PATTERN AND CHRONOLOGY OF PREBASIC MOULT IN WOOD-WARBLERS (PARULIDAE)

by

Christine Anne Debruyne

A thesis presented in partial fulfillment of the requirements for the degree of
Master of Science
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GENERAL ABSTRACT

Pattern and chronology of prebasic moult in wood-warblers (Parulidae)

Masters Degree in Biology, 2003

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This study compared the pattern and chronology of the prebasic moult in seven warbler species (Parulidae) at two locations in Ontario. Yellow Warblers (*Dendroica petechia*) were the earliest to start flight feather moult. Ovenbirds (*Seiurus aurocapillus*) underwent the most rapid flight feather moult, being only 22 days. Yellow-rumped Warblers (*D. coronata*) had the longest moult period (62 days) and were the last species to finish moult. These findings suggested that some warblers overlap the early and final stages of moult with the later stages of breeding and/or the onset of migration. Furthermore, a positive correlation between the duration of moult and timing of migration for all species, except Ovenbirds, suggested that earlier migrants moult more quickly and later migrants take a longer period to moult. Ovenbirds may be anomalous with regard to moult scheduling and migration because of their atypical ecological and behavioural attributes or their systematic position among parulids. A combination of external and internal factors may explain variations in the relationship between breeding, moult, and migration in warblers, allowing each species to fine-tune the onset of prebasic moult accordingly.

I examined the relationship between raggedness scores and moult rates among five species of wood-warblers with similar moult patterns to determine if raggedness could be used as an index of moult rates. Positive correlations between raggedness and moult rates derived from pooled recaptures, least squares linear regressions, and individual species recapture methods suggested that average raggedness for the primary and secondary scores within a determined primary moult score range is a good index of the rate of moult in warblers. Therefore, mean raggedness scores may be a useful tool for (1) providing baseline moult rate assessments in populations with insufficient recaptures, allowing for comparisons to other populations with known moult rates; and (2) estimating the rate and duration of moult in some species.

I compared the timing and patterns of the prebasic body moult between Hatch Year and After Hatch Year American Redstarts (*Setophaga ruticilla*), and Hatch Year and After Hatch Yellow Warblers. Both species displayed no difference in the number of moulting individuals in each designated body region. In addition, moult started in early July and lasted until mid-August for both age classes of American Redstarts. In contrast, Hatch Year Yellow Warblers started body moult in late June to early July, whereas adults began body moult in mid-

July. Both American Redstarts and Yellow Warblers displayed differences in intensity and timing of moult among specific body regions between age classes. In addition, After Hatch Year individuals of both species underwent body moult concurrently with primary moult. Extrinsic and intrinsic factors may contribute to the variations in body moult scheduling observed in these two species.

ACKNOWLEDGEMENTS

To begin with, I would like to thank my graduate supervisor, Janice Hughes, for her support and advice and for sharing her knowledge, not only of avian biology, but also of Middle-earth. Furthermore, she has enhanced my skills as an author and has taught me that sometimes "more is more" in the field of scientific writing. I also thank David Hussell for all of his time helping me out in the field and his constant assistance via the Internet. I thank my advisory committee: Rob Mackereth for his much-appreciated statistical advice and Dave Thomson for his support in my research.

I thank everyone at Birds Studies Canada especially Michael Bradstreet, Jon McCracken, Denis Lepage, and Debbie Badzinski for allowing me to conduct my fieldwork at the Long Point and Thunder Cape Bird observatories, and for providing me with the migratory data needed for my analysis. Also, I am very grateful to all of the volunteers at Thunder Cape, Innis Point, and Long Point bird observatories who collected moult data over the years; this study would not have been possible without all of their long hours of hard work.

I thank Jody Allair and John Woodcock for their assistance and hospitality at the Thunder Cape Bird Observatory. In addition, I am grateful to the many Thunder Cape volunteers who have helped me with my research: Maureen Woodcock, Kenneth Burrell, Peter Biederman, Christian Friis, and Adam Blake.

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PREFACE TO THE THESIS

As a graduate student, I agreed to submit for publication all chapters of this thesis as they were completed. Since each manuscript has to stand alone, I am required to include some duplicate explanatory information in some sections of certain chapters.

Below is a list of chapters, as they will be published.

CHAPTER 1: Timing and duration of the prebasic moult of wood-warblers (Parulidae) in Ontario.

CHAPTER 2: Raggedness as an indicator of moult rates in Parulids.

CHAPTER 3: Age-related timing and patterns of prebasic body moult in wood-warblers (Parulidae).

GENERAL INTRODUCTION

New World warblers are more commonly known as wood-warblers to distinguish them from other warblers of the world, such as Old World Warblers of the Sylviinae. There are about 115 species of these small, primarily insectivorous songbirds of the family Parulidae, of which approximately 37 species are found in Ontario (Dunn and Garrett 1997, Hughes 2001). Most wood-warblers are long distance migrants, traveling thousands of kilometers twice a year between their breeding grounds in North America and wintering grounds as far south as South America (Dunn and Garrett 1997). Considered precious gems in the world of bird watching, this family is also prized for their diversity and song repertoire that has fascinated naturalists and biologists around the globe.

OVERVIEW OF SPECIES STUDIED

The American Redstart (*Setophaga ruticilla*) is monotypic, being the only North American warbler in the genus *Setophaga*. Found throughout most of Canada and eastern United States, this sexually dimorphic warbler is easily distinguished in all plumages. Hatch Year (HY) birds are deep olive brown with pale lemon yellow portions on most flight feathers with dull green edging on their tips. The spring After Hatch Year (AHY) female has gray on the crown, hindneck, and sides of head; tinged with olive on the back and rump; and has pale yellow to pale orange patches on the breast, wing, and tail. Males do not acquire full adult plumage until their first potential breeding season has passed.

The spring After Second Year (ASY) male is glossy black with similar breast, wing, and tail patches as the female, which are bright salmon orange in colour, rather than yellow. In eastern North America, the American Redstart prefers interior woodlands with large, intact tracts of habitat for breeding. Some individuals depart for their wintering grounds in South America in early July, but peak migratory movements typically occur from late August through mid-September (Dunn and Garrett 1997, Sherry and Holmes 1997).

The genus *Vermivora* includes primarily smaller-sized warbler species with sharply pointed bills, relatively little sexual dimorphism, and simple songs and calls. The Nashville Warbler (*Vermivora ruficapilla*) has two breeding subspecies, which are geographically separated in eastern and western regions of North America (*Vermivora ruficapilla ruficapilla, V. r. ridgwayi*, respectively). This ground-nesting warbler prefers second growth open deciduous forest or mixed forests with shrubby undergrowth. Breeding adults have a gray head with a rufous crown patch and bold white eye ring, olive green upperparts, and a bright yellow throat and underparts with some white on the belly; the female is slightly more drab in colour than the male. The western population can be distinguished by its overall brighter plumage and longer tail. Fall migration of the eastern population of Nashville Warblers typically ranges from mid-August to mid-October. Migration of the western population through the Pacific coastal states peaks in mid September. Both arrive at their wintering grounds, which extend from Mexico through Central America, from mid-October to mid-November (Williams 1996b).

Dendroica warblers are the most diverse genus of warblers. They vary in size, song structure, and habitat preferences, but most species exhibit contrasting plumage marks, such as wing bars and tail spots. The Yellow Warbler (*Dendroica petechia*) is abundant across North America and has the broadest distribution of any *Dendroica* warbler, breeding mostly in wet, deciduous thickets consisting predominantly of willows, and in disturbed and early successional habitats. It is the brightest yellow *Dendroica* in North America. The breeding male has a bright yellow body, with chestnut streaking on the underparts, yellowish edges on the wing feathers, and diagnostic yellowish tail spots; the female is similar, but with a more drab appearance. Age variation can be substantial, with immature birds ranging from dull olive-brown to a brighter yellow. Members of eastern Yellow Warbler populations are early migrants that may leave their breeding grounds in mid-July; although, most typically depart around mid-August. Their wintering grounds extend from Mexico, south through South America (Dunn and Garrett 1997, Lowther et al. 1997).

The Magnolia Warbler (*Dendroica magnolia*) is a common warbler found throughout most boreal forests in Canada and the northeastern United States, with preferred nesting habitat of dense young growth of spruce (*Picea* spp.) or hemlock (*Tsuga canadensis*). The AHY breeding male has a black back, yellow rump, yellow underparts heavily streaked with black, gray head with a black mask, and white wing bars; in contrast, the AHY breeding female lacks the face mask and has fainter breast striping. In fall, adult males and immatures are similar in plumage to AHY breeding females, although the dark ventral striping is reduced. Fall migration of the Magnolia Warbler to their wintering grounds throughout the southern United States to northern South America occurs typically from mid-August through early October, with peak movements during late September into early October (Hall 1994).

Another common wood-warbler, the Yellow-rumped Warbler (*Dendroica coronata*), was once classified as two distinct species. However, the Myrtle Warbler (*D. c. coronata*) and Audubon's Warbler (*D. c. auduboni*) were found to be genetically similar, often hybridizing where their breeding ranges overlapped. The Myrtle Warbler is found in most coniferous forests across Canada, north to Alaska and south into the northeastern United States. The Audubon's Warbler is restricted to the western part of North America. Both subspecies can be distinguished from all other warblers by their yellow rumps. The AHY breeding male Myrtle Warbler has gray upperparts with black streaks on the back, yellow crown patch, black breast with yellow patches on sides, white wing bars and tail spots, and a distinct black and white face pattern. The adult breeding female has a brown or gray face, brown upperparts, and streaked underparts. Hatch Year birds are duller overall in appearance, with males being more distinctly marked than females. The Yellow-rumped Warbler is among the most ecologically generalized warblers in North America, employing various types of habitat for breeding, feeding, and wintering. Furthermore, they are one of the last warblers to migrate in fall — Myrtle Warblers having a slightly longer migration period — and can remain in their breeding areas well into October, after which they move south to the southern United States through to the West Indies to winter (Hunt and Flaspohler 1998).

The Bay-breasted Warbler (*Dendroica castanea*) is one of the larger *Dendroica* warblers inhabiting boreal forests throughout Canada and the Eastern United States, where populations may fluctuate depending on the severity of spruce budworm outbreaks (*Choristoneura fumiferana*), which they exploit as a major food source. The AHY breeding male can be distinguished by a black face, chestnut-coloured upperparts and cream-coloured underparts, and two distinct white wing-bars. The AHY breeding female also has two white wing-bars, but lacks the black face, and is duller overall with limited chestnut colouration. Both HY birds and AHY birds in fall plumage may be confused with HY and AHY Blackpoll (*Dendroica striata*) and Pine (*Dendroica Pinus*) warblers, but Bay-breasted Warblers can be distinguished by their buffy undertail-coverts, and black legs, feet, and toes. In addition, males have traces of chestnut on their flanks. The Bay-breasted Warbler is a regular trans-Gulf migrant, leaving its breeding grounds in mid-August, and arriving south from Panama throughout northern South America in October. During fall migration, it is often found in mixed-species flocks, particularly with Blackpoll warblers (Williams 1996a, Dunn and Garrett 1997).

The Ovenbird (*Seiurus aurocapillus*) is found throughout most largely forested areas across Canada and throughout eastern United States. This thrush-like warbler forages primarily on the forest floor and is dissimilar to most wood-warblers in appearance with its bulky form, olive-gray upperparts, large eyes with a bold white eye ring, an orange crown stripe lined with black, white belly with large black spots, and long thick pink legs. Unlike most wood-warblers, the two sexes of Ovenbirds are identical. HY birds are drabber in appearance than AHY individuals, with a more obscure crown patch and buffy tipped wing coverts. Fall migration of the Ovenbird usually occurs between September to early October, with arrivals at their wintering areas – ranging from Florida throughout the Caribbean Islands and Central America – in early to mid-October (Van Horn and Donovan 1994, Dunn and Garrett 1997).

Despite numerous studies about species distribution, habitat requirements, and nesting behaviour conducted on wood-warblers, little is known about their prebasic moult patterns, particularly its relation to the timing of fall migration. Many individuals for each species are required to fully establish respective moult and migration timelines, a task that is often difficult to achieve in the field. Consequently, this has lead to the assumption that most warblers follow similar moult and migration patterns as other passerines, which may not necessarily be the case.

Most eastern members of the Parulidae can be found throughout Ontario, often breeding in the same region, allowing several species to be examined simultaneously. My study of the prebasic moult of warblers: (1) describes the moult patterns of several warbler species in Ontario; and (2) provides a new method for comparing the rate of primary feather moult between passerines with similar moult patterns, and (3) examines the chronology of prebasic moult relative to migration.

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CHAPTER 1: Timing and duration of the prebasic moult of wood-warblers (Parulidae) in Ontario

Abstract. — This study compared the pattern and chronology of the prebasic moult of American Redstarts (*Setophaga ruticilla*), Magnolia (*Dendroica magnolia*), and Yellow-rumped (*D. coronata*) warblers at Thunder Cape Bird Observatory, Ontario; and Ovenbirds (*Seiurus aurocapillus*), Yellow (*D. petechia*), Bay-breasted (*D. castanea*), and Nashville (*Vermivora ruficapilla*) warblers at Long Point Bird Observatory, Ontario. Yellow Warblers and American Redstarts displayed no difference in the timing of prebasic moult between sexes. Yellow Warblers were the earliest to start flight feather moult (July 9); however, they did not have the shortest moult duration. Ovenbirds underwent a rapid moult beginning in late July, with a duration of only 22 days. Yellow-rumped Warblers had the longest moult period (62 days) and were the last species to finish moult (Sept 25). American Redstarts and Magnolia Warblers had similar moult durations (31 and 39 days, respectively). Primary moult in Bay-breasted Warblers lasted 33 days, but began in August 3, about 13 days later than American Redstarts and Magnolia Warblers. Although Nashville Warblers started moult July 31, it continued through September 20. These findings suggest that some warblers overlap early and final stages of moult with later stages of breeding and/or onset of migration. There was a positive correlation between the duration of moult and timing of migration for all species, except Ovenbirds, suggesting that earlier migrants moult more quickly and later migrants take a longer period to moult. Ovenbirds had a shorter moult duration relative to timing of migration than the other species; however, they may be anomalous with regards to moult scheduling and migration because of their atypical ecological and behavioural attributes or its systematic position among parulids. Both external and internal factors may explain variations in the relationship between breeding, moult, and migration in warblers, allowing each species to fine-tune the onset of prebasic moult accordingly.

Introduction

Plumage sequences and moult patterns in birds have been studied extensively throughout the last century in an attempt to understand the complexities of feather replacement and its concomitant relationship with feeding, reproductive, and locomotory strategies. Humphrey and Parkes (1959) were instrumental in defining plumage sequences, and subsequently developed the most commonly used terminology for plumages and moults. According to their descriptions, birds display an *alternate plumage* during the breeding period, which is often brightly coloured with characteristic signal patches to attract mates. On the other hand, the *basic plumage*, typically duller in appearance, is displayed throughout non-breeding periods. In most North American migratory passerines, the prebasic moult occurs between the breeding and migration seasons. Consequently, the prebasic moult of adult passerines, that have only one plumage per cycle such as wood-warblers, is performed in the fall to attain the *basic plumage* (Humphrey and Parkes 1959).

Moult plays an important role in the life cycle of birds because feathers have multiple functions, such as display during courtship (e.g., Beehler 1983) and thermoregulation (Schieltz and Murphy 1997). Moult may also prevent infestations by dermal parasites (Post and Enders 1970). Most importantly, birds must replace their feathers before wearing impedes flight (Ginn and Melville 1983). However, the complete moult is a major undertaking that consumes large amounts of energy and protein reserves for both feather production and compensation for the effects of poorer insulation and decreased flight efficiency (Dolnik and Gavrilov 1979, Murphy and King 1991, 1992). In order to maximize efficiency, birds typically schedule moult during times when food is abundant, and to avoid undue overlap with other energetically demanding activitles, such as reproduction and migration (Payne 1972). For example, Samson (1976) found that although moult overlapped with the end of the breeding season in Cassin's Finch (*Carpodacus cassinni*) only during years where conditions were highly favorable for breeding, it did not overlap with migration. Furthermore, Hahn et al. (1992) suggested that the timing and rate of the prebasic moult could be fine-tuned in response to various environmental factors including change in day length, food availability, temperature, and social cues such as parental behaviour, and inter- and intra-sexual interactions.

Migration is costly for birds, and benefits must outweigh the energetic demands. Although migration typically secures a better climate for living and abundant, unfailing sources of food, birds tend to migrate when the costs and hazards of migration are lowest (Ketterson and Nolan 1983). As with moult, the timing of migration is influenced by both environmental factors (i.e., photoperiod, day length, and favorable weather conditions) and internal physiological rhythms, known as *zugunruhe* or migratory restlessness. Berthold (1973) found that the timing and duration of migration was often associated with *zugunruhe* in fall migrants of several species of Old World warblers (Sylviinae).

Consequently, the intricate factors involved in both moult and migration has fueled the need for further research in these areas.

MOULT AND MIGRATION IN WOOD-WARBLERS

Wood-warblers, such as the *Dendroica* warblers, belong to the family Parulidae (except the Olive Warbler, *Peucedramus taeniatus,* of the family Peucedramidae; Dunn and Garrett 1997). They are small, primarily insectivorous songbirds that forage and breed in many different habitat types throughout North America. Most wood-warblers are long distance migrants, traveling thousands of kilometers twice a year between their breeding grounds in North America and wintering grounds as far as South America (Dunn and Garrett 1997). There are about 115 species of wood-warblers, of which approximately 37 species are found in Ontario (Hughes 2001).

Typically, adult warblers (also known as After Hatch Year or AHY) undergo a complete prebasic moult, replacing nearly all feathers while still on the breeding grounds prior to fall migration. Most species of North American migratory wood-warblers share prebasic moult patterns and plumage sequences (Dunn and Garrett 1997) that follow a similar feather loss and replacement pattern; however, the timing and rate of moult, which varies among species, has been poorly documented. D. J. T. Hussell (pers. comm.) hypothesized that the differences in the timing and rate of moult among species may be related to the timing of fall migration. However, previous studies that documented the rate and timing of moult for an individual warbler species failed to compare their results to other warbler species. For example, Rimmer (1988) determined that most adult Yellow Warblers (*Dendroica petechia*) nesting at James Bay, Ontario undergo a rapid moult, becoming almost flightless after breeding. He suggested that they do so because the insect food supply and optimal migrating conditions decline in later summer, thus threatening survival during the long distance migration.

Conversely, it could be argued that most warblers have similar diets and migration ranges yet appear not to follow the same moult and migration strategies as the Yellow Warbler. Baird (1967) documented two cases of adult Tennessee Warblers (*Vermivora peregrina*) exhibiting arrested moult. Rimmer and McFarland (1998) suggested that factors other than food supply may dictate scheduling of both moult and migration for this species because some individuals remain on the breeding grounds throughout their prebasic moult. Regardless, diet likely plays a role in the late migration of the Yellow-rumped Warbler (*Dendroica coronata*) as this species is also frugivorous during the fall (Hunt and Flaspohler 1998). The addition of fruit to an otherwise insectivorous diet could prolong their stay on the breeding grounds, and may even allow some populations to winter in the northern coastal regions of North America (Hunt and Flaspohler 1998).

After breeding, most warblers prepare for their long distance flight to wintering grounds by increasing their nutritional intake and moulting prior to migration (Dunn and Garrett 1997). However, Woodrey and Chandler (1997) suggested that in some species of warblers moult could delay the departure of adults from the breeding grounds by several days; therefore, timing of moult should play a critical role in scheduling migration to minimize the energetic demands. Examining moult patterns of various warblers will allow a better understanding of its timing and rate in relation to migration for species found throughout Ontario and eastern North America.

Apparently, many factors may dictate moult and migration strategies for each of the above-mentioned species, and further study will be required to elucidate them. Unfortunately, even less is known about the timing of prebasic moult in relation to migration for American Redstarts (*Setophaga ruticilla*), Ovenbirds (*Seiurus aurocapillus*), and Magnolia (*Dendroica magnolia*), Bay-breasted (*Dendroica castanea*), and Nashville (*Vermivora ruficapilla*) warblers. Although the duration and scheduling of moult are known for a few species of warblers, such as the Orange-crowned Warbler (*Vermivora celata*; Foster 1967) and the Prairie Warbler (*Dendroica discolor*; Nolan 1978), more studies examining these patterns between species are required.

In this study, I compared the timing and duration of primary moult of American Redstarts, Ovenbirds, and Nashville, Yellow, Magnolia, Yellow-rumped, and Bay-breasted warblers in relation to the breeding period and timing of migration. In addition, I explored the adaptive significance of different moult strategies observed in these species. I hypothesize that the duration and timing of primary moult will vary among warbler species in relation to the timing of their respective breeding periods and timing of fall migration, such that (1) birds that migrate earlier will have to moult rapidly to complete their moult before they migrate, and (2) later migrants have the option of moulting more slowly than early migrants, thus extending the increased energy requirements associated with moult over a longer period of time.

