and needs further investigation.

Based on weight gain data, Newton (1966) concluded that molt probably does not impose a significant physiological strain on bullfinches. Molting Yellow Warblers were heaviest during mid-molt, indicating that the energetic and nutritional demands of molt may not be high relative to the demands of parental care and migration (see also Payne 1972). However, the decrease in mean weights during late molt and the lack of discernible body-fat accumulation suggest that insect food may become limiting in late summer and that progressively lower temperatures may take an energetic toll on molting birds with reduced feather insulation. Although I did not collect data on insect food abundance, qualitative observations indicated a substantial decline in many insect groups during the second half of August. I believe that diminishing food supplies and deteriorating weather may stress the energy budgets of adult Yellow Warblers, causing the observed reduction in mean weights and precipitating migration during the final phase of re-

migratory molt. I suggest that James Bay breeders begin to migrate "with low intensity" (e.g., Dolnik and Blyumenthal 1967), accumulating fat reserves during stopover periods after one or a series of short flights away from the inhospitable coast.

THE RELATIONSHIP BETWEEN BREEDING, MOLT, AND MIGRATION

Most north-temperate passerines stagger the periods of reproduction, molt, and migration, beginning molt shortly after the termination of parental care and completing it prior to migration. Yellow Warblers at James Bay depart slightly from this pattern by overlapping prebasic molt with care of dependent fledglings and with the beginning of migration. Breeding, molt, and migration each require energy expenditure above that of normal metabolic activity (Payne 1972, King 1974). Assuming the scheduling of these events to be adaptive, I examined factors that may have determined their integration into the annual cycle of Yellow Warblers.

Molt-breeding overlap has been reported in several species of temperate and north-temperate breeding passerines. Tiainen (1981) found that Willow Warblers (*Phylloscopus trochilus*) regularly begin molt during nesting. He noted considerable variation among males in molt onset, some individuals starting to molt during incubation, others delaying molt until late in the fledgling care period. He concluded that both sexes begin molt independently of the breeding stage, and he suggested that endogenous rhythms might control the fine tuning of molt onset in individuals. Nonmigratory Great Tits (*Parus major*) and Willow Tits (*P. montanus*) in Finland frequently overlap molt and nesting (Orell and Ojanen 1980). Males do so more commonly than females, and both sexes overlap molt with repeat or true second nesting attempts significantly more often than with first attempts. Overlap between molt and care of nestlings or fledglings has been reported in individuals of several other migratory passerines from both temperate and northern latitudes (e.g., Northern Waterthrush [*Seiurus noveboracensis*], Eaton 1957; Lesser Redpoll [*Carduelis flammea cabaret*], Evans 1966; Redwing [*Turdus iliacus*], and Pine Grosbeak [*Pinicola enucleator*], Haukioja 1971b; Snow Bunting, Green and Summers 1975).

Bullfinches (Newton 1966) and Prairie Warblers (Nolan 1978) with dependent young tend

to have later and slower molts than birds without dependent young. Nolan also found significantly later mean dates of molt onset in Prairie Warblers of both sexes that tended fledglings to independence than in birds whose last nest failed. Both authors suggested that parental care and molting are incompatible in those species. Although Yellow Warblers at James Bay regularly began molt while tending fledglings, only six (27%) of 22 known breeders started within the first week after young fledged. Since fledgling mobility increases and dependence decreases during the postfledging period, demands on parental time and energy must also progressively decrease. The delay in molt onset by most breeders until the late stages of fledgling care suggests a mechanism tending to reduce molt-breeding overlap. However, as early a start as possible should be advantageous for individuals at this latitude, either in allowing a slower, less stressful molt or in enabling an earlier completion. The earlier molt of apparently nonbreeding SY males suggests this.

In several species an earlier emancipation from parental care by one sex has been shown to correspond to an earlier molt schedule in that sex (e.g., White-crowned Sparrow, Morton and Welton 1973; Common Reed-Bunting [*Emberiza schoeniclus*], Bell 1970; Northern Oriole, Sealy 1979; Willow Warbler, Tiainen 1981). In most migratory passerines that divide parental duties equally during the postfledging period, the onset of prebasic molt is similar in males and females (e.g., Lesser Redpoll, Evans 1966; Cassin's Finch, Samson 1976; Prairie Warbler, Nolan 1978). I found no evidence that one sex of Yellow Warblers consistently terminated fledgling care before the other. However, I suggest that females, constrained by the energetic demands of nest construction, egg synthesis, incubation, brooding, and nestling-feeding duties, may be unable to mobilize sufficient physiological resources to begin molt as soon after nesting as males. Although energetic demands on incubating and brooding females may actually be less than those on their nonincubating mates (Walsberg and King 1978, Bancroft and Woolfenden 1982, Walsberg 1983), several studies have indicated increased metabolic rates during incubation (e.g., Mertens 1980). Female Yellow Warblers may be able to accumulate energy reserves after terminating parental care, possibly allowing for their more rapid molt than males. While most females decreased in weight during nestling and fledgling care, their

weights increased steadily through mid-molt (Table 6). Although males' weights also increased during this time, they may have expended relatively more energy during molt, since many continued to sing and apparently maintained territories. Females may have devoted more time to feeding during molt than males, thus obtaining relatively more energy for feather synthesis.