Materials and Methods

STUDY AREAS

Moult data were obtained for American Redstarts, Ovenbirds, Nashville, Yellow, Magnolia, Yellow-rumped, and Bay-breasted warblers captured at Thunder Cape Bird Observatory (TCBO), and Long Point Bird Observatory (LPBO) between 1976-2002. TCBO is situated at the tip of the Sibley Peninsula, on the Northwest shore of Lake Superior, approximately 80 km from Thunder Bay, Ontario (48° 18'04", 88° 56'18"; Fig. 1.1). The area is predominantly forested, consisting mostly of coniferous trees and shrubs, providing suitable habitat for most boreal breeding warbler species, such as the Nashville Warbler, Black-throated green Warbler (*Dendroica virens*), and Mourning Warbler (*Oporornis philadelphia*). LPBO has monitoring stations throughout the Long Point peninsula on the northwestern shore of Lake Erie (from 42°35'00", 80°24'00" to 42°32'55", 80°3'00"; Fig. 1.2). Located in the only Carolinian Forest region in Ontario, its

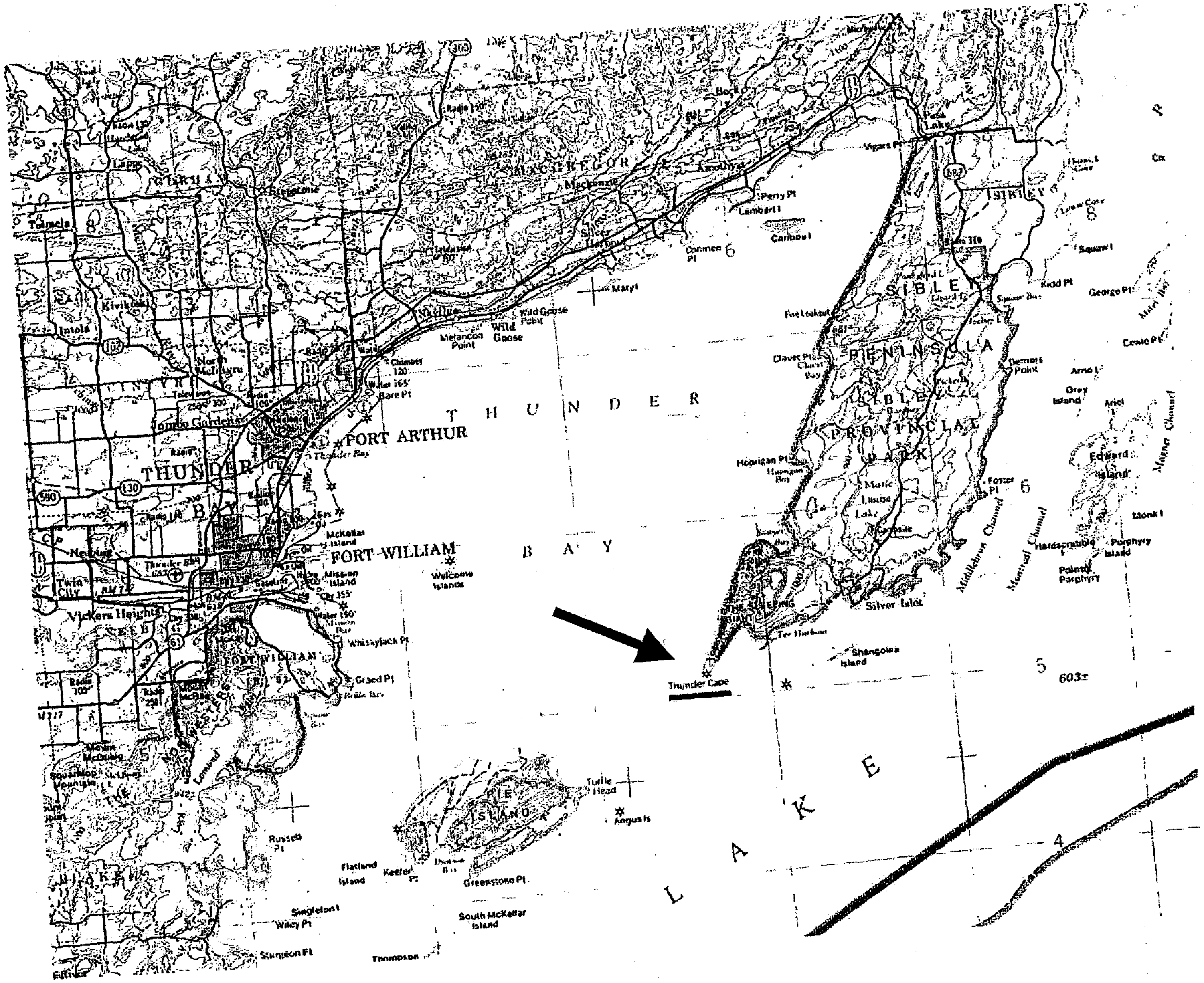

Fig. 1.1. Location of Thunder Cape Bird Observatory, Ontario, Canada.

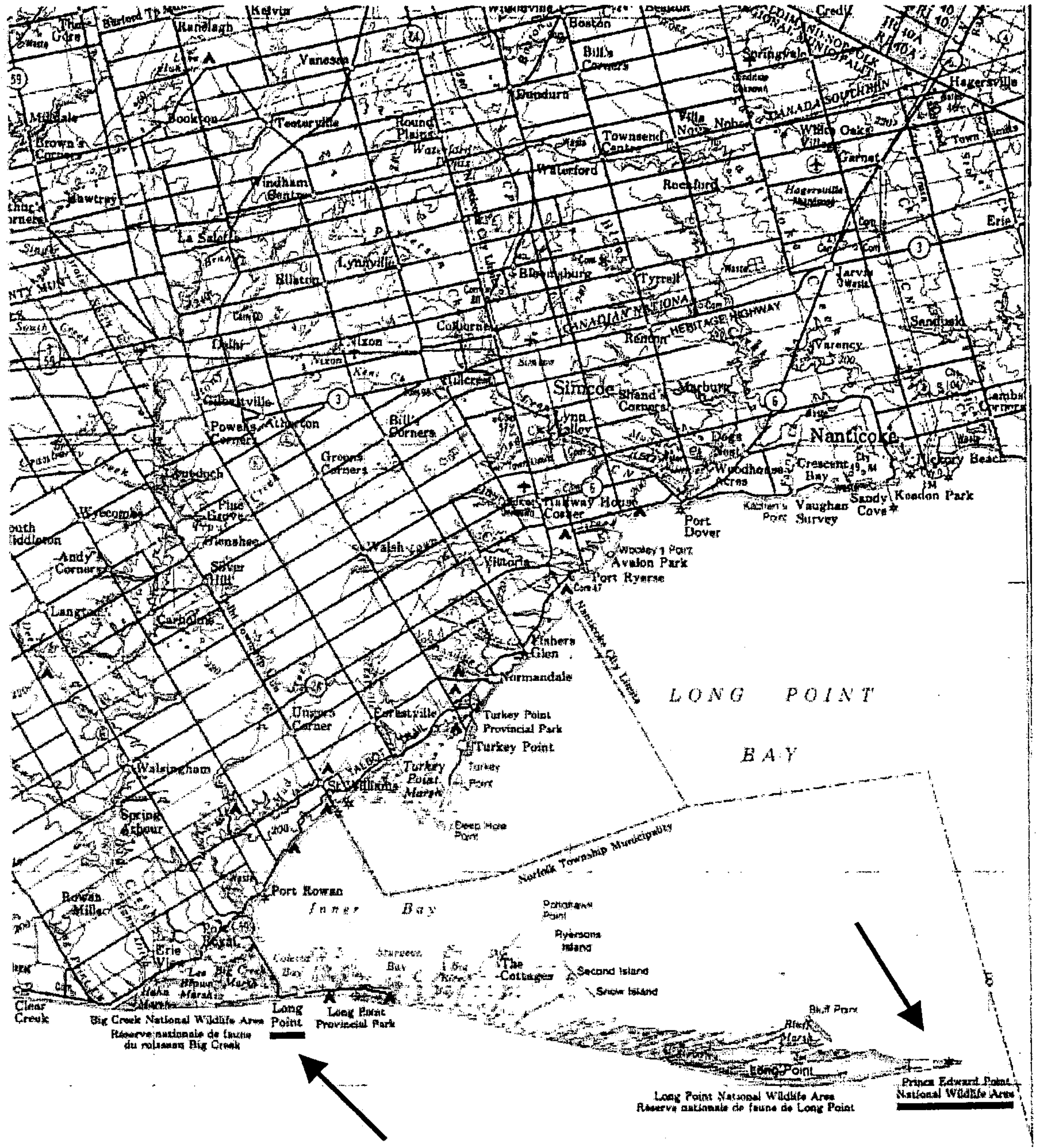

Fig. 1.2. Locations of the Long Point Bird Observatories, Ontario, Canada.

diverse range of breeding habitats, including marshes, wetlands, and deciduous forest allows various warbler species, from the threatened Hooded warbler (*Wilsonia citrina*) to the very common Yellow Warbler, to be found breeding there. In addition to supplying breeding habitat, both sites are known to be major stopover areas for migrating warblers, and allow birds to rest and replenish fat reserves along their migration route. These attributes confer that both locations are ideal for monitoring warbler migration, providing ample numbers to be examined during the course of this study.

FIELD PROCEDURES

A total of 238 birds were captured from July to October throughout their moult and migration periods using mist nests with a mesh size of 30mm (1 1/4 inch) and Heligoland traps, according to TCBO and LPBO standard protocols. Moult data for After Hatch Year (AHY) warblers were obtained according to Newton (1966) and Ginn and Melville (1983), with feathers scored on a scale of 0 to 5. Using their methods, old feathers are scored as 0; missing or in pin (completely in the feather sheath) as 1; feather out of pin to 1/3 full grown as 2; 1/3 to 2/3 full grown as 3; greater than 2/3 full grown with sheath present as 4; full-grown new feather with no sheath as 5. Each feather is scored independently, then the total score is summed for the group of primary feathers for that wing (Fig. 1.3). The vestigial primary number 10 was excluded from the primary moult score (Rimmer 1988), therefore, the moult score ranged from 0

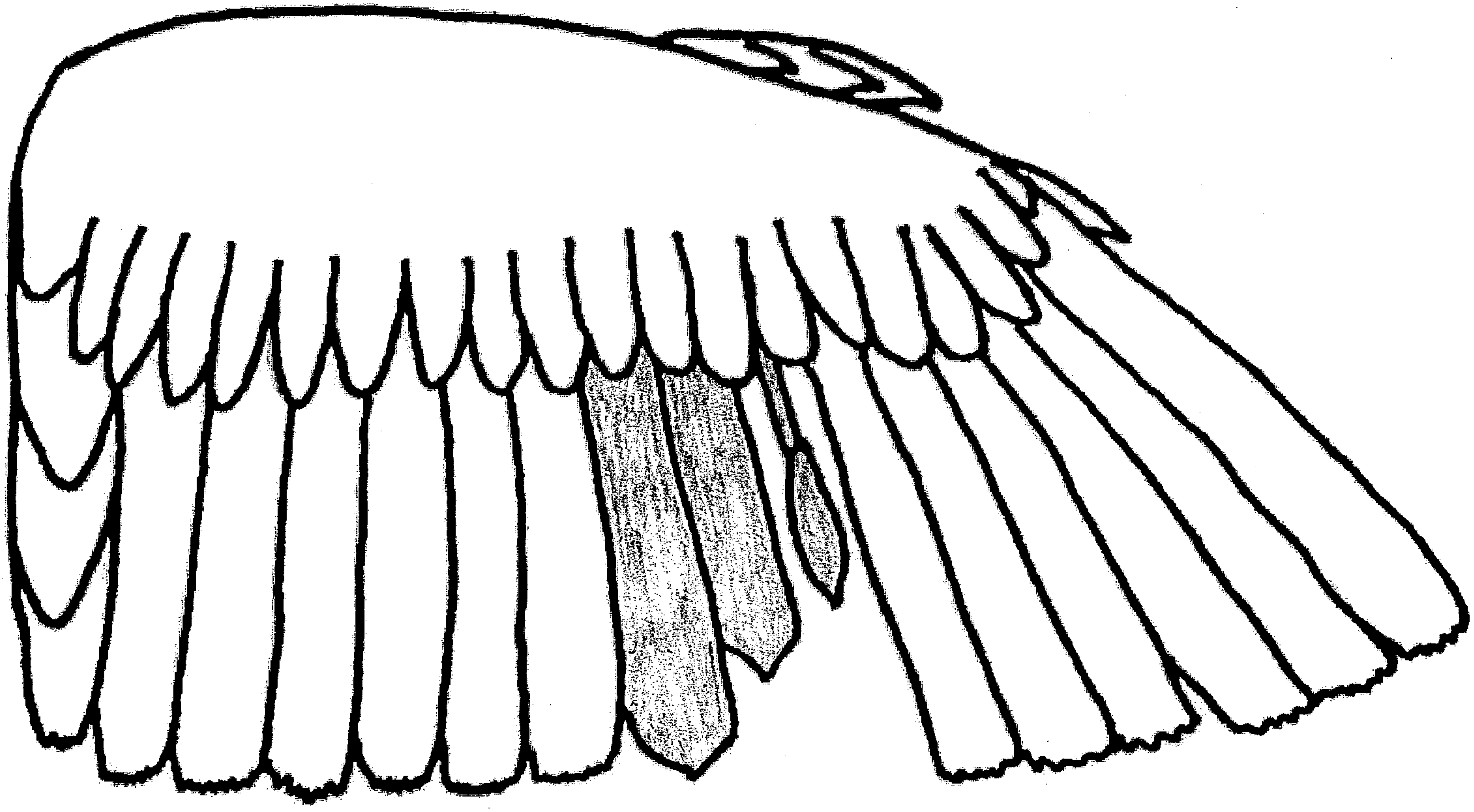

Fig. 1.3. Description of the method for estimating the primary score (new feathers represented by shading; after Bensch and Grahn 1993).

(no moult) to 45 (primary moult complete). Moult data were recorded for the right wing, unless the moult was obviously asymmetrical, in which case both sides were recorded. To get a representative sample of the population, primary feather moult scores were calculated on all birds captured (or on a random sample if large numbers were captured), whether they were moulting or not (D. J. T. Hussell, pers. comm.).

AHY warblers were differentiated from Hatch Year (HY) warblers by plumage and skulling methods with AHYs having fully ossified skulls and HYs ranging on a scale of 0 to 3. Sexes were distinguished by plumage characteristics or wing chord length (Pyle 1997). Some species of warblers, such as Ovenbirds, are sexually monotypic in size and plumage. These individuals were pooled because sexual determination was unreliable; in addition, species with unequal sex ratios were pooled (Green and Summers 1975, Mewaldt and King 1978).

STATISTICAL ANALYSES

Three-way analyses of covariance (ANCOVA; Sokal and Rohlf 1995) — using primary moult score as the dependant variable, sex as the independent variable, and date captured as the covariate — were performed to test for differences in timing of moult between sexes in American Redstarts and Yellow Warblers because energetic constraints associated with breeding may influence moult scheduling. As there were insufficient individuals to determine a difference between the sexes in Ovenbirds, Yellow-Rumped, Nashville, Magnolia, and Bay-breasted warblers, moult data for males and females were correspondently pooled for each species. Furthermore, the data were pooled for each species across all years to increase sample sizes (e.g., Foster 1967, Sealy 1979, Voelker and Rohwer 1998). Rimmer (1988) found that many moulting Yellow Warblers were reclusive in their vulnerable state, suggesting that warblers, in general, might be difficult to trap at this time. Only birds moulting flight feathers were used to determine the timing of moult because the timing of moult in non-moulting birds cannot be predicted with accuracy.

Least squares linear regressions were used to estimate the mean duration, starting dates, and completion dates of primary flight feather moult for each species as depicted in Pimm (1976), which regressed capture date against moult score to estimate an individual's duration of moult. Although, newer techniques have since been developed to determine moult duration (Underhill and Zucchini 1988, Bensch and Grahn 1993), this technique is still commonly used due to its ease of use (Yuri and Rowher 1997, Voelker and Rohwer 1998).

The median migration date was determined for each species at both locations using migration data collected at TCBO from 1991-2001 and LPBO from 1984-2001. The median migration date was calculated from the median of the average of the estimated totals of birds seen migrating on each day over 9 years at TCBO and 17 years at LPBO. In addition, a bivariate correlation was performed to examine the relationship between the duration of primary moult for each species and its timing of fall migration. A significant, positive correlation would support the suggestion that the longer it takes for a bird to complete moult, the later it will migrate. All tests were performed using SPSS (Version 10.07a) for Apple Macintosh (SPSS Inc. 2000), with a significance level of $p<0.05$.

Results

MOULT SCHEDULE AND DURATION

Analyses of the effect of sex, with the primary score held constant as a covariate, on the timing of moult indicated that there was no difference for the two species with sufficient individuals sampled to be tested (American Redstart: $F=0.649$, $p=0.429$, $n=25$; Yellow Warbler: $F=1.904$, $p=0.175$, $n=47$).

Table 1.1 illustrates the estimates of start and end dates, and the duration of primary feather moult for all species examined. The Yellow Warbler was the earliest to start flight feather moult, beginning in early July (9 Jul ± 6 days) and ending in early August (7 Aug ± 3 days); however, with a duration of 29 days ± 6, it did not have the shortest moult duration (Fig. 1.4). Although the Ovenbird began flight feather moult in late July (27 Jul ± 12 days), it underwent a rapid moult, with a duration of only 22 days ending in mid-August (18 Aug ± 9 days; Fig. 1.5). The Yellow-rumped Warbler had the longest moult period of 62 days starting at the end of July (25 Jul ± 7 days). This species had the latest end

Table 1.1. Estimates of start and end dates, and duration of primary feather moult ± 95% confidence intervals using the least squares linear regression model for seven warbler species. Day 1=1 July, with calendar dates in parentheses.

Species	Location	Start Date	End Date	Duration (Days)
Bay-breasted Warbler	LPBO	34 (Aug 3) ± 8 d	67 (Sep 5) ± 7 d	33 ± 8
Ovenbird	LPBO	27 (Jul 27) ± 12 d	49 (Aug 18) ± 9 d	22 ± 12
Nashville Warbler	LPBO	31 (Jul 31) ± 13 d	82 (Sep 20) ± 10 d	51 ±13
Yellow Warbler	LPBO	9 (July 9) ± 6 d	38 (Aug 7) ± 3 d	29 ± 6
American Redstart	TCBO	22 (Jul 22) ± 7 d	53 (Aug 22) ± 6 d	31 ± 7
Magnolia Warbler	TCBO	21 (Jul 21) ± 8 d	60 (Aug 29) ± 7 d	39 ± 11
Yellow-rumped Warbler	TCBO	25 (Jul 25) ± 7 d	87 (Sep 25) ± 10 d	62 ± 7

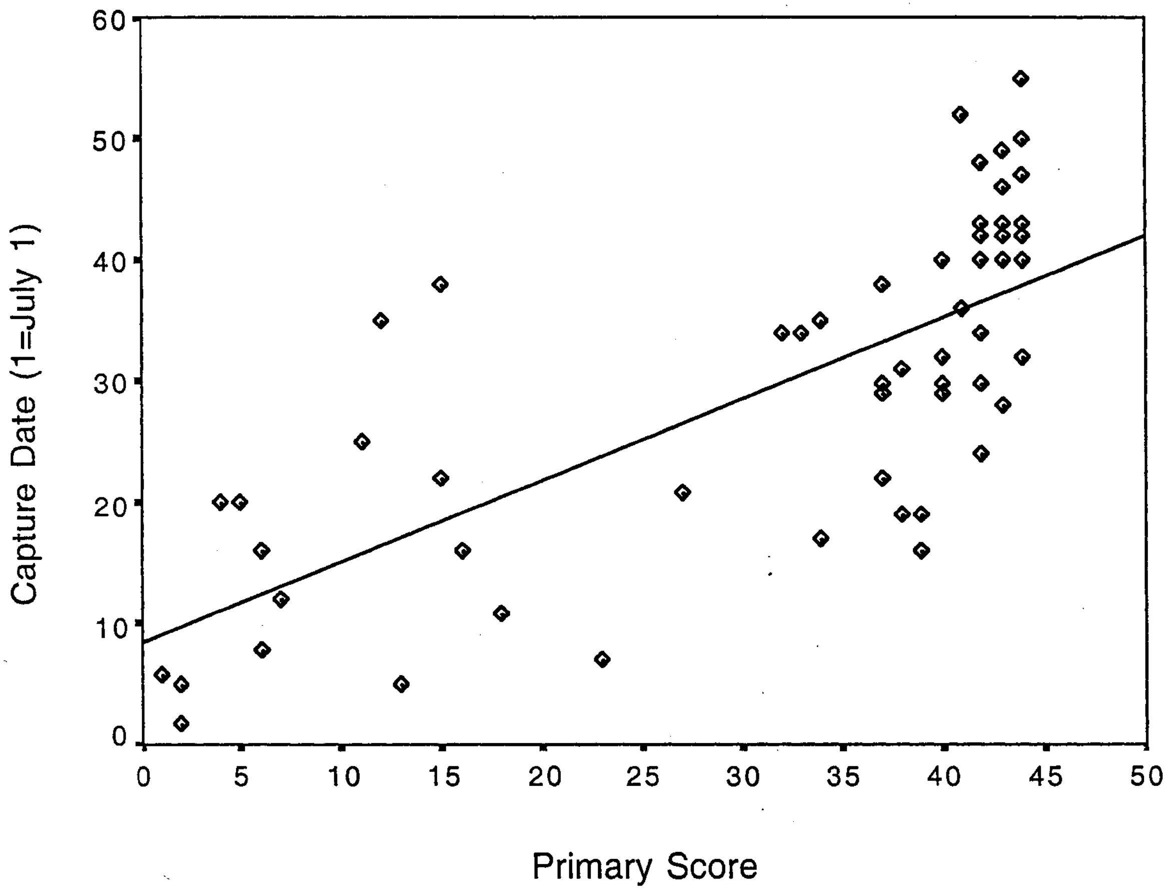

Fig. 1.4. Relationship between capture date and primary score for Yellow Warblers at LPBO (Y=0.673x+8.340, *n*=60, data from 1975-1997).

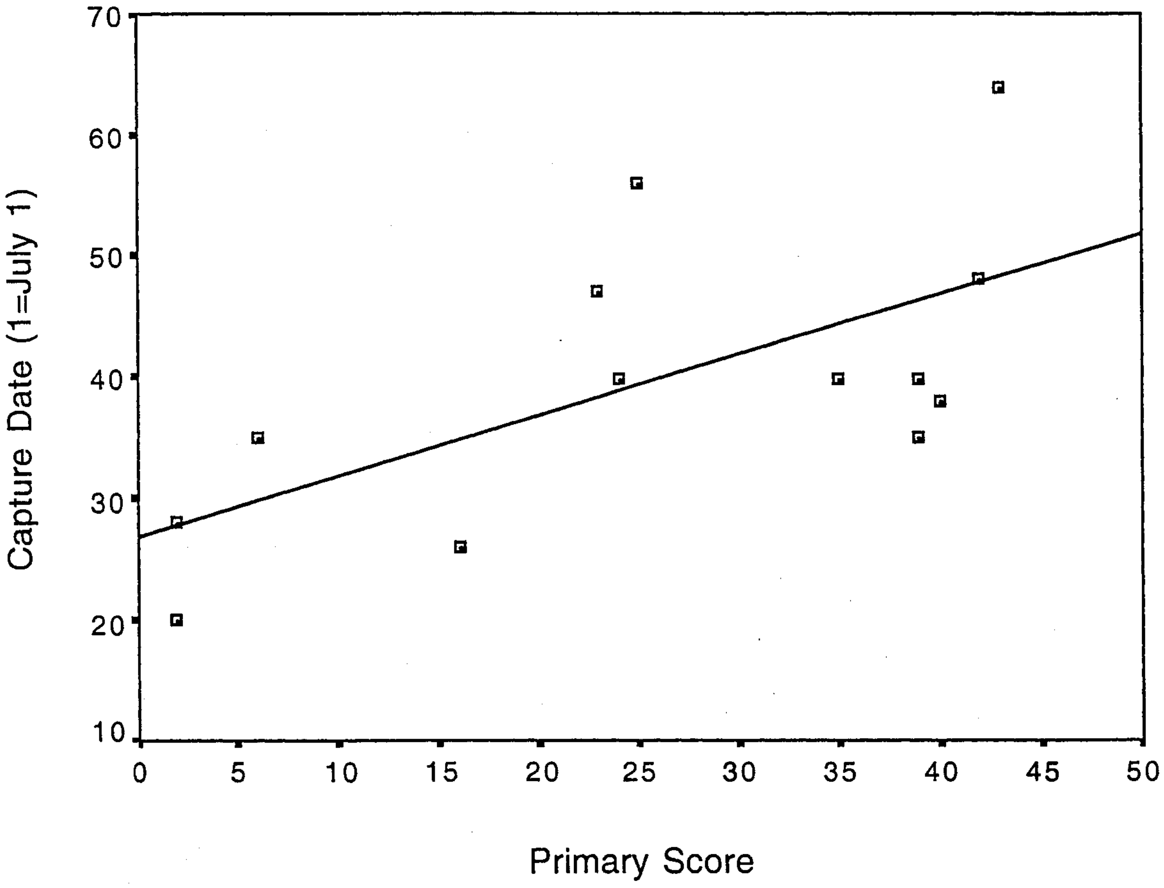

Fig. 1.5. Relationship between capture date and primary score for Ovenbirds at LPBO (Y=0.500x+26.840, *n*=13, data from 1988-1995).

date of moult, lasting until the end of September (25 Sep ± 10 days; Fig. 1.6). Both American Redstarts (Fig. 1.7) and Magnolia Warblers (Fig. 1.8) had similar moult durations (31 days ± 7 and 39 days ± 11, respectively), starting at the end of July (22 July ± 7 days and 21 July ± 8 days) through to the end of August (22 Aug ± 6 days and 29 Aug ± 7 days). With a moult duration of 33 ± 8 days, the Bay-breasted Warbler was similar to the American Redstart and Magnolia Warbler, but began moult in early August (3 Aug ± 8 days; Fig. 1.9), approximately 13 days later than the other two species. Although the Nashville Warbler started flight feather moult during late July (31 Jul ± 13 days), the moult continued through late September (20 Sep ± 10 days; Fig. 1.10).

MOULT AND MIGRATION

Table 1.2 illustrates the median fall migration dates for all species examined. There was a positive correlation between the duration of moult and timing of migration for all species ($r=0.764$, $p=0.038$, $n=6$) except for the Ovenbird, suggesting that earlier migrants moult more quickly and later migrants take a longer period to moult. In contrast, the Ovenbird had a shorter moult duration relative to its timing of migration (8 Sep ± 7 days) than the other species (Fig. 1.11).

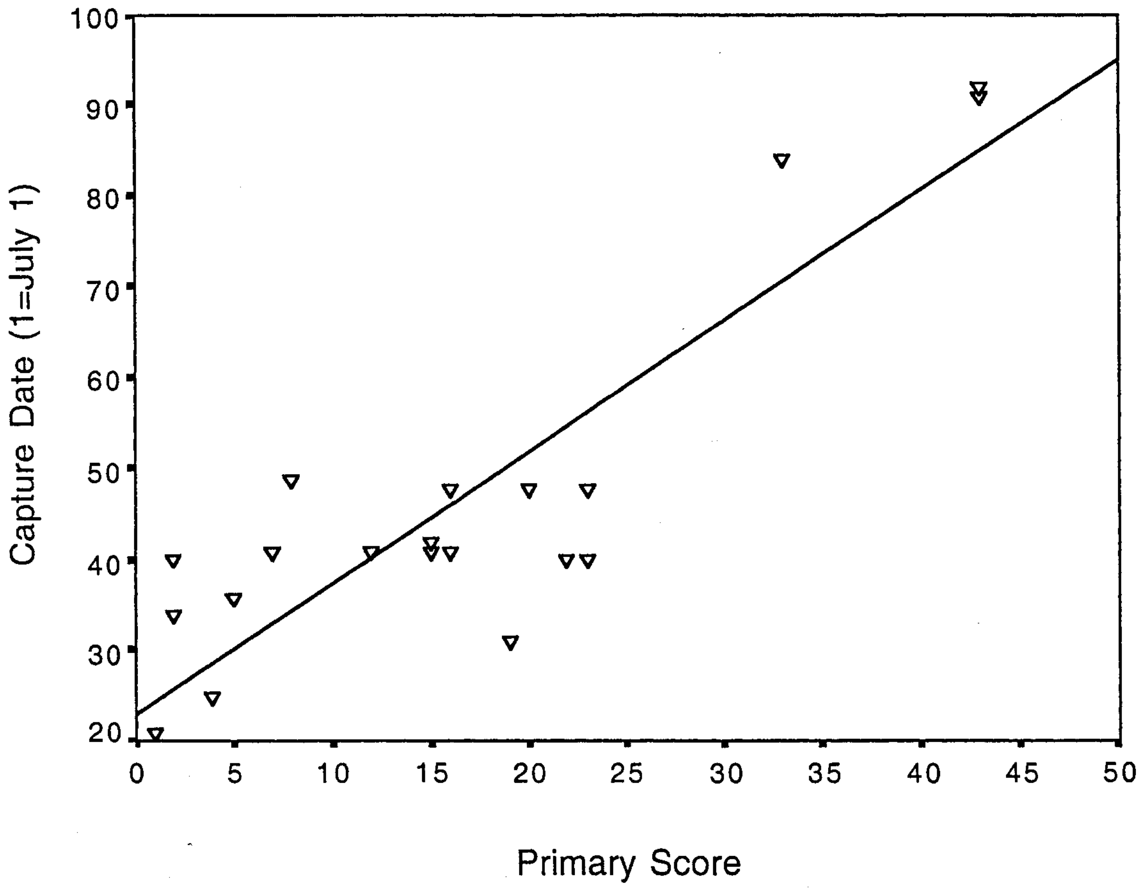

Fig. 1.6. Relationship between capture date and primary score for Yellow-rumped Warblers at TCBO (Y=1.441x+23.063, *n*= 22, data from 1998-2002).

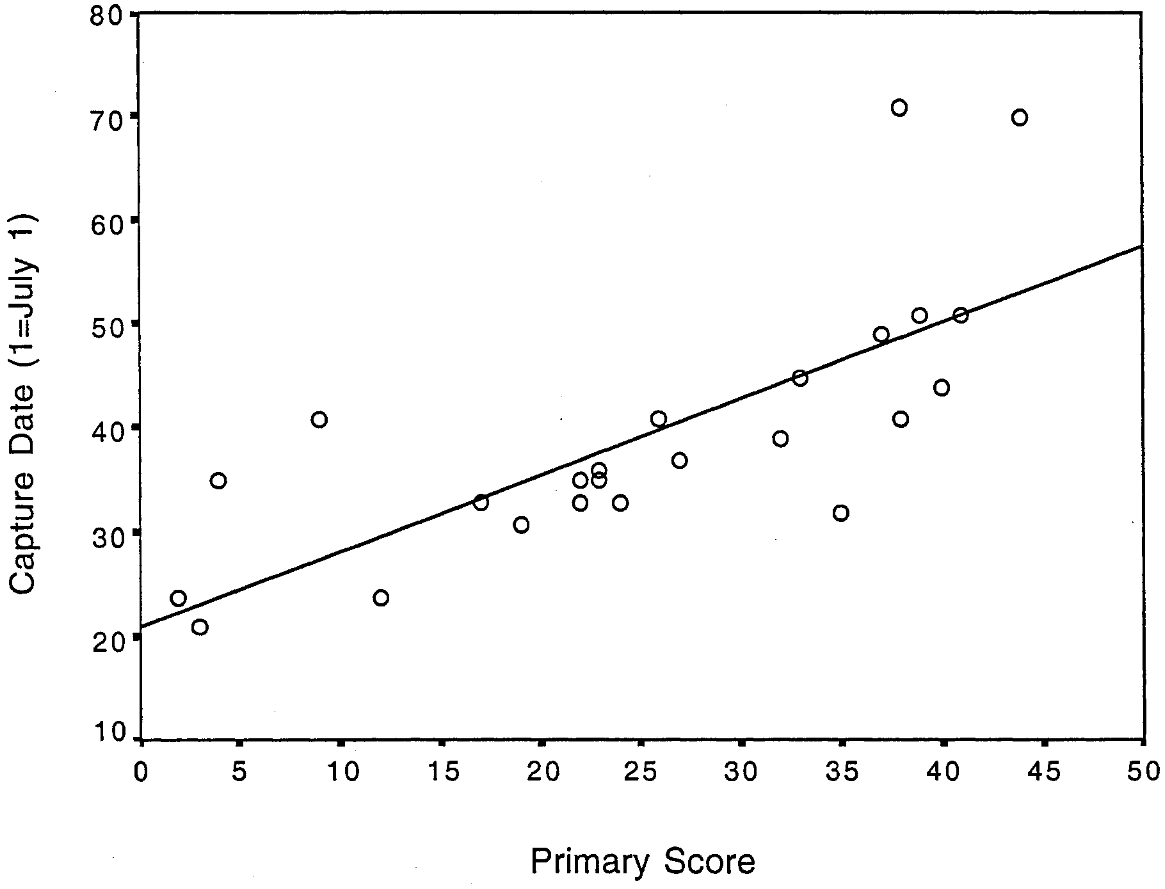

Fig. 1.7. Relationship between capture date and primary score for American Redstarts at TCBO (Y=0.732x+20.969, *n*=25, data from 1998-2002).

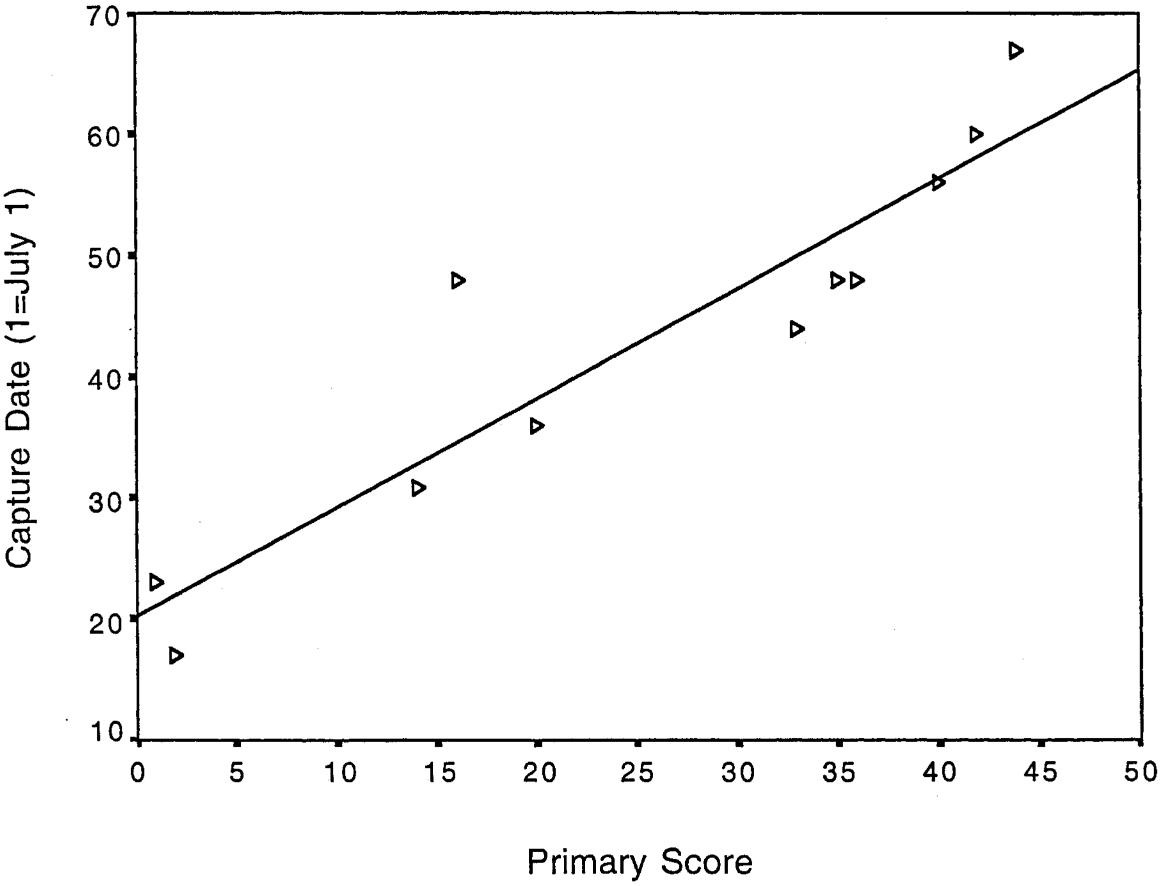

Fig. 1.8. Relationship between capture date and primary score for Magnolia Warblers at TCBO (Y=0.905x+20.178, *n*=11, data from 1998-2002).

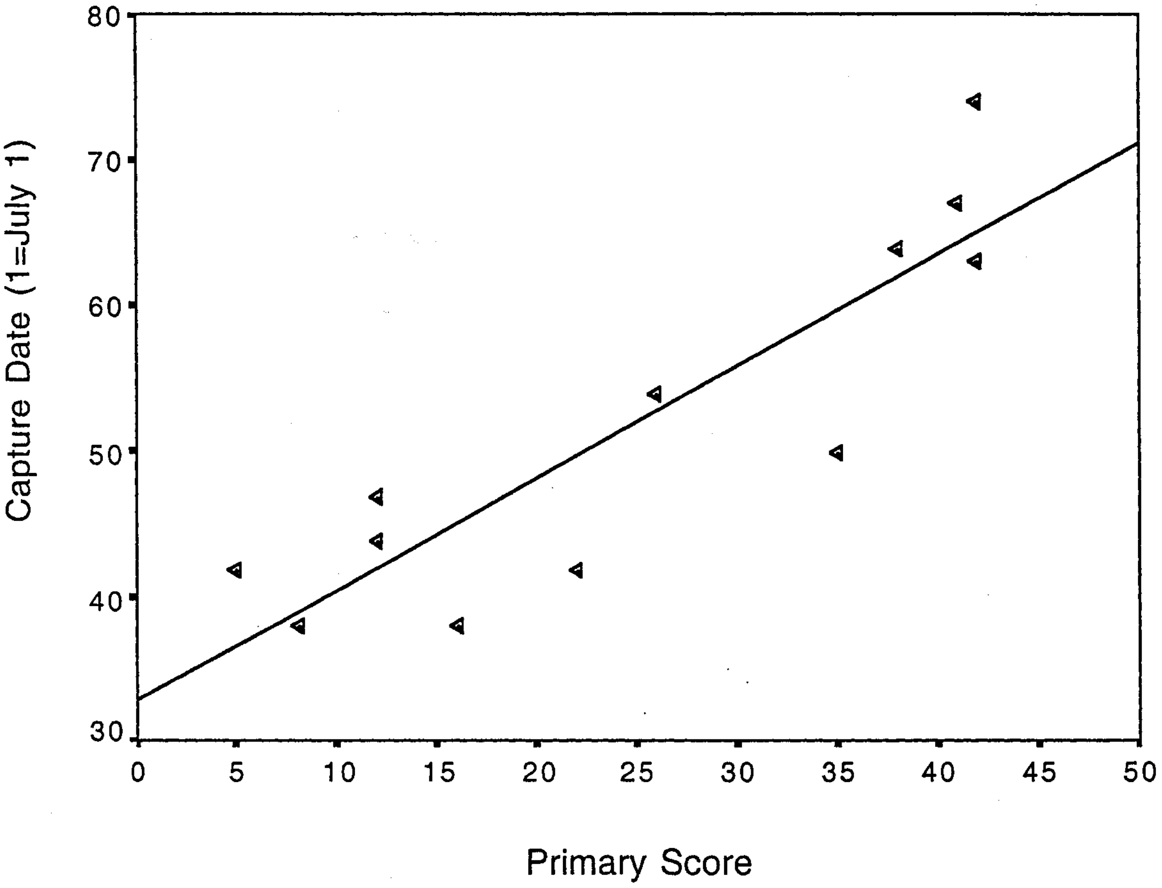

Fig. 1.9. Relationship between capture date and primary score for Bay-breasted Warblers at LPBO (Y=0.766x+32.823, *n*=12, data from 1975-1978).