Early- and late-molting individuals of both sexes did not differ significantly in their rate of molt. This suggests that molt rates may be maximal in this population. Although molt may not impose an exhaustive energetic strain on a day-to-day basis (Payne 1972), metabolic rates do increase during molt (Lustick 1970). Perhaps the needs to maintain thermoregulatory abilities in the event of severe weather, to maintain high rates of feeding to offset the energetic costs of molting, and to prepare physiologically for the impending long-distance migration, set an upper limit on the molt rate in James Bay Yellow Warblers. Further adjustments to the short summer may necessitate slight overlaps between breeding and molt and between molt and migration.

Maintenance of peak flight efficiency may have selected for the timing and duration of molt in Yellow Warblers. Bancroft and Woolfenden (1982) found that remigial molt in Scrub Jays coincided with periods of activity in their annual cycle that required the least amount of flying. In Yellow Warblers the early postfledging period of young may require full flight abilities of parents, due to the limited mobility and high food demands of fledglings. This may also be a period in which detection and distraction of predators is especially critical. Thus, potential losses in offspring survival through impaired flight of adults, either from reduced feeding efficiency or increased vulnerability to predators, may have favored delaying molt onset until young are nearly independent and capable of full flight themselves.

Few passerines are known to overlap molt and migration. Dolnik and Blyumenthal (1967) reported that chaffinches and other passerines breeding at high latitudes in Finland and Russia apparently begin migrating while in molt. Late-molting individuals of three cardueline finch species in Britain occasionally migrate with the outer one or two primaries and innermost secondaries incompletely grown (Newton 1968b). Evans (1966) reported that, while most Lesser Redpolls complete molt prior to migration, some

individuals may begin migration before finishing wing molt. Sealy (1979) speculated that SY male Northern Orioles begin moving southward early in the molt, since they were absent from his study area after mid-July. Niles (1972) described molt-migration overlap in Purple Martins (*Progne subis*) and reported that the pattern is typical of migratory hirundinids. He suggested that the family's characteristic slow, diurnal migration, with frequent feeding intervals, reduces the concurrent energetic demands of molt and migration.

Yellow Warblers regularly began migrating during the final phase of remigial molt, when flight efficiency was probably close to maximal. With all rectrices full-grown and only the distal one or two primaries and proximal three or four secondaries in late growth stages, wing loading would be only slightly greater than normal. The energetic costs of molt are probably low at this time, as evidenced by the decreased remex rates of individuals near the end of molt. Since Yellow Warblers actually lost weight late in molt and did not visibly accumulate premigratory fat, their departure may be more closely keyed to aerodynamic than physiological readiness. This and the very rapid rate of their molt suggest that strong selection pressures are operating on their migration schedule.

SUMMARY

The phenology of ecological events on the James Bay coast ultimately dictates the allocation of time and energy by breeding Yellow Warblers. In this strongly periodic environment, spring arrives late and fall begins early. Yellow Warblers spend only 10 to 12 weeks in the region, during which they must breed, molt, and prepare for southward migration. Their insect food resources are abundant through the breeding and early-molting periods, but appear to decline rapidly after mid-August. Temperatures regularly drop to freezing point in late August. Severe storms off the bay, which pose a constant threat even during the breeding season, increase in frequency and intensity as autumn approaches. This brief period of favorable feeding and climatic conditions appears to have forced compromises in the partitioning of breeding, molt, and migration in Yellow Warblers. The prebasic molt intrudes upon the period of postfledging parental care, and migration overlaps with the end of molt. The molt itself is rapid and intense, involving

up to eight primaries simultaneously, and probably results in the virtual flightlessness of some birds. The short duration of 35 to 45 days is possible, presumably because peak food supplies and long photoperiods in which to forage persist through the period of heaviest molt. The importance of maintaining thermoregulatory abilities and high rates of feeding may constrain further shortening of the molt. The need for maintenance of good flying ability during fledging care and migration may, in part, have determined molt timing and duration in the population. Although a complex of endogenous and environmental factors are known to influence molt onset, breeding chronology seems to most closely dictate the individual scheduling of prebasic molt in James Bay Yellow Warblers.

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