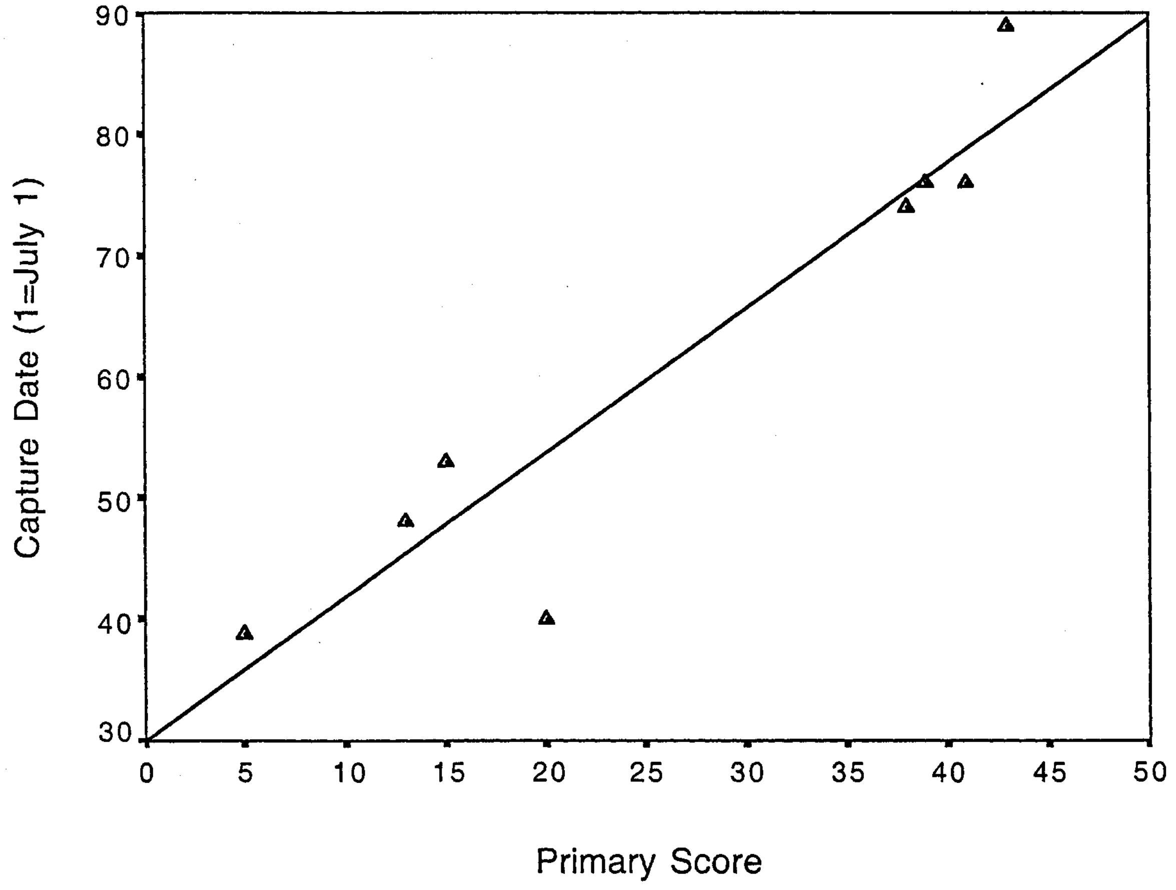

Fig. 1.10. Relationship between capture date and primary score for Nashville Warblers at LPBO (Y=1.190x+30.038, *n*=8, data from 1975-1996).

Table 1.2. Estimates of fall median migration dates ± 95% confidence intervals for seven warbler species. Day 1=1 July, with calendar dates in parentheses.

Species	Location	Median Migration Date
Bay-breasted Warbler	LPBO	67 (Sep 5) ± 8 d
Nashville Warbler	LPBO	82 (Sep 20) ± 8 d
Ovenbird	LPBO	70 (Sep 8) ± 7 d
Yellow Warbler	LPBO	45 (Aug 14) ± 9 d
American Redstart	TCBO	58 (Aug 27) ± 9 d
Magnolia Warbler	TCBO	55 (Aug 24) ± 8 d
Yellow-rumped Warbler	TCBO	74 (Sep 12) ± 10 d

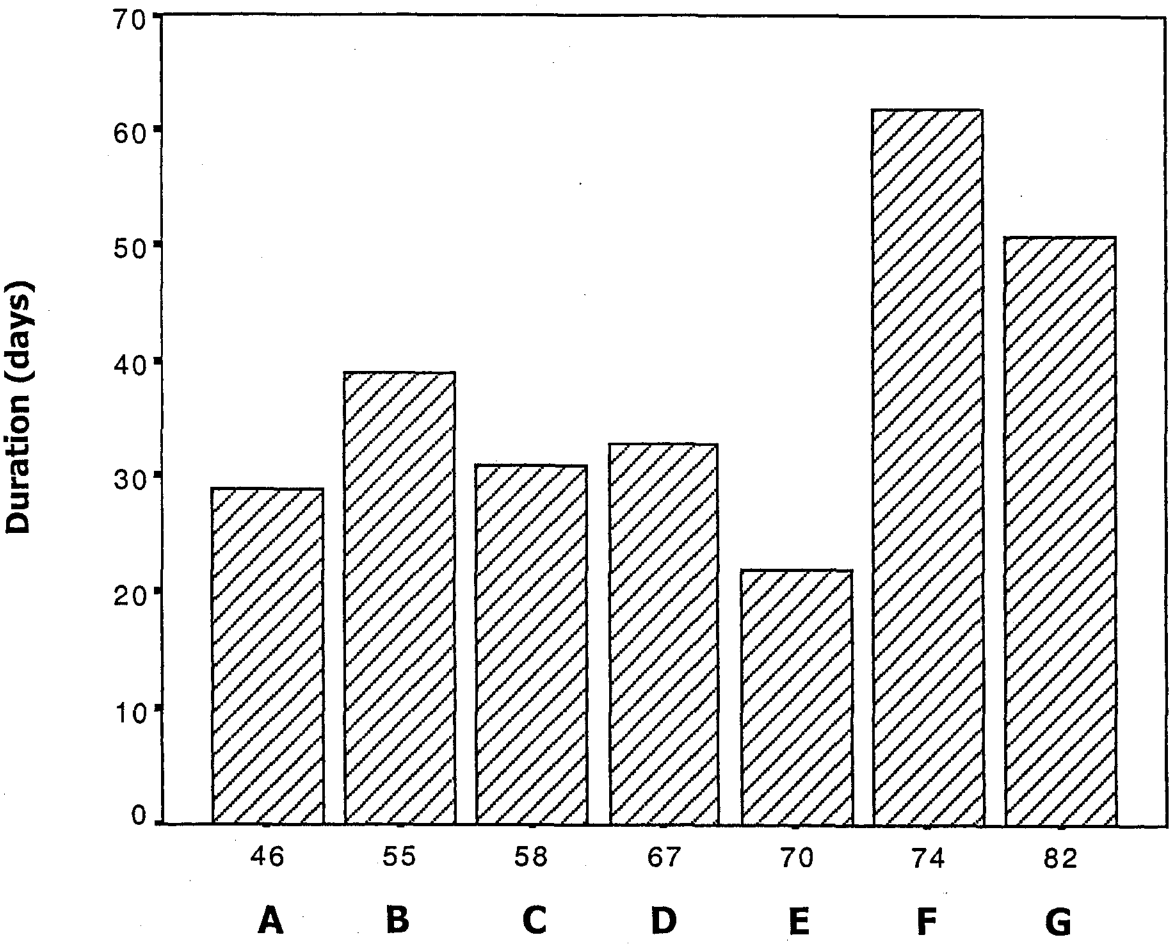

Fig. 1.11. Relationship between duration of moult and median migration date (1=July 1) for seven warbler species. A=Yellow Warblers; B=Magnolia Warblers; C=American Redstarts; D=Bay-breasted Warblers; E=Ovenbirds; F=Yellow-rumped Warblers; G=Nashville Warblers.

Discussion

Rimmer (1988) noted that there have been few moult studies performed on discrete wood-warbler populations in central and northern regions of North America. Moreover, the timing and duration of moult for most North American wood-warblers has been insufficiently examined; in particular, none have compared differences in the scheduling and duration of primary moult between several warbler species from a geographic region of North America. This novel study compared various features such as the duration and timing of the prebasic moult of warbler populations found at two locations in Ontario.

TIMING OF MOULT

The scheduling of moult must be precisely timed to ensure minimum energetic losses while still proving to be adequately efficient to prepare for fall migration. Moreover, a bird's annual cycle must be structured to optimally fulfill its reproductive, migratory, and moult requirements. Factors such as the timing of spring arrival to the breeding grounds will set the timeline required to fulfill all of the tasks associated with breeding and raising young.

I found that the American Redstart, and Yellow-rumped and Magnolia warblers at TCBO started their prebasic moult at the end of July. These three species also had similar spring arrival dates at TCBO (median spring migration arrival dates ± confidence intervals): May 29 ± 6 days, May 21 ± 7 days, and

May 28 ± 6 days, respectively. Their time of arrival also coincided with Ontario nest records for these species, which ranged from the end of May through to the end of July, peaking in mid-June (Peck and James 1987). In addition, the breeding period from the first egg laid until the fledging of young for American Redstarts, and Yellow-rumped and Magnolia warblers were all approximately 20 to 25 days, and adults may feed their young for about two weeks to one month after they have left the nest (Hall 1994, Sherry and Holmes 1997, Hunt and Flaspohler 1998). Furthermore, with parallel breeding schedules, I found that the timing of prebasic moult for all three species appears to be associated with the final stages of their breeding periods. Similarly, Jackson et al. (1992) noted that for male Hermit (*Dendroica occidentalis*) and Townsend's (*Dendroica townsendi*) warblers — which frequently hybridize in overlapping breeding ranges — most of the prebasic moult was completed on their breeding grounds. They suggested that their breeding areas, which are situated mostly in moist and humid regions, have enough nutrients to allow birds to moult before leaving the area.

Similarly, Ovenbirds and Yellow, Nashville, and Bay-breasted warblers appear to arrive at LPBO at the same time in spring (median spring migration arrival dates ± confidence intervals): May 16 ± 7 days; May 19 ± 7 days, May 13 ± 6 days, and May 22 ± 7 days, respectively. Although all species examined at both sites had similar nest record dates to each other, the warbler species at LPBO had a larger time range than those examined at TCBO. The four above mentioned LPBO species have nest records lasting from mid-May through the end of July, with the Yellow and Nashville warblers peaking during the first two weeks in June, and Ovenbird and Bay-breasted Warblers peaking during the second half of June (Peck and James 1987). However, the breeding period from the first egg laid until the fledging of young for the Ovenbird and Yellow, Bay-breasted, and Nashville warblers were also similar (about 20 to 25 days) to those of American Redstarts and Yellow-rumped and Magnolia warblers. Moreover, parental care of young after leaving the nest ranged from one week to one month (Van Horn and Donovan 1994, Williams 1996a, Williams 1996b, Lowther et al. 1999).

Although there was a wider range of breeding schedules in the warbler species examined at LPBO, I found that the Ovenbird, and Bay-breasted and Nashville warblers all initiated prebasic moult from the end of July through to the beginning of August. Unfortunately, I could not compare these to other findings because there are no published studies of prebasic moult for these species. On the other hand, I determined that the Yellow Warbler population at LPBO started prebasic moult in early July, implying that they have a surprisingly short time period in which to complete all tasks required for breeding and raising young prior to preparing for the long migration south. Although I did not perform any breeding analysis on Yellow Warblers in the LPBO area, my findings suggest that the initiation of moult must begin towards the end of the breeding season. Similarly, Rimmer (1988) found that the prebasic moult of Yellow Warblers in the

James Bay, Ontario region typically overlapped with breeding, primarily during the fledgling stage, when parental time and energetic demands gradually decrease as the young get older. Zalas and Breitwish (1990) found moult-breeding overlap during the fledgling stage of Northern Mockingbirds (*Mimus polyglottos*) in Florida, also suggesting that both activities could occur in tandem with sufficient energetic and nutritional reserves. In addition, Vega Rivera et al. (1998) suggested that the Wood Thrush (*Hylocichla mustelina*) could overlap moult with fledgling care because their young are relatively independent at this time and could, therefore, procure some of their own food. The timing of moult in this species coincided with fall fruit and berry production, which is used as an easily attainable supplimental food resource. In addition, Stevenson and Anderson (1994) noted that Yellow Warblers occasionally eat fruits, which are likely to be found in Ontario during the fall.

However, Rimmer (1988) determined that female Yellow Warblers initiated moult later than males in the James Bay region, suggesting that energetic demands for breeding and raising young does not allow enough time to acquire sufficient resources to begin moult as early as males. Although I did not find any significant difference in the initiation of moult between the sexes in the American Redstarts and Yellow Warblers, Rimmer (1988) also suggested that differences in moult scheduling might be less apparent between males and females at lower latitudes because of the reduced energetic demands of breeding. For example, Nolan (1978) found no difference in the initiation of moult between the sexes for Prairie Warblers in the southeastern region of the United States. Furthermore, eastern populations of Northern Rough-winged Swallow (*Stelgidopteryx serripennis*; Yuri and Rohwer 1997) and Florida populations of Northern Mockingbirds (Zalas and Breitwisch 1990) showed no difference between the sexes in the onset of flight feather moult because both sexes share equally in parental duties.

My findings suggest that Yellow Warblers at LPBO overlap the early stages of moult with the later stages of breeding. Furthermore, they imply that this may well be so for other species I examined, including American Redstarts, Magnolia Warblers, and Yellow-rumped Warblers. Accordingly, Nolan (1978) also detected moult in adult Prairie Warblers that were tending to recently fledged young. This supports the notion that the energetic demands of breeding may not be the critical factor in determining the onset of moult in warblers. Hahn et al. (1992) indicated that the timing and rate of prebasic moult could be adjusted in response to environmental cues such as photoperiod, nutritional resource availability, and social interactions. Similarly, Samson (1976) suggested that the consistency of photoperiod could regulate the onset of moult in the Cassin's Finch (*Carpodacus cassinii*). Hahn et al. (1992) also suggested that the rate of moult could be regulated daily depending on the availability of nutritional resources in order to minimize conflicts in distribution of nutrients and energy with other processes such as breeding. Although my findings suggest that moult rates remained relatively constant throughout the moult period, it is possible that under examination the warbler species use a combination of external and internal factors to determine the scheduling of moult. Consequently, this allows warblers to fine-tune the onset of prebasic moult creating a slight overlap with the termination of breeding, providing more time to prepare for their long-distance fall migration south.

DURATION OF MOULT

Although warblers examined at TCBO had similar breeding schedules and initiation dates for primary moult, there were variations in their duration of primary moult. Both American Redstarts and Magnolia Warblers had similar moult durations of 31 (± 7 C.I.) and 39 (± 11 C.I.) days, respectively. Similarly, Bay-breasted and Yellow warblers at LPBO both had moult durations of approximately one month (33 ± 8 C.I., 29 ± 6 C.I., respectively). Although a moult duration of approximately 30 to 40 days is considered to be a short and intense moult for migratory passerines (Rimmer 1988, Haukioja 1971), this duration appears to be the average length for the warbler species that I examined at both locations.

In contrast, the primary moult of Yellow-rumped Warblers at TCBO lasted approximately 60 days from the end of July until late September. The Yellow-rumped Warbler may be able to prolong the duration of moult — thus reducing daily energy requirements — because, unlike most warblers, it utilizes a diverse range of foraging habitats (Hunt and Flaspohler 1998) and is considered a generalist forager (MacArthur 1958, Morse 1968) that consumes insects, small invertebrates, and fruits such as bayberry (*Myrica* spp.) and wax myrtle (*Myrica cerifera*; Bent 1953). Similarly, Foster (1967) found that Orange-crowned Warblers took approximately two months to complete their prebasic moult. Like the Yellow-rumped Warbler, Sogge et al. (1994) described varying degrees of migratory behaviour in Orange-crowned Warblers from short-distant migrants of coastal populations to highly migratory northern populations, in concert with a more extensive diet consisting of invertebrates, fruits and berries, and suet from feeders in winter. These similarities in nutritional choices and migratory behaviour suggest that Yellow-rumped Warblers could prolong moult without experiencing detrimental energetic losses.

At LPBO, Nashville Warblers had the longest primary moult period of approximately 50 days. No previous study on moult has been conducted on this species, and potential ecological explanations for my findings remain obscure. However, it is possible that Nashville Warblers display a longer primary moult duration due to phylogenetic constraint. Protein electrophoresis has demonstrated that the Nashville Warblers may be closely related to the Orange-crowned Warbler (Barrowclough and Corbin 1978), which has a similarly long prebasic moult duration (Foster 1967). It is also possible that the Nashville Warbler has a longer moult duration because it had the latest migration date of the other species I examined. Hussell (pers. comm.) suggested that species that migrate later during the fall have more time to prepare for migration, and hence, have a longer moult period.

In contrast, Ovenbirds at LPBO had the shortest primary moult duration of only 22 days. Although this high rate of moult may leave this species flightless (Haukioja 1971), it may have an ecological advantage over many other warbler species in this regard because it breeds and feeds primarily on the ground (Van Horn and Donovan 1994). Consequently, it can maintain daily activities while in active moult. In addition, the Ovenbird may forage opportunistically in trees and shrubs during spruce budworm (*Choristoneura fumiferana*) outbreaks (Zach and Falls 1975), thus allowing a larger range of food choices. Feeding and nesting habitats of the Ovenbird do not usually overlap with warblers of similar habitats, such as the Louisiana Waterthrush (*Seiurus motacilla*), Kentucky Warbler (*Oporornis formosus*), and Worm-eating Warbler (*Helmitheros Vermivora*; Wenny 1989, Van Horn 1990), which likely reduces competition for food. This suggested advantage of ground foraging options in Ovenbirds is also observed in Wood Thrushes (Holmes and Robinson 1988). Vega Rivera et al. (1998) found that although the rapid flight feather moult for Wood Thrushes decreased flight capabilities during this period, this species could survive because they became very secretive, remained in areas with dense vegetation, and fed primarily on the ground. Ovenbirds may adapt similar tactics to successfully undergo a short, intensive moult.

MOULT AND MIGRATION

Another factor that could contribute to observed differences in the timing and length of moult in warblers is their respective timing of fall migration. Moult scheduling and duration for American Redstarts, and Yellow-rumped and Magnolia warblers at TCBO and Yellow, Bay-breasted, and Nashville warblers at LPBO were consistent with their timing of migration, indicating that an earlier migration date decreased the duration of moult. However, there might also be overlap with the termination of primary moult with the start of fall migration for the species that I examined, including Yellow-rumped and Magnolia warblers. Similarly, Rimmer (1988) noted that the Yellow Warblers in the James Bay region began migrating with the last two primaries in final growth stages and suggested that the energetic costs associated with this incomplete stage of moult were small enough to do so. He also found a decrease in body weight during later stages of moult because individuals departed without the typical accumulation of premigratory fat. Consequently, he suggested that migration may be regulated to flight efficiency rather than physiological readiness to adhere to their migration schedule. As well, Hedenström and Sunada (1999) found minimal effects on flight performance in birds with narrow wing gaps due to moulting and suggested that this may be the reason why some bird species can moult during fall migration. These studies may provide explanation for the overlap of moult with the onset of migration in warblers in my study. Further examination of flight energetics in warblers would provide invaluable information in this regard.

In contrast, short moult period did not imply an early migration date for Ovenbirds at LPBO. Although this species had the shortest moult of all warblers examined, fall migration occurred in mid-September, later than the Yellow Warbler and Bay-breasted Warblers at LPBO. The Ovenbird is larger in size than most other warblers (Van Horn and Donovan 1994). It is possible that the short moult duration could provide the necessary time to prepare for fall migration; however, studies examining moult scheduling in relation to migration in species of similar size have found varying results (e.g., Evans 1966, Morton et al. 1969) suggesting that this may not be the case. However, the Ovenbird may be anomalous with regards to moult scheduling and migration because of its atypical ecological and behavioural attributes or its systematic position among parulids. Lovette and Bermingham (2002) found the Ovenbird to be in a basal position as sister taxon lying outside a clade including all other parulids that they examined, with the exception of the Yellow-breasted Chat (*Icteria virens*) which they concluded was probably not a parulid. Further study is needed to fully comprehend atypical moult and migration scheduling displayed by the Ovenbird.

Although, timing of moult is consistent with timing of fall migration for most species in this study, one could question the mechanisms underlying the range of moult scheduling and migration observed. It is likely that a combination of both internal (i.e., physiological) and external (i.e., environmental) factors (Hahn et al. 1992) that are characteristic to each species determine the scheduling of moult and migration. Moreover, ecological constraints, such as food availability, might prevent species from prolonging their stay at the breeding grounds. However some species, such as the Yellow-rumped Warbler, which demonstrated a protracted moult, also had a later migration period, which also coincides with Hussell's (pers. comm.) suggestion that late migrants have a longer moult period. Hunt and Flashpohler (1998) suggested that protracted fall migration of Yellow-rumped Warblers allows them to disperse early from their breeding grounds to forage while undergoing moult. In addition, Terrill and Ohmart (1984) found that migrating Yellow-rumped Warblers could shift to geographically closer wintering areas depending on the food resources and climatic suitability of the region. Seasonal frugivory of Yellow-rumped Warblers may allow them to remain further north than other migratory warblers because fruits contain large amounts of fatty acids necessary for building specific depot lipids (Bairlein 2002). The accumulation of lipids is essential because energetic demands are exceptionally high during migration (Moore and Simm 1985).

This study provides a foundation for future research of several wood-warblers species in eastern North America. External factors, such as food availability and geographical distribution, provided some explanation for moult and migration scheduling for the majority of warbler species examined. Further examination of the many biological and environmental aspects of moult and migration in birds, and specific phylogenetic relationships among parulids will contribute to a better understanding of moult and migration in wood-warblers.

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CHAPTER 2: Raggedness as an indicator of moult rates in Parulids

Abstract. — Traditional methods of analyzing moult in birds have been criticized for their inaccuracy; however, newer, more precise methods require complex mathematical interpretations and unrealistic sample sizes. I examined the relationship between raggedness scores and moult rates among five species of wood-warblers (Parulidae) with similar moult patterns to determine if raggedness could be used as an index of moult rates. Positive correlations between raggedness and moult rates derived from pooled recaptures, least squares linear regressions, and individual species recapture methods in this study suggested that average raggedness for the primary and secondary scores within a determined primary moult score range is a good index of the rate of moult in warblers. Therefore, mean raggedness scores may be a useful tool for (1) providing baseline moult rate assessments in populations with insufficient recaptures, allowing for comparisons to other populations with known moult rates; and (2) estimating the rate and duration of moult in some species.

Introduction

Ginn and Melville (1983) noted the difficulties in determining the rate and duration of primary moult in birds because no method to date could completely satisfy the statistical reasoning for its use. Even so, traditional methods of analyzing moult are still being used to date. Although new methods have since been developed, further research is still needed to apply these techniques in comparative moult studies between species. Detailed examination of moult patterns and chronology may aid in the realization of a standard, practical way of determining primary moult.

Plumage sequences and moult patterns have been studied extensively throughout the last century, in an attempt to understand the complexities of feather replacement. Humphrey and Parkes (1959) were instrumental in defining the various plumage sequences found in birds and subsequently developed the most commonly used terminology for plumages and moults. Many North American migratory passerines display an *alternate plumage* during the breeding period, which is often brightly coloured or has characteristic signal patches to attract mates. Conversely, the *basic plumage* displayed throughout non-breeding periods is often duller in appearance. Consequently, the prebasic moult of adult passerines, such as wood-warblers that have only one plumage per cycle, is performed in autumn – between breeding and migration – to attain the *basic plumage*.

With the increase in studies on moult, the British Trust for Ornothology developed moult cards to standardize data collection and facilitate the exchange of moult data between countries. Primary moult is typically scored with a system that ranks each feather on a scale; 0 being an old feather, 1 – 4 are growing feathers at certain stages, and 5 being a fully grown new feather (Newton 1966, Ginn and Melville 1983).

Moult plays an important role in the life cycle of birds because feathers have multiple functions, such as display during courtship (e.g., Beehler 1983) and thermoregulation (Schieltz and Murphy 1997). Moult may also prevent infestations by dermal parasites (Post and Enders 1970). Moreover, birds must replace their feathers before wearing impedes flight (Ginn and Melville 1983). However, the complete moult is a major undertaking that consumes large amounts of energy and protein reserves for both feather production, and compensation for the effects of poorer insulation and decreased flight efficiency (Dolnik and Gavrilov 1979, Murphy and King 1991, 1992). In order to maximize efficiency, birds typically schedule moult during times to avoid undue with other energetically demanding activities, such as reproduction and migration, and when food is abundant (Payne 1972).

Estimation of moult duration of bird populations have been previously analyzed by regressing capture dates of individuals on the moult score (Pimm 1976, Summers et al. 1983). Although this approach has been criticized for its inaccuracy (Underhill and Zucchini 1988, Bensch and Grahn 1993), it is still utilized because of its ease of use compared to more recently developed techniques (Yuri and Rohwer 1997, Voelker and Rohwer 1998). For instance, Underhill and Zucchini (1988) developed a method for the estimation of duration of primary moult through a mathematical model using both moult scores and primary feather masses. Although this model may be a more effective way to determine the moult duration, it requires mean primary feather masses for each species studied, which are not easily obtained from live specimens.

In addition, the rate and duration of moult can be calculated from individuals re-trapped throughout their moult period. Although it has been suggested that this may be the most accurate method in determining the rate and duration of moult, large numbers of moulting individuals must be examined to determine the variation in individual moult duration (Bensch and Grahn 1993). Rimmer (1988) found that moulting Yellow Warblers (*Dendroica petechia*) were reclusive in their vulnerable state, suggesting that birds might be difficult to trap at this time.

An additional approach to wing moult was realized to further improve the accuracy in calculating the duration of moult. Haukioja (1971b) introduced the term "wing raggedness" and developed a scoring method that scores the size of the gap in the wing relative to the corresponding moult score. Raggedness is scored by subtracting the moult score for each feather from five resulting in raggedness scores ranging from zero (for both old and fully replaced feathers) to four (for missing feathers).

Bensch and Grahn (1993) found that wing raggedness could predict the speed of moult of Willow Warblers (*Phylloscopus trochilus*). They subsequently developed the Residual Raggedness Value (RRV) method that made the raggedness value independent of the stage of moult. This allowed for the estimation of moult duration for individuals captured only once during a moulting period, which greatly amplified the sample size and improved the accuracy of the results. Unfortunately, in order to confirm if the RRV method can be applied to a particular species, a large sample of birds must first be recaptured to establish the constancy of RRV over a major part of an individual's moulting period.

Following this, a significant correlation between RRV and moult speed must be demonstrated (Bensch and Grahn 1993).

Although these newer techniques have been shown to produce more accurate results, their drawbacks have resulted in them being used primarily to examine individual populations of a particular species. In contrast, my study will demonstrate how raggedness scores can be used as an index of rate of moult within, and among, different species of warblers. Wood-warblers are an appropriate taxon with which to examine this technique because they have similar moult patterns. Most eastern members of the Parulidae can be found in Ontario, often breeding in the same region, allowing several species to be examined simultaneously (Dunn and Garrett 1997). If an association between average raggedness and rate of moult can be demonstrated within warblers, this method may be applicable to other taxa.

Materials and Methods

STUDY AREAS

Moult data for the primary and secondary flight feathers were obtained for the American Redstarts (*Setophaga ruticilla*), Nashville (*Vermivora ruficapilla*), Yellow, Magnolia (*Dendroica magnolia*), and Yellow-rumped (*Dendroica coronata*) warblers captured at Thunder Cape Bird Observatory (TCBO), Innis Point Bird Observatory (IPBO), and Long Point Bird Observatory (LPBO) between

1976-2002. TCBO is situated at the tip of the Sibley Peninsula, on the Northwest shore of Lake Superior, approximately 80 km from Thunder Bay, Ontario (48° 18' 04", 88° 56'18"; Fig. 2.1). The area is predominantly forested, consisting mostly of coniferous trees and shrubs, providing suitable habitat for most boreal breeding warbler species, such as the Nashville and Magnolia warblers. IPBO is located approximately 12 km from Ottawa, Ontario (45°22'55", 75°53'30"; Fig. 2.2). Situated near Shirley's Bay on the property of the Department of National Defense along the southwest bank of the Ottawa River, the surrounding habitat provides ideal breeding grounds for numerous warbler species such as the Black-and-White Warbler (*Mniotilta varia*) and Common Yellowthroat (*Geothlypis trichas*). LPBO has monitoring stations throughout the Long Point peninsula on the Northwest shore of Lake Erie (from 42°35'00", 80°24'00" to 42°32'55", 80°3'00"; Fig. 2.3). Located in the only Carolinian Forest region Ontario, its diverse range of breeding habitats such as marshes, wetlands, and deciduous forest allows various warbler species, from the threatened Hooded Warbler (*Wilsonia citrina*) to the very common Yellow Warbler, to be found breeding there. In addition to supplying breeding habitat, these sites are known to be major stopover areas for migrating warblers, and allow birds to rest and replenish fat reserves along their migration route. These attributes confer that the three locations are ideal for monitoring warbler migration, providing ample numbers to be examined during the course of this study.

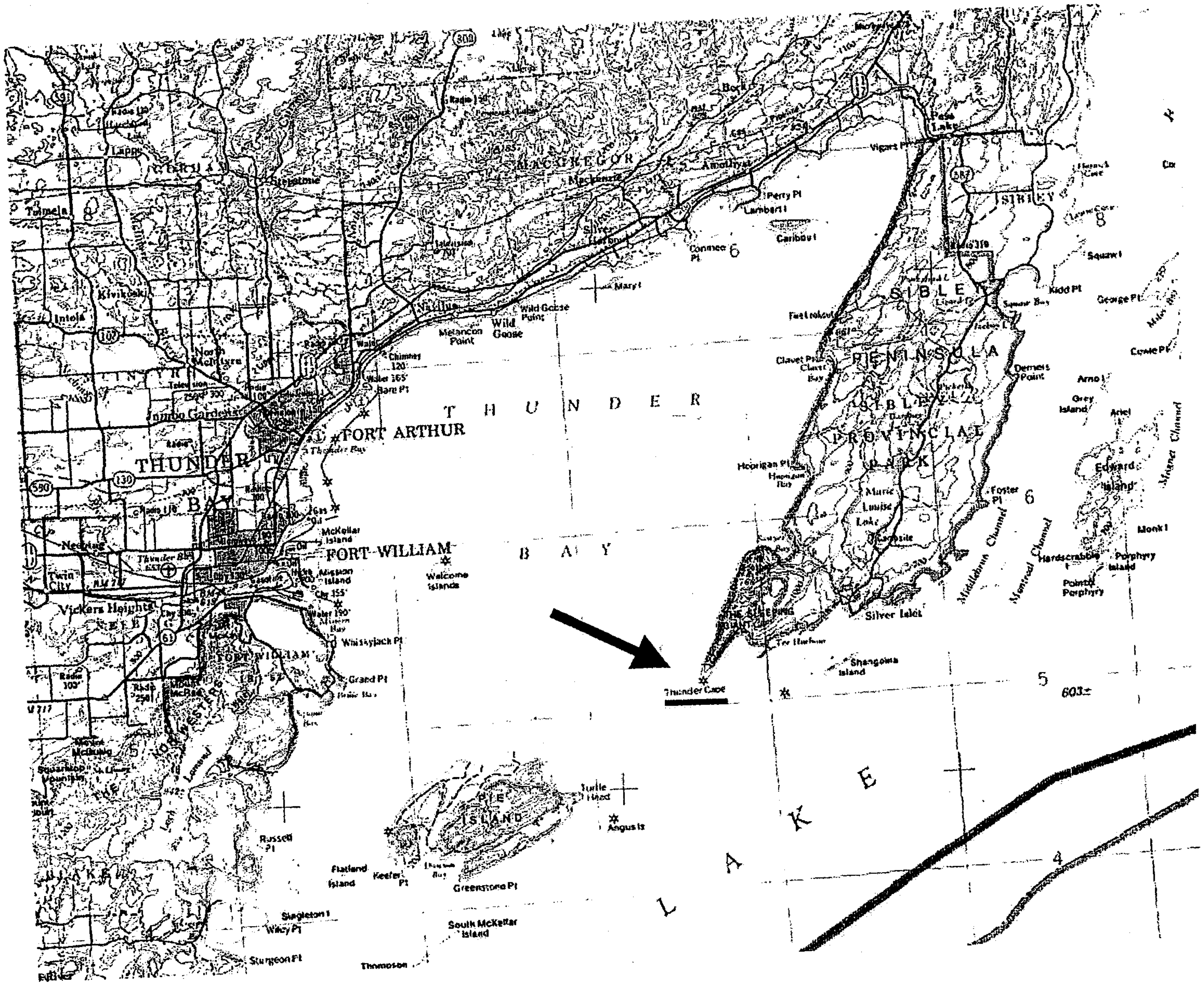


Fig. 2.1. Location of Thunder Cape Bird Observatory, Ontario, Canada.

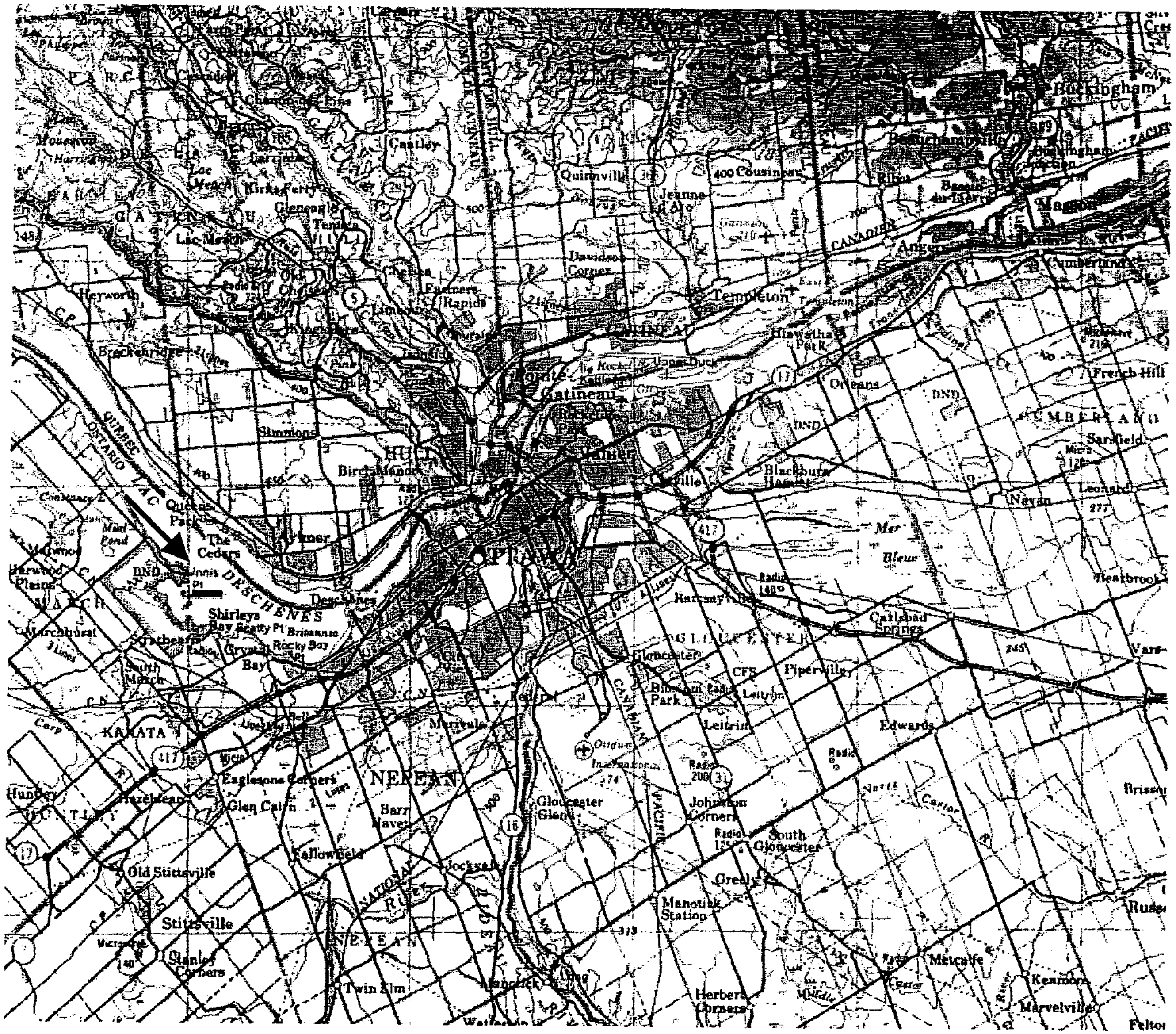


Fig. 2.2. Location of Innis Point Bird Observatory, Ontario, Canada.

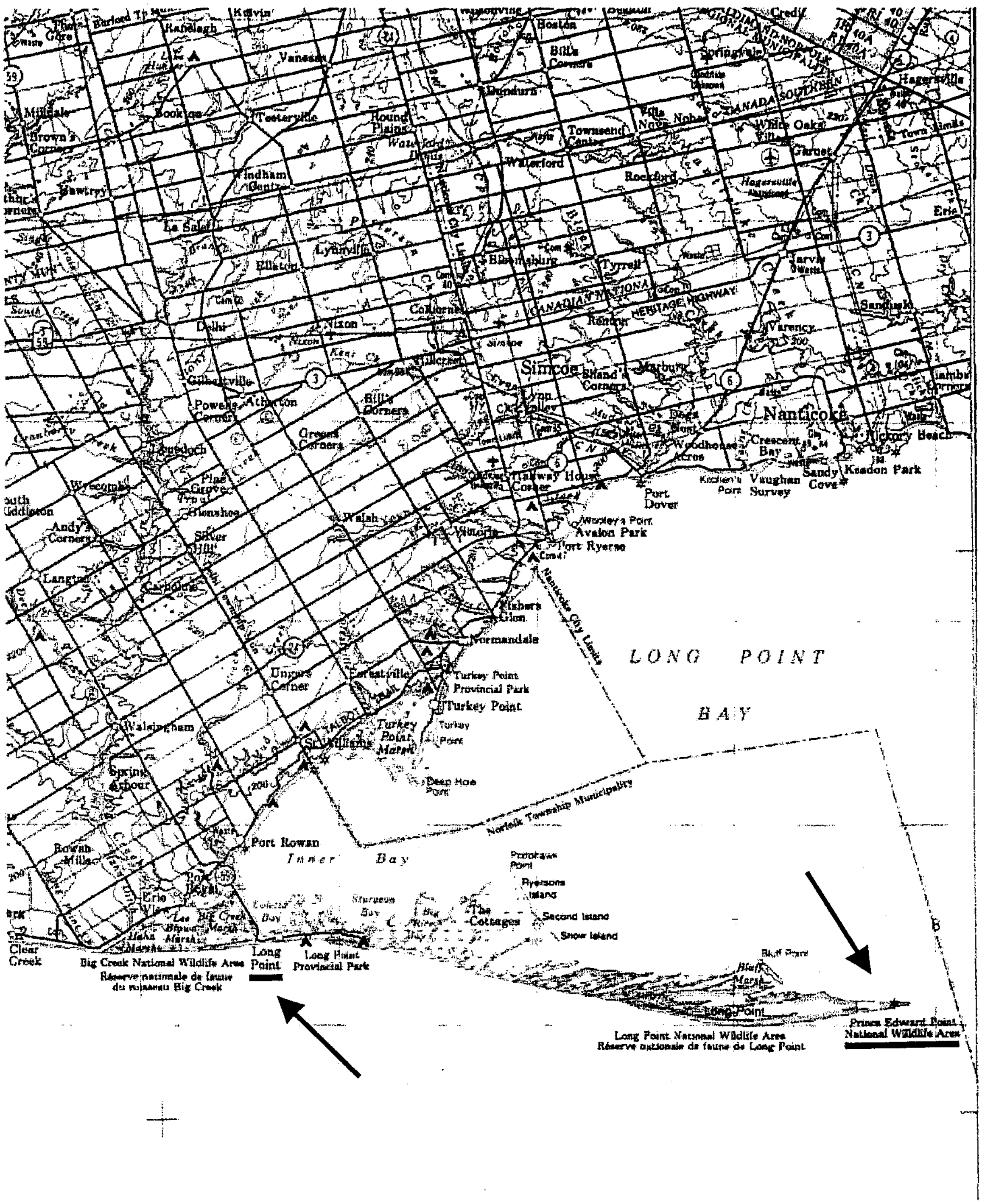
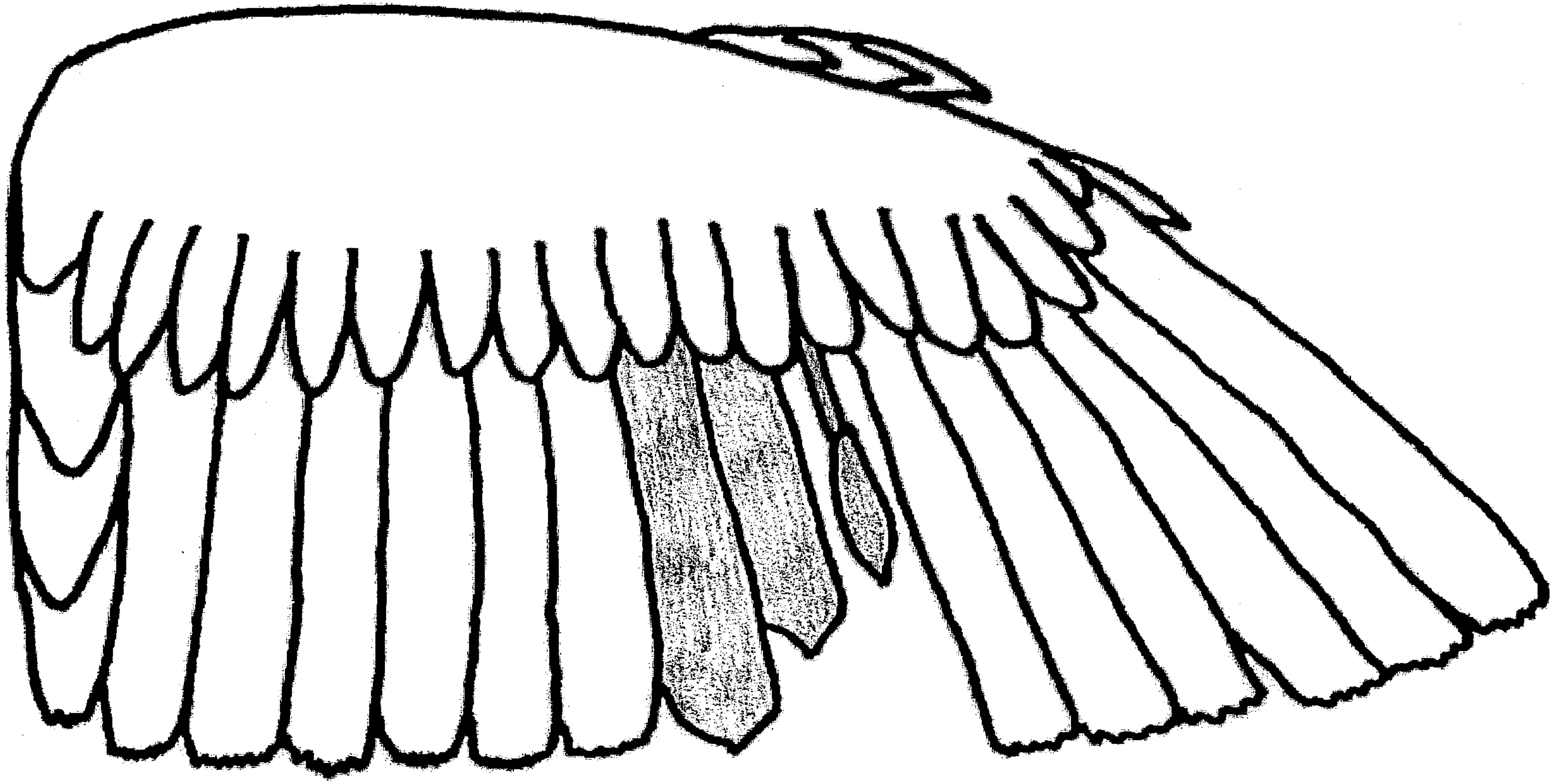


Fig. 2.3. Locations of the Long Point Bird Observatories, Ontario, Canada.

FIELD PROCEDURES

A total of 298 individuals was captured from July to October throughout their moult and migration periods using mist nests with a mesh size of 30mm (1 1/4 inch) and Heligoland traps, according to TCBO, IPBO and LPBO standard protocols. Moult data for the primary feathers for After Hatch Year (AHY) warblers were obtained according to Newton (1966) and Ginn and Melville (1983), scoring feathers on a scale of 0 to 5. Using their methods, old feathers are scored as 0; missing or in pin (completely in the feather sheath) as 1; feather out of pin to 1/3 full grown as 2; 1/3 to 2/3 full grown as 3; greater than 2/3 full grown with sheath present as 4; full-grown new feather with no sheath as 5. Each feather is scored independently, then the total score is summed for the group of primary feathers for that wing (Fig. 2.4). The vestigial primary number 10 was excluded from the primary moult score (Rimmer 1988); therefore, it ranged from 0 (no moult) to 45 (primary moult complete). Moult data were recorded for the right wing only, unless the moult was obviously asymmetrical, in which case both sides were recorded. To get a representative sample of the population, primary moult scores were calculated on all birds captured (or on a random sample if large numbers were captured), whether they were moulting or not (D. J. T. Hussell, pers. comm.). AHY warblers were differentiated from Hatch Year (HY) warblers by plumage and skulling with AHYs having fully ossified skulls and HYs ranging on a scale of 0 to 3. Furthermore, the sexes were distinguished by plumage characteristics or wing chord length



Primary Score = 5 + 4 + 3 = 12

Raggedness Score = 0 + 1 + 2 = 3

Fig. 2.4. Description of the method for estimating the primary score with corresponding raggedness scores (new feathers represented by shading; after Bensch and Grahn 1993).

(Pyle 1997). Species with unequal sex ratios were pooled (Green and Summers 1975, Mewaldt and King 1978). In addition, the data was pooled for each species across all years to increase sample sizes (e.g., Foster 1967, Sealy 1979, Voelker and Rohwer 1998).

The rate of feather growth per day, as indicated by the change in moult score, was determined using individuals recaptured at intervals greater than seven days because the recapture method is likely to produce rate estimates with high variance when individuals caught within a few days of each other are included (Ginn and Melville 1983, Bensch and Grahn 1993). In addition, raggedness scores were calculated for all individuals to examine the size of the gap created in the wing due to moulting feathers using methods developed by Haukioja (1971a), moult score for each feather is subtracted from 5 resulting in a raggedness score of 0 for both old and fully replaced feathers, and a corresponding raggedness score of 4 for a primary moult score of 1; raggedness score of 3 for a primary moult score of 2; raggedness score of 2 for a primary moult score of 3; and raggedness score of 1 for a primary moult score of 4 (Fig. 2.4). Raggedness scores were calculated for both primary and secondary flight feathers to lengthen the time during which raggedness values can differ between individuals (Haukioja 1971a) since wood-warblers typically complete secondary moult soon after the completion of primary moult (D. J. T. Hussell, pers. comm.). Raggedness scores have little variation at very low (PS<3) and very high primary scores because few feathers are moulting at these times (PS>42; Haukioja

1971a, Bensch and Grahn 1993), therefore, only individuals with a primary score of 5-41 were used.

STATISTICAL ANALYSES

A three-way analysis of covariance (ANCOVA; Sokal and Rohlf 1995) was performed to determine differences in raggedness score in relation to primary score between the sexes for American Redstarts and Yellow Warblers. Differences in raggedness scores between the sexes would require them be analyzed separately. In addition, to demonstrate that raggedness score can be used as an index of rate of moult, a correlation between rate of moult and raggedness was performed with all recaptured individuals, regardless of species, throughout all years. Least squares linear regressions were then used to estimate the rate (i.e., increase of primary score per day) of primary flight feather moult for each species as suggested by Pimm (1976). This method of regressing date captured (dependant variable) against moult score provides an estimation of an individual's timing and duration of moult.

Substantiation that raggedness scores could be used as an index of moult speed was determined in a bivariate correlation between average raggedness scores (for each species) versus their moult rates derived from the least squares linear regression method. A significant correlation could demonstrate possible relationships between the average raggedness and rate of moult. In addition, I performed a bivariate correlation between average raggedness scores for each species and average rate of moult derived from recaptured individuals. A significant correlation between these two variables would additionally confirm that raggedness could be used as an index of moult speed (Sokal and Rohlf 1995). All tests were performed using SPSS (Version 10.07a) for Apple Macintosh (SPSS Inc. 2000), with a significance level of $p<0.05$.

Results

Analyses of the effect of sex, with the primary score held constant as a covariate, on the raggedness score indicated that there was no difference for the two species with sufficient individuals sampled to be tested (American Redstart at TCBO, F=0.001, p=0.980, *n*=20; American Redstart at IPBO, F=0.096, p=0.762, *n* =15; Yellow Warbler at LPBO, F=0.091, p=0.766, *n*=22; Yellow Warbler at IPBO, F=0.041, p=0.842, *n*=20). In addition, there was a significant positive correlation between all recaptured individuals and rate of moult (r=0.697, p=0.013, *n*=20; Fig. 2.5), suggesting that mean raggedness for a species is a good indicator of its moult speed.

Furthermore, Table 2.1 illustrates moult rates for each species examined using the least squares linear regression method. Moreover, the mean primary and secondary raggedness for individuals with primary scores, ranging from 5 to 41 for each species, significantly correlated with their rate of moult derived from the linear regression method (r=0.697, p=0.027, *n*=8; Fig. 2.6), which suggests

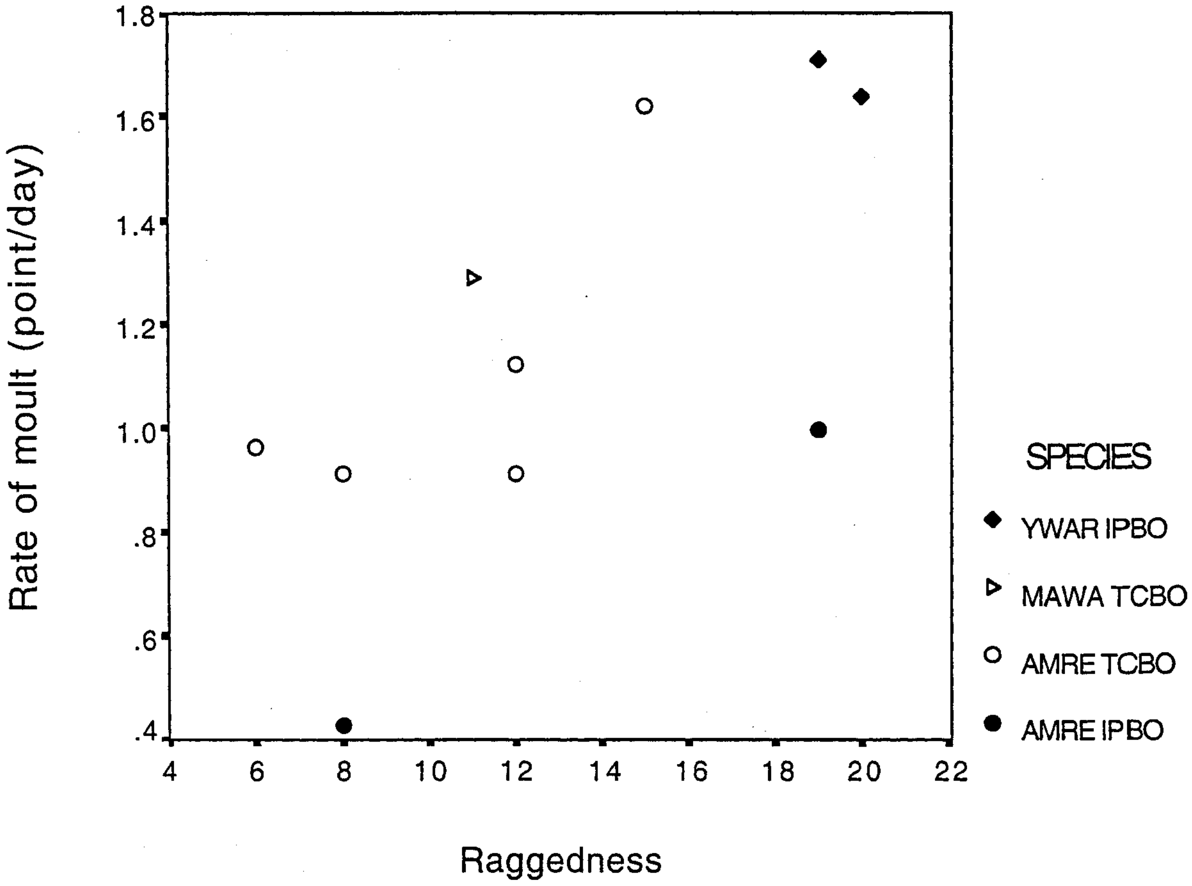


Fig. 2.5. Relationship between rate of moult and raggedness scores for three species of recaptured warblers. YWAR=Yellow Warbler; MAWA=Magnolia Warbler; AMRE=American Redstart.

Table 2.1. Moult rates derived from the least squares linear regression method for six warbler species.

Species	Location	*n*	Rate of moult (point/day)
Yellow-rumped Warbler	TCBO	22	0.7097
Nashville Warbler	LPBO	8	0.8627
American Redstart	IPBO	17	1.0732
Magnolia Warbler	TCBO	11	1.1282
Nashville Warbler	IPBO	15	1.1579
American Redstart	TCBO	25	1.4194
Yellow Warbler	LBPO	60	1.5172
Yellow Warbler	IPBO	36	1.7600

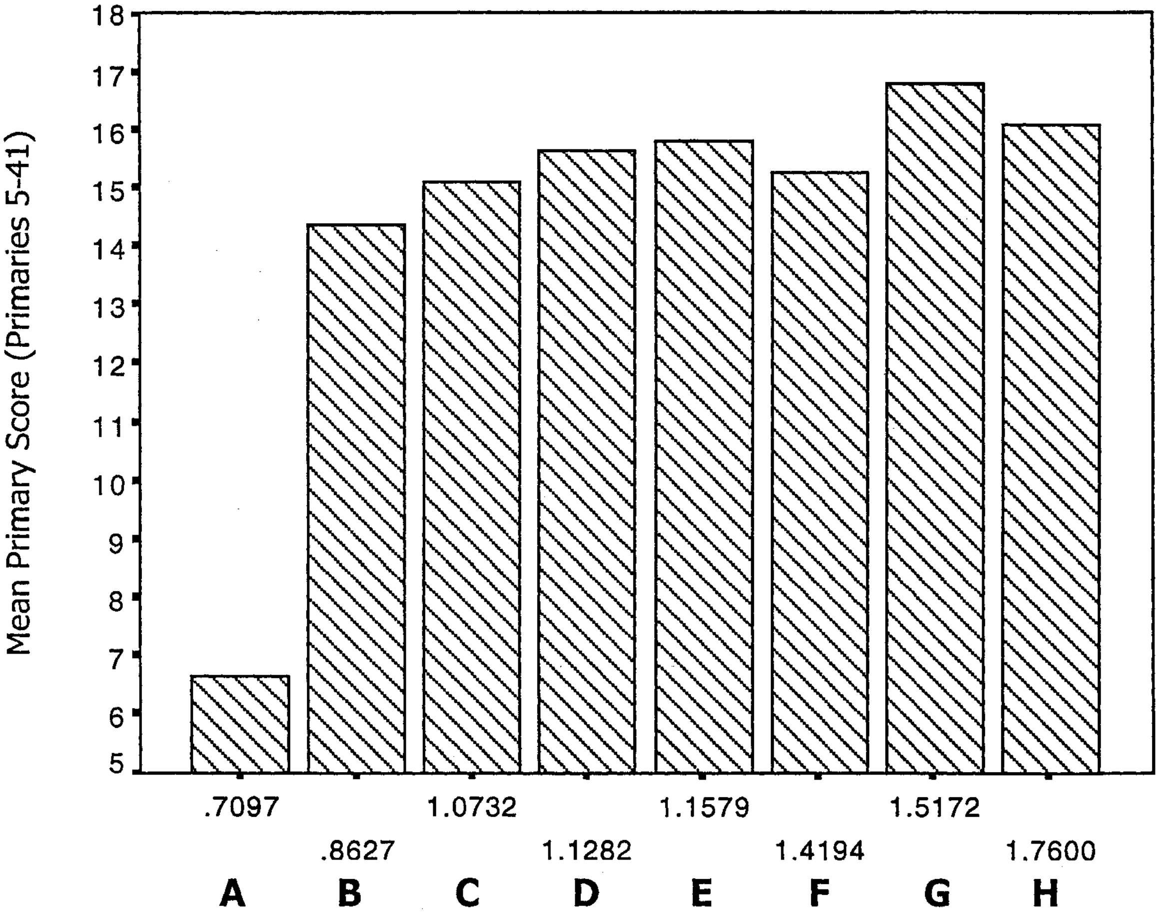


Fig. 2.6. Relationship between mean primary scores and moult rates (point/day) derived from the least squares linear regression method. A=Yellow-rumped Warblers (TCBO); B=Nashville Warblers (LPBO); C=American Redstarts (IPBO); D=Magnolia Warblers (TCBO); E=Nashville Warblers (IPBO); F=American Redstarts (TCBO); G=Yellow Warblers (LPBO); H=Yellow Warblers (IPBO).

that species with raggedness scores also have high moult rates. In addition, mean moult speed of each species of recaps correlated with mean raggedness (r=0.992, p=0.039, *n*=4; Fig. 2.7), which further strengthens the positive association between average raggedness and moult speed.

Discussion

Knowing the rate of feather moult could offer insight to the many biological and environmental factors that play a role in the process of feather replacement. This study presents a comparative method of examining moult rates that could provide a foundation for additional moult analyses. The positive correlations between raggedness and moult rates derived from the pooled recaptures, linear regressions, and species recapture methods in this study suggest that average raggedness for the primary and secondary scores within a determined primary moult score range is a good index of the rate of moult in warblers.

My results are supported by Rimmer (1988) who found that the Yellow Warblers at James Bay showed high raggedness values, which he suggested had coincided with their rapid rate of moult. Moreover, Haukioja (1971a), using similar methods reported high raggedness values in several European passerines that putatively associated with high moult rates, which caused these species to be flightless during part of their moult. In addition, Bensch et al. (1991) used average raggedness scores to compare moult rates between different species of

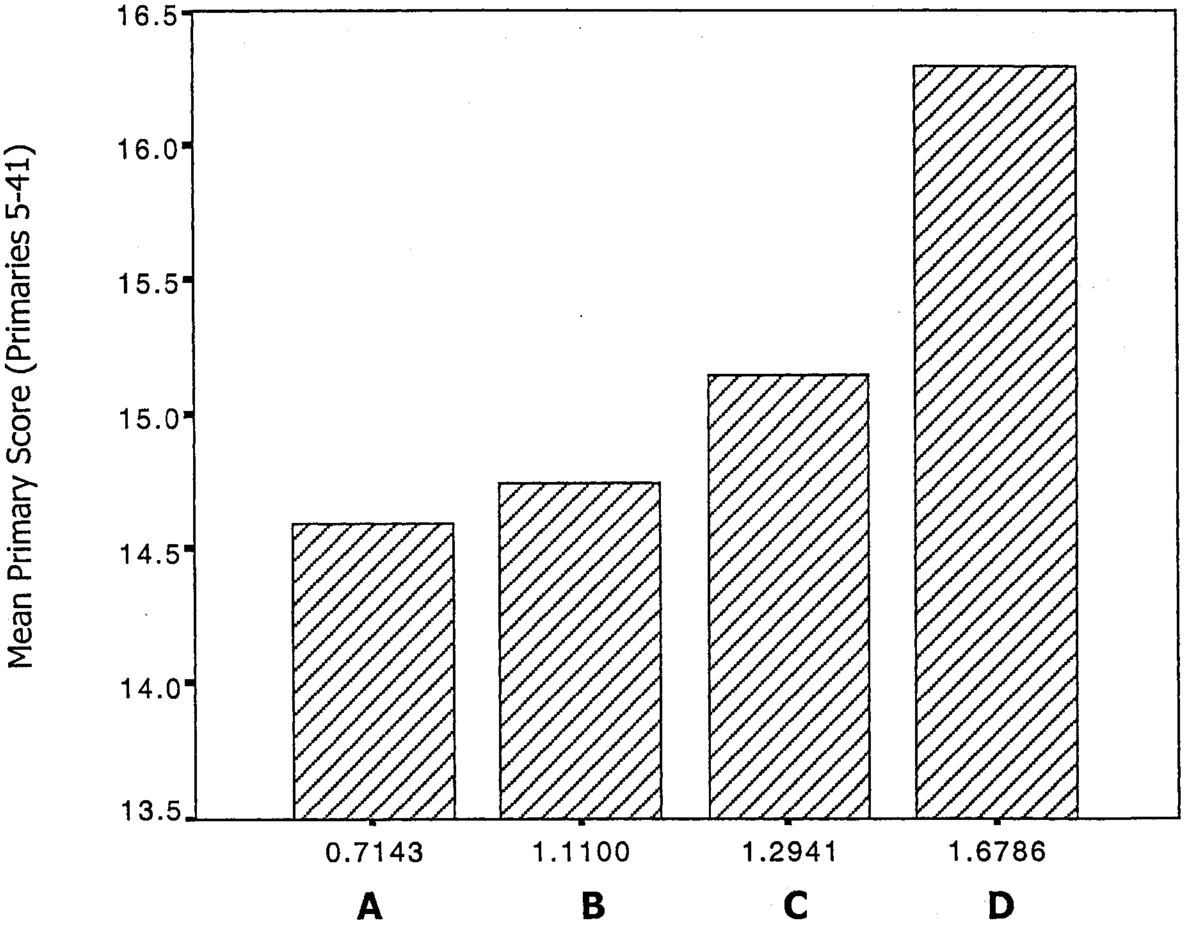


Fig. 2.7. Relationship between mean primary scores and moult rates (point/day) derived from the recapture method. A=American Redstarts (IPBO); B=American Redstarts (TCBO); C=Magnolia Warblers (TCBO); D=Yellow Warblers (IPBO).

Old World Warblers, claiming they could do so since there were only slight variations in feather growth rates between species; however, they did not provide any statistical justification for its use.

Bensch and Grahn (1993) also established that individual raggedness values indicated either a high speed or later stage of moult for Willow Warblers. They developed the Residual Raggedness Value (RRV) for estimating moult rates and moult durations of individual birds captured only once during a moulting period. Unfortunately, for moult comparison studies between species, individual Residual Raggedness models require unrealistic numbers of recaptured individuals. Recapturing banded birds is a relatively rare event. For example, approximately 1.1 million birds were banded in the United States and Canada in 2001, resulting in only 65,000 recoveries (including recaptured individuals) of which only 28% were nongame birds (USGS 2001). In addition, moulting passerines with reduced flight capabilities tend to be more secretive and are less likely to be caught (Ginn and Melville 1983).

On the other hand, the average raggedness method used in the present study may be used to validate the moult rates derived from the linear regression method. Furthermore, using average raggedness scores compensates for any slight changes in moult speed during the primary score interval and allows for comparisons between species with individuals captured only once. As with the RRV method, however, the utility of average raggedness as a predictor of rate of moult is not without constraint. For example, it may not be useful for species that do not display a sequential moult pattern, such as most Anseriformes that moult all of their flight feathers simultaneously (Ginn and Melville 1983). Therefore to use average raggedness as an index for the rate of moult of populations, all species examined should have similar raggedness trends. The area in which raggedness increases linearly when plotting raggedness against primary score will indicate what range of primary score to use. In addition, one must ensure that the population examined has an even distribution of primary scores throughout the primary range determined or raggedness scores could be skewed in either direction, increasing or decreasing moult rates.

Primary moult scores of 5-41 were appropriate for species examined in this study, but may not necessarily be so for species that have varied moult speeds and patterns. Bensch and Grahn (1993) used primary moult scores ranging from 5-35 Willow Warblers, but suggested that these limits are not rigidly set because feather growth rates may differ with species and, thus, should be determined accordingly.

Raggedness values are proving to be a valuable resource not only in moult studies but also in other areas. Hedenström (1998) found that raggedness could be used to estimate the reduction of wing area during moult in several European passerines, such as the Willow Warbler and the Reed Bunting (*Emberiza schoeniclus*). In addition, Haukioja (1971a) used raggedness values to compare flight capabilities in moulting northern European passerines such as the Whitethroat (*Sylvia communis*) and White Wagtail (*Motacilla alba*).

It is likely that the average raggedness method used in the present study is most effective with comparable species, such as confamilials or species displaying similar moult patterns. Furthermore, it may be a useful tool to provide baseline moult rate assessments in populations with insufficient recaptures, allowing for comparisons to other populations with known moult rates. In brief, this method may be used to strengthen other techniques utilized to estimate the rate and duration of moult, thus, serving as a foundation for future avian moult studies.

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CHAPTER 3: Age-related timing and patterns of prebasic body moult in wood-warblers (Parulidae)

Abstract. —This study compared the timing and patterns of the prebasic body moult between Hatch Year and After Hatch Year American Redstarts (*Setophaga ruticilla*) at Thunder Cape Bird Observatory, Ontario, and Hatch Year and After Hatch Yellow Warblers (*Dendroica petechia*) at Innis Point Bird Observatory, Ontario. Both species displayed no difference in the number of moulting individuals in each designated body region. In addition, there was no difference in the overall timing of body moult between age classes in American Redstarts; moult started in early July and lasted until mid-August. In contrast, Hatch Year Yellow Warblers started body moult in late June to early July, whereas adults began body moult in mid-July. Both American Redstarts and Yellow Warblers displayed differences in intensity and timing of moult among specific body regions between age classes. In addition, After Hatch Year individuals of both species underwent body moult concurrently with primary moult. External factors (e.g., food availability and geographical distribution), and internal factors (e.g., physiological status) may contribute to the variations in body moult scheduling observed in these two species.

Introduction

Moult plays an important role in the life cycle of birds because feathers have multiple functions, such as display during courtship (e.g., Beehler 1983), thermoregulation (Schieltz and Murphy 1997), and prevention of dermal parasites (Post and Enders 1970). Most importantly, birds must replace their feathers before wearing impedes flight (Ginn and Melville 1983). However, moult is a major undertaking that consumes large amounts of energy and protein reserves for both feather production, and compensation for the effects of poorer insulation and decreased flight efficiency (Dolnik and Gavrilov 1979, Murphy and King 1991, 1992). In order to maximize efficiency, birds typically schedule moult during times when food is abundant, and to avoid undue overlap with other energetically demanding activities, such as reproduction and migration (Payne 1972). For example, Samson (1976) found that although moult overlapped with the end of the breeding season in Cassin's Finch (*Carpodacus cassinni*) during years where conditions were favorable for breeding, it did not overlap with migration. In addition, Hahn et al. (1992) suggested that the timing and rate of prebasic moult could be fine-tuned in response to various environmental factors including day length, food availability, temperature, and social cues, such as parental behaviour, and inter- and intra-sexual interactions.

Most birds typically replace all of their feathers at least once a year, but many feathers groups may be replaced more frequently per year due to wear or change in function, such as display or camouflage (Ginn and Melville 1983). In many North American migratory passerines, the basic plumage, often duller in appearance than the alternate (or nuptial) plumage, is displayed throughout non-breeding periods. Consequently the prebasic moult of many adult passerines (also known as After Hatch Year: AHY), including wood-warblers that have only one plumage per cycle, is performed in the fall between breeding and migration to attain the basic plumage (Humphrey and Parkes 1959). In contrast, Hatch Year (HY) birds first grow a juvenal plumage in the nest, with body feathers typically being weaker and looser in texture than the basic plumage. The flight and tail feathers from juvenal plumage are typically retained during the first prebasic moult in HY birds (Ginn and Melville 1983). Consequently, HY birds attain their winter plumage through a first prebasic moult, which is considered to be partial moult because it only replaces certain feather groups (Pyle 1997).

Wing primary feather moult is typically scored with a system that ranks each feather on a scale; 0 being an old feather, 1 – 4 are growing feathers at specific stages, and 5 being a fully grown new feather (Newton 1966, Ginn and Melville 1983). On the other hand, there is no standard method for scoring body moult and various methods have been used to study body moult patterns and trends. For example, Niles (1972) scored body moult in Purple Martins (*Progne subis*) on a scale of 0 – 2 by the proportion of actively moulting feathers in each region. Similarly, Yuri and Rohwer (1997) used a proportion technique to score body moult for each assigned region in Northern Rough-winged Swallows (*Stelgidopteryx serripennis*); however, they ranked moult on scale of 0 – 4. These inconsistencies may cause difficulties when comparing body moult between species and a goal of future study of body moult should be to adopt a standard, reliable method to record its progress.

MOULT IN WOOD-WARBLERS

Wood-warblers belong to the family Parulidae (except the Olive Warbler, *Peucedramus taeniatus*, of the family Peucedramidae; Dunn and Garrett 1997).

They are small, primarily insectivorous songbirds that forage and breed in various habitats throughout North America. Most wood-warblers are long distance migrants, traveling thousands of kilometers twice a year between their breeding grounds in North America and wintering grounds as far as South America (Dunn and Garrett 1997). There are about 115 species of wood-warblers, of which approximately 37 species are found in Ontario (Hughes 2001).

Most species of North American migratory wood-warblers share prebasic moult patterns and plumage sequences that follow a similar feather loss and replacement regime (Dunn and Garrett 1997). Typically, adult warblers (AHY) undergo a complete prebasic moult, replacing nearly all feathers while still on the breeding grounds prior to fall migration. On the other hand, HY warblers typically undergo a partial, first prebasic moult, replacing only the contour feathers covering the body and most of the wing coverts.

After breeding, most warblers prepare for their long distance flight to wintering grounds by increasing their nutritional intake and moulting prior to migration (Dunn and Garrett 1997). However, Woodrey and Chandler (1997) suggested that, in some species of warblers, moult could delay the departure of adults from the breeding grounds by several days; therefore, timing of moult should play a critical role in scheduling migration to minimize the energetic demands. Although HY warblers do not moult as extensively as AHYs, preparations for migration, including moult, may be limited by the timing of fledging. Examining the differences in body moult patterns and scheduling between HY and AHY warblers will allow a better understanding of its timing and rate in relation to breeding and migration for species found throughout Ontario and eastern North America.

Materials and Methods

STUDY AREAS

Moult data were obtained for American Redstarts (*Setophaga ruticilla*) captured at Thunder Cape Bird Observatory (TCBO) and Yellow Warblers (*Dendroica petechia*) captured at Innis Point Bird Observatory (IPBO). TCBO is situated at the tip of the Sibley Peninsula, on the Northwest shore of Lake Superior, approximately 80 km from Thunder Bay, Ontario (48° 18'04", 88° 56'18"; Fig. 3.1). The area is predominantly forested, consisting mostly of coniferous trees and shrubs, providing suitable habitat for most boreal breeding birds including several warbler species, such as the Nashville Warbler (*Vermivora ruficapilla*), Black-throated green Warbler (*Dendroica virens*), and Mourning Warbler (*Oporornis philadelphia*).

IPBO is located approximately 12 km from Ottawa, Ontario (45°22'55", 75°53'30"; Fig. 3.2). Situated near Shirley's Bay on the property of the Department of National Defense along the southwestern bank of the Ottawa River, the surrounding habitat provides ideal breeding grounds for numerous warbler species, such as the Black-and-White Warbler (*Mniotilta varia*), and

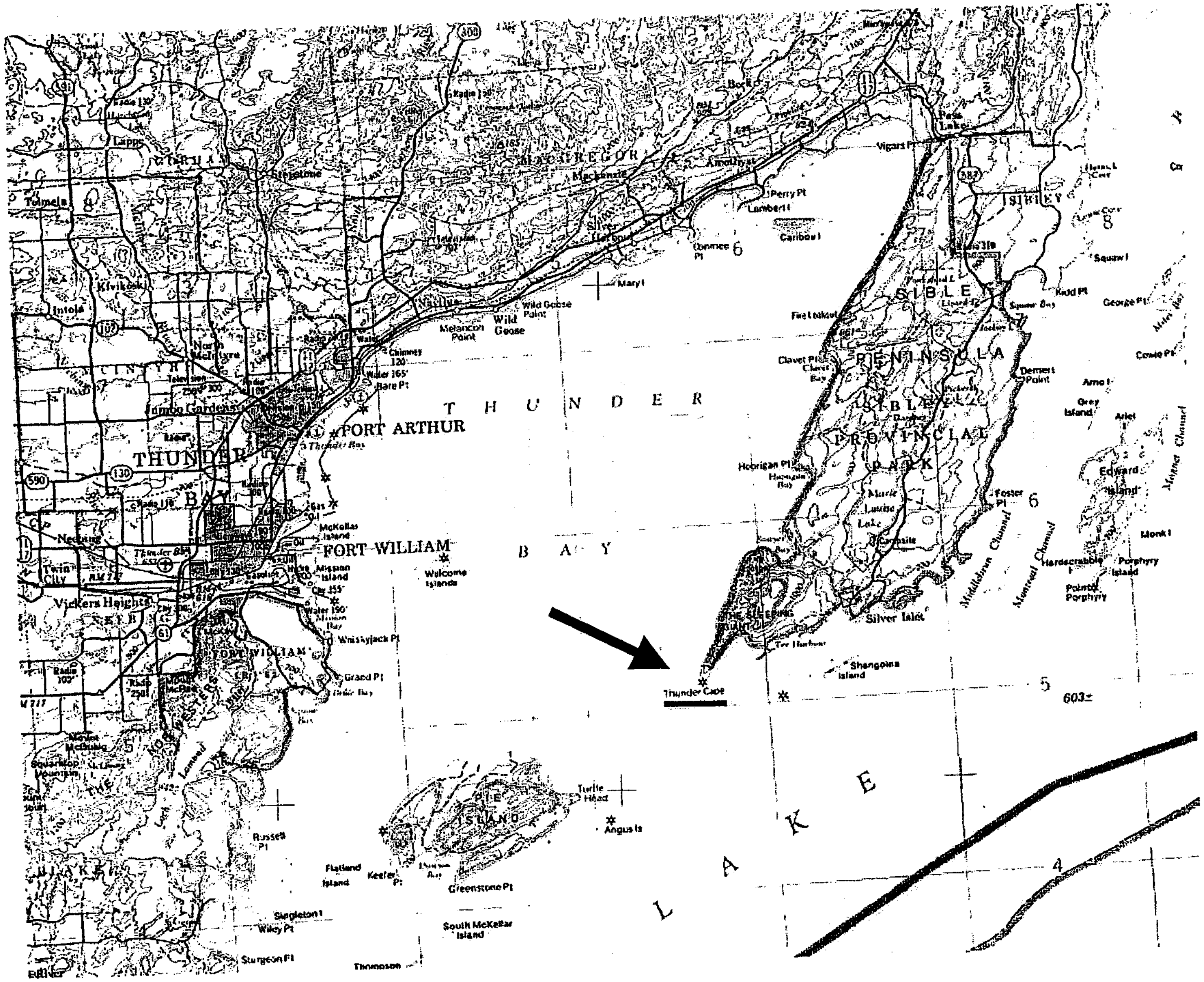


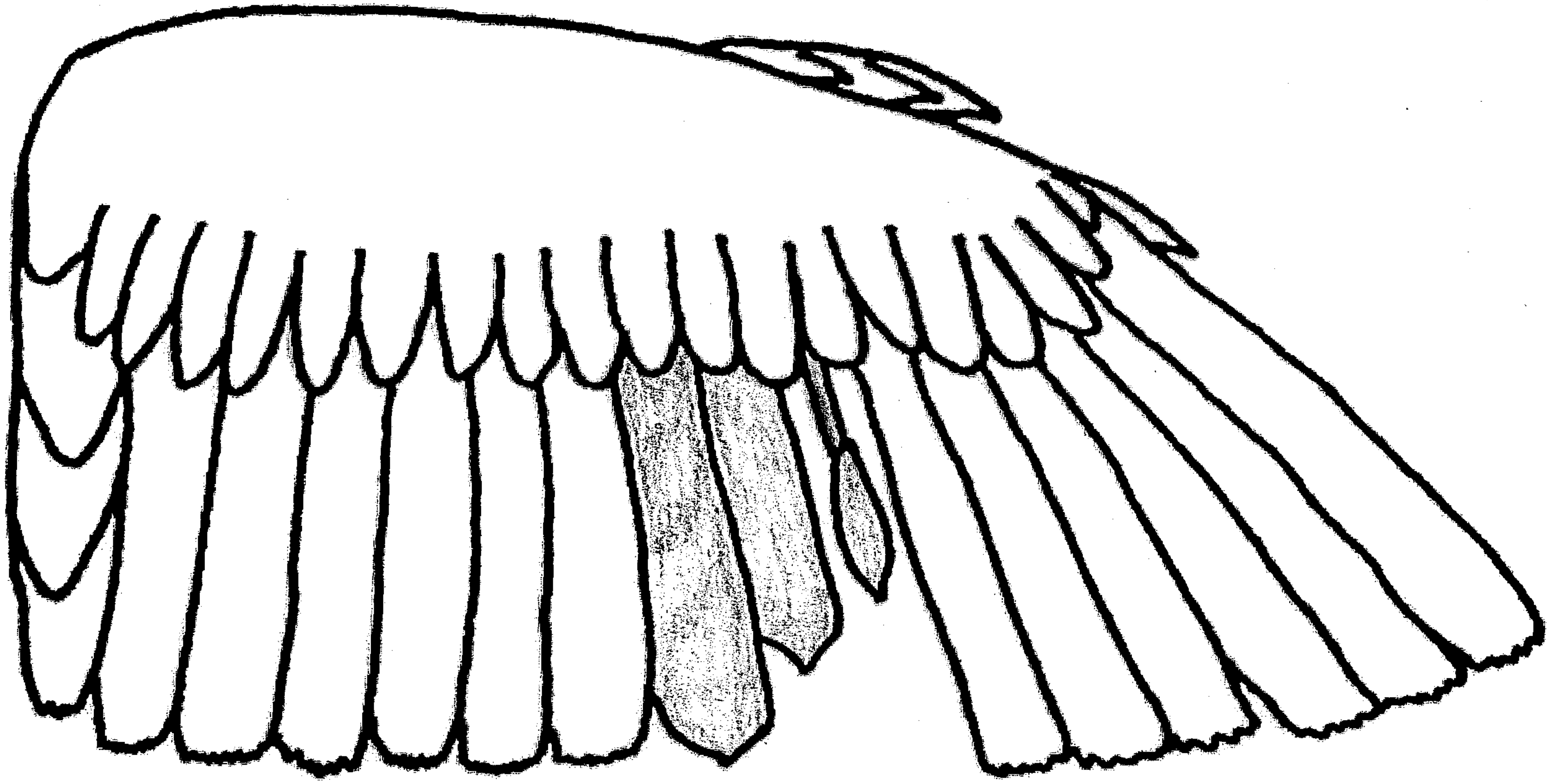
Fig. 3.1. Location of Thunder Cape Bird Observatory, Ontario, Canada.

Fig. 3.2. Location of Innis Point Bird Observatory, Ontario, Canada.

Common Yellowthroat (*Geothlypis trichas*). In addition to supplying breeding habitat, both sites are known to be major stopover areas for migrating warblers, and allow birds to rest and replenish fat reserves along their migration route. These attributes confer that both locations are ideal for monitoring warbler migration, providing ample numbers to be examined during the course of this study.

FIELD PROCEDURES

A total of 187 individuals were captured from July to October – throughout their moult and migration periods – using mist nests with mesh size of 30mm (1 1/4 inch) and Heligoland traps according to TCBO and IPBO standard protocols. Primary feather moult data for After Hatch Year (AHY) were obtained according to Newton (1966) and Ginn and Melville (1983), with feathers scored on a scale of 0 to 5. Using their methods, old feathers are scored as 0; missing or in pin (completely in the feather sheath) as 1; feather out of pin to 1/3 full grown as 2; 1/3 to 2/3 full grown as 3; greater than 2/3 full grown with sheath present as 4; full-grown new feather with no sheath as 5. Each feather is scored independently, after which total score is summed for primary feathers for each wing (Fig. 3.3). Vestigial primary number 10 was excluded from the primary moult score (Rimmer 1988); therefore, the potential moult score for all individuals ranged from 0 (no moult) to 45 (primary moult complete).



Primary Score = 5 + 4 + 3 = 12

Fig. 3.3. Description of the method for estimating the primary score (new feathers represented by shading; after Bensch and Grahn 1993).

Body moult data for AHY and Hatch Year (HY) warblers were also obtained for five body regions (crown, back, belly, upper tail coverts, and under tail coverts) using standard moult scores according to Ginn and Melville (1983), with the exception of scoring moult for each region when at least 50% of the feathers observed to be moulting at a particular score ranging from 0 to 5. Total body moult for each individual was determined by summing the moult scores for all body regions. Consequently, body moult scores ranged from 0 to 25.

Moult data was recorded for the right wing and right side of body only, unless the moult was obviously asymmetrical, in which case both sides were recorded. To get a representative sample of the population, primary feather and body moult scores were calculated on all birds captured (or on a random sample if large numbers were captured), whether they were moulting or not (D. J. T. Hussell, pers. comm.).

AHY warblers were differentiated from HY warblers by plumage and skulling methods, with AHYs having fully ossified skulls and HYs ranging on a scale of 0 to 3. In addition, the sexes were distinguished by plumage characteristics or wing chord length (Pyle 1997). The data was pooled for each species across all years to increase sample sizes (e.g., Foster 1967, Sealy 1979, Voelker and Rohwer 1998).

STATISTICAL ANALYSES

Log-linear models with G-tests using Williams' correction (Sokal and Rohlf 1995) were used to analyze the relationship of moult scores among body regions between HY and AHY warblers with respect to time captured (Yuri and Rohwer 1997). For American Redstarts, capture dates were categorized into three consecutive 17-day blocks. In addition, moult scores were grouped into five classes (0-20%, 40%, 60%, 80%, and moult complete) to satisfy samples size requirements of log-linear models (Sokal and Rohlf 1995). Similarly, capture dates for Yellow Warblers were divided into three consecutive 16-day blocks. However, due to an unequal ratio of moult scores among body regions, moult scores were categorized into only three group classes (0-60%, 80%, and moult complete) for the same statistical reasoning as above.

Three-way analyses of covariance (ANCOVA; Sokal and Rohlf 1995) — using total body moult score as dependant variable, age as independent variable, and date captured as the covariate — were performed to test for differences in timing of body moult, for all body regions combined, within the determined moult period between HYs and AHYs for American Redstarts and Yellow Warblers. A bivariate correlation was performed on AHY warblers to examine the relationship between body moult and primary moult. Using this test, a significant, positive correlation would indicate that body moult occurs throughout the same moult period as primary moult. All tests used SPSS (Version 10.07a) for Macintosh (SPSS Inc. 2000), with a significance level of $p<0.05$.

Results

There was no difference in the number of moulting individuals in each body region for HY and AHY American Redstarts analyzed together or separately (HY: G_{adj}=4.5434, df=8, p>0.75; AHY: G_{adj}=4.7743, df=8, p>0.75; AHY and HY: G_{adj}=5.242 df=8, p>0.50). Body moult in all regions occurred from mid-July through early September (Fig. 3.4). Additionally, Yellow Warblers displayed no difference in the number of moulting individuals in each body region with respect to time (HY: G_{adj}=0.197, df=8, p>0.999; AHY: G_{adj}=1.521, df=8, p>0.99; AHY and HY: G_{adj}=0.5195, df= 8, p>0.995). Moult occurred in this species from early July through mid-August for all body regions (Fig. 3.5).

Analyses of the effect of age, with the total body moult score held constant as a covariate, indicated no difference in the timing of moult, within the given moult period, for American Redstarts (F=0.965, p=0.329, *n*=94; Fig. 3.6). In contrast, there was a difference in the timing of moult within the established moult period between age classes of Yellow Warblers (F=6.517, p=0.014, *n*=50). HY Yellow Warblers began body moult, on average, earlier than AHY individuals (Fig. 3.7).

Despite similarities in the timing of moult among body regions in American Redstarts, moult scores in each body region differed between HYs and AHYs (G_{adj}=79.1683, df=16, p<0.001). In particular, there was a large difference in moult scores in the under tail covert region between the age classes (Fig. 3.8).

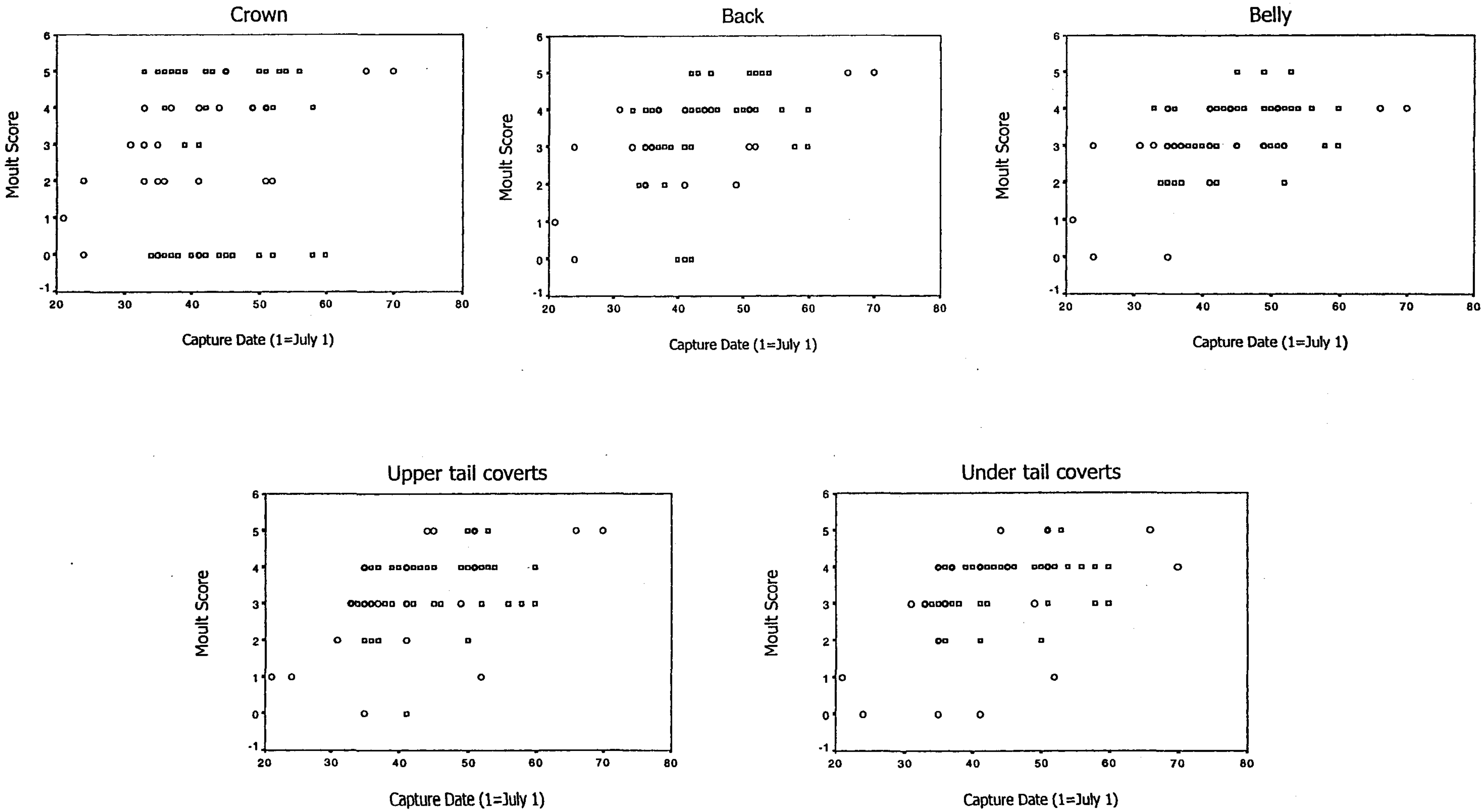
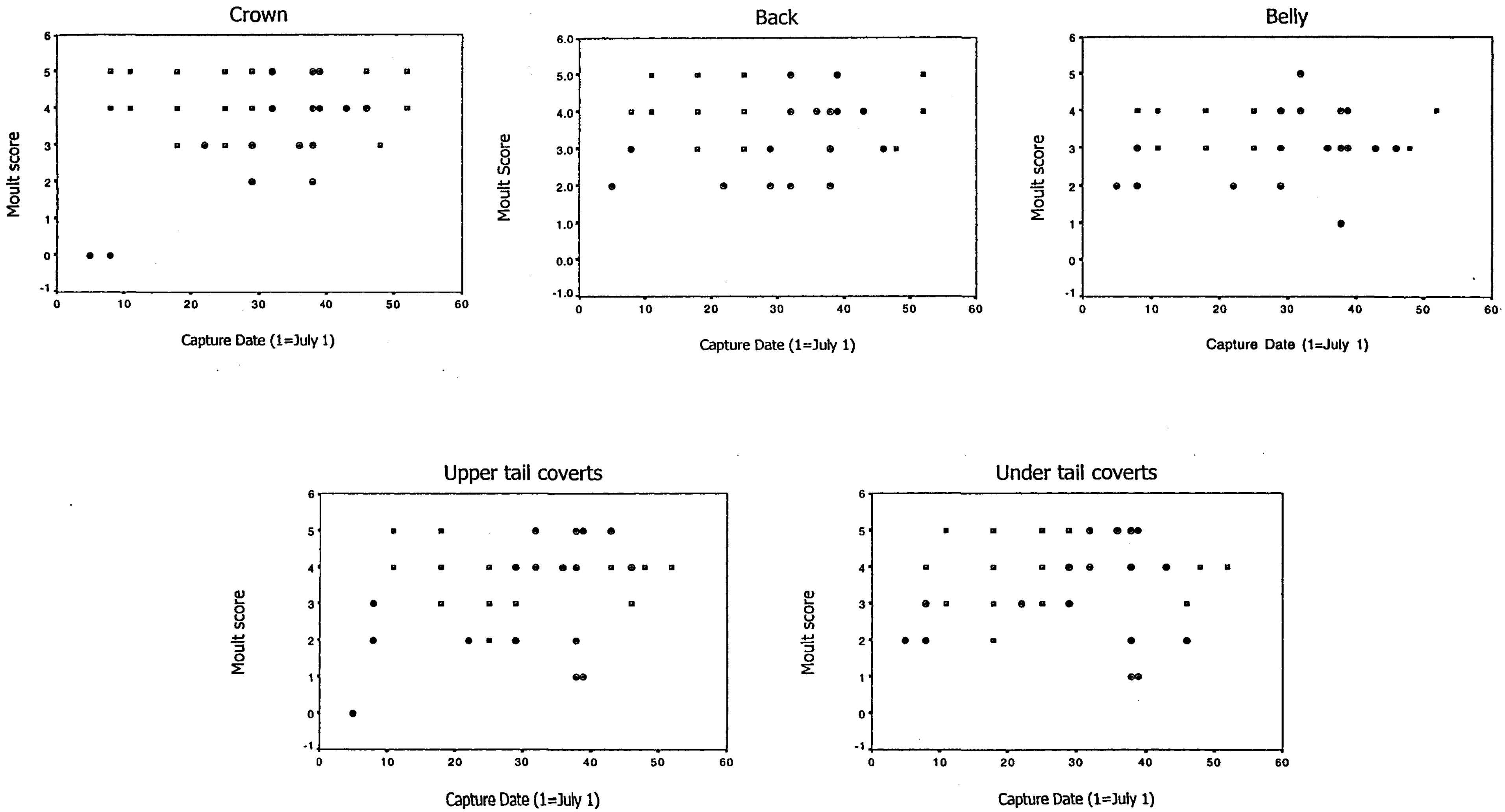


Fig. 3.4. Relationship between moult scores and capture date for each body region in HY (☐) and AHY (○) American Redstarts at TCBO.



Crown

Back

Belly

Upper tail coverts

Under tail coverts

Fig. 3.5. Relationship between moult score and capture date for each body region in HY (⊡) and AHY (⊙) Yellow Warblers at IPBO.

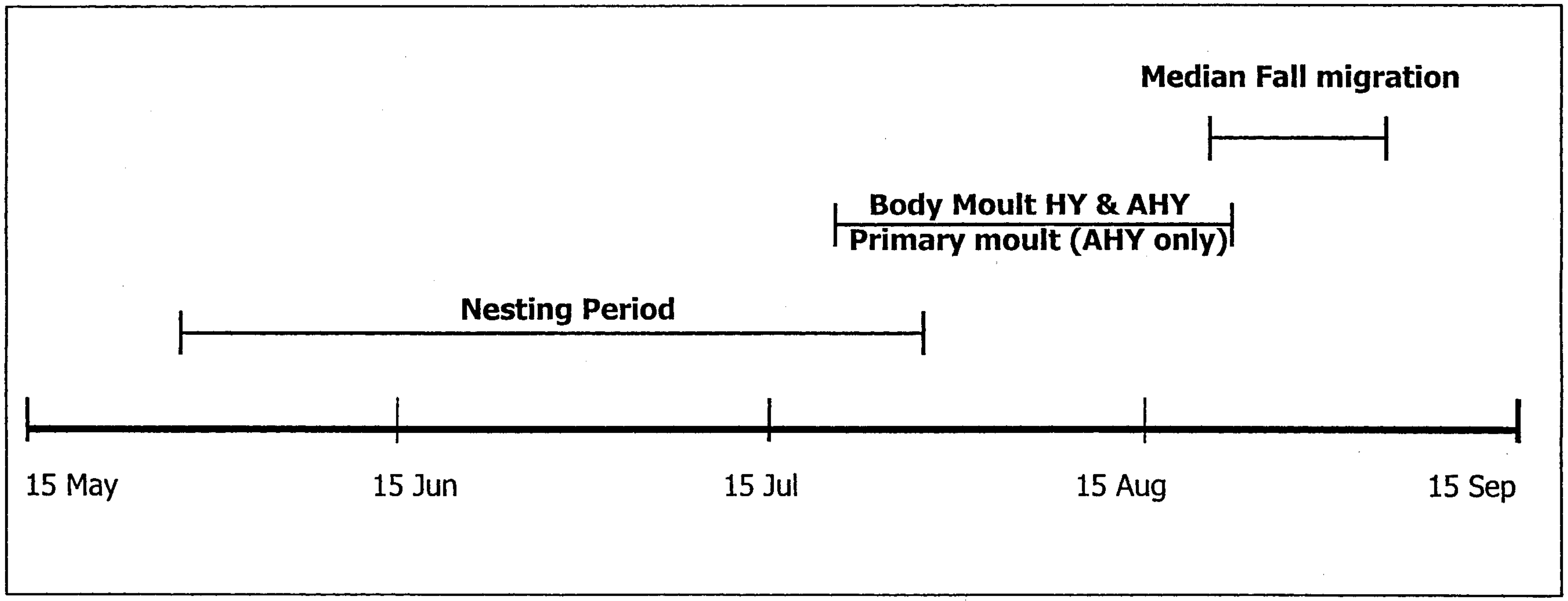


Fig. 3.6. Temporal distribution of nesting, moult, and migration periods for HY and AHY American Redstarts at TCBO.

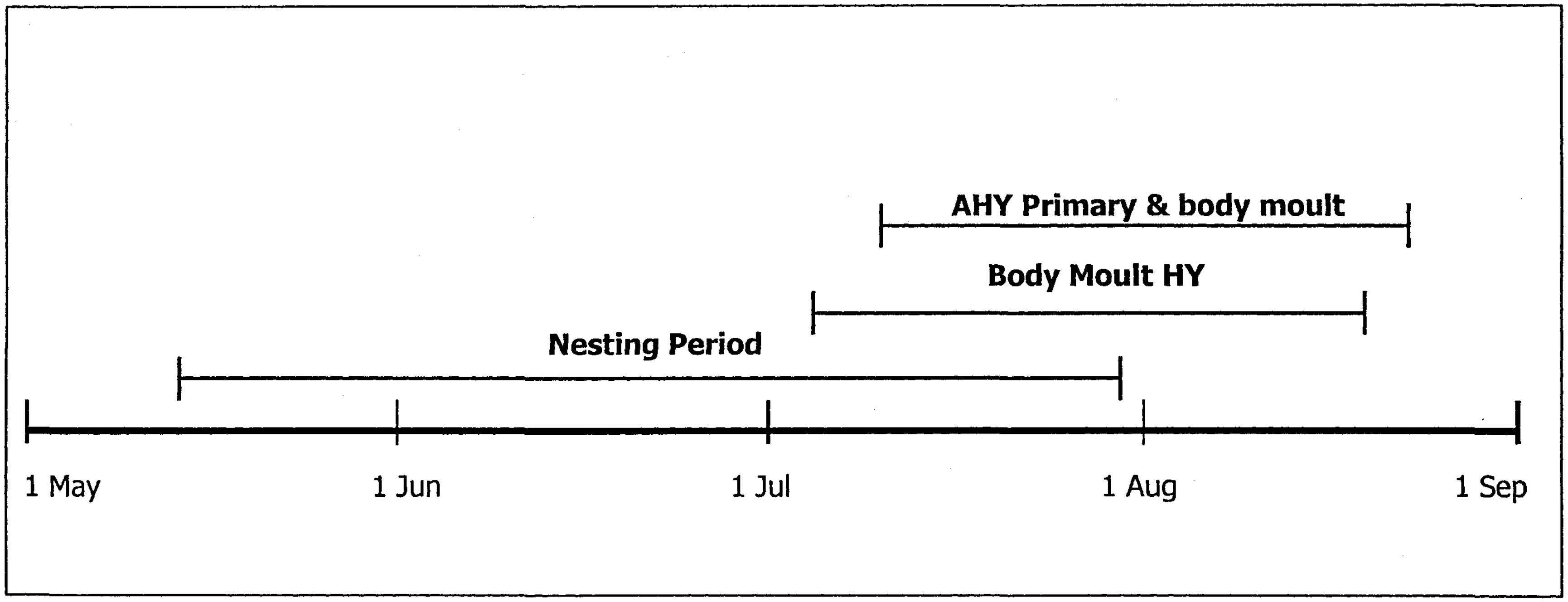


Fig. 3.7. Temporal distribution of nesting and moult periods for HY and AHY Yellow Warblers at IPBO.

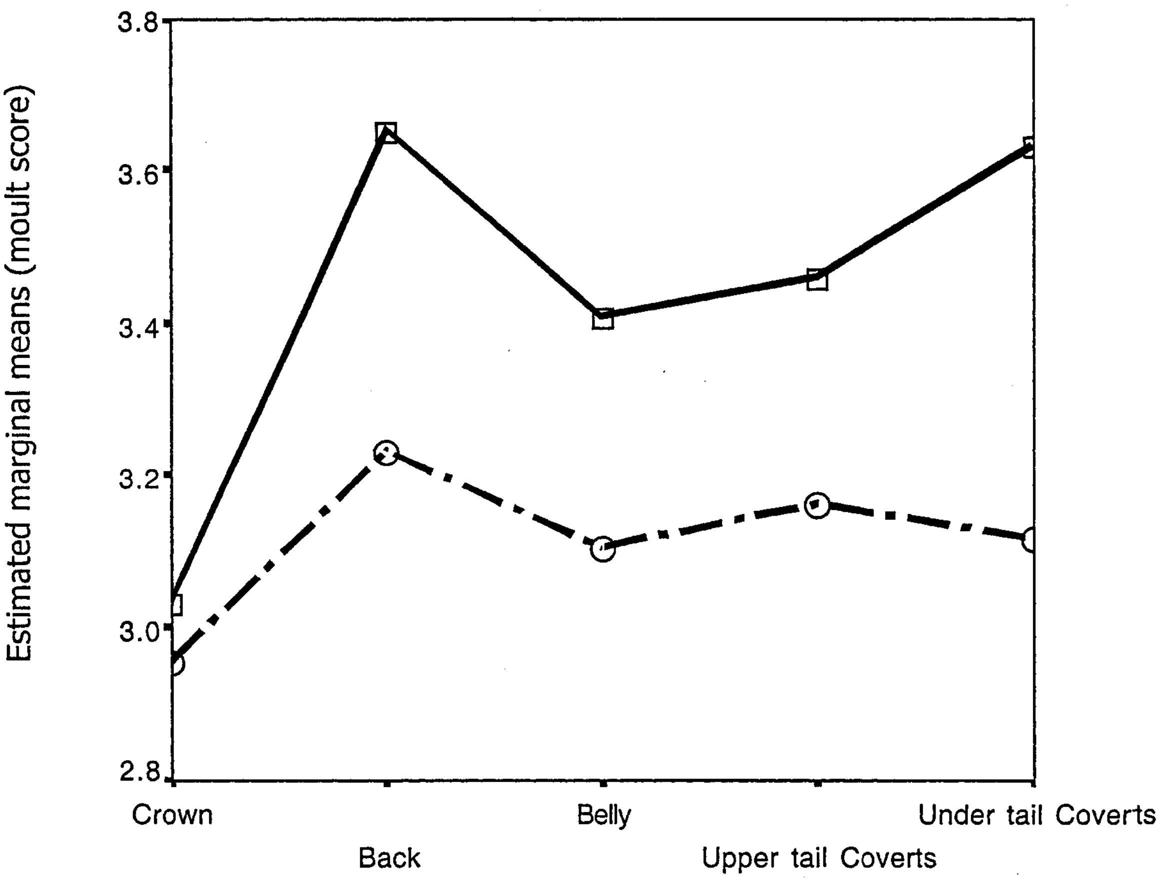


Fig. 3.8. Estimated marginal mean moult scores among body regions between HY (□) and AHY (O) American Redstarts at TCBO.

Similarly, moult scores in each body region differed between age classes in Yellow Warblers (G_{adj}=16.494, df=8, $p<0.05$). For example, moult scores differed greatly in the crown and back regions between age classes of this species (Fig. 3.9).

Both species displayed differences in moult scores with respect to time between HY and AHY individuals (American Redstarts: G_{adj}=42.136, df=8, $p<0.001$; Yellow Warblers G_{adj}=17.7389, df=4, $p<0.005$). There was a large difference in moult scores between age classes in the time period extending from August 25 to September 10 for American Redstarts. The estimated marginal mean moult score for AHY American Redstarts was 4.6, whereas HYs had an estimated marginal mean moult score of 3.2 during that time period. In addition, body moult in HY birds peaked in early August. For AHY individuals, however, it increased somewhat linearly with time (Fig. 3.10). In contrast, moult scores differed greatly between age classes of Yellow Warblers from July 5 to July 21. The estimated marginal mean moult score for AHY Yellow Warblers was 3.0, whereas HYs had an estimated marginal mean moult score of 3.9 for that time period. Body moult in HY Yellow Warblers decreased slightly from July 22 through to August 6, but AHY Yellow Warblers showed a similar linear increase in body moult with time as did American Redstarts (Fig. 3.11).

Among adults, there was a strong positive correlation between body moult and primary moult for both species (American Redstarts: $r=0.955$, $p=0.001$,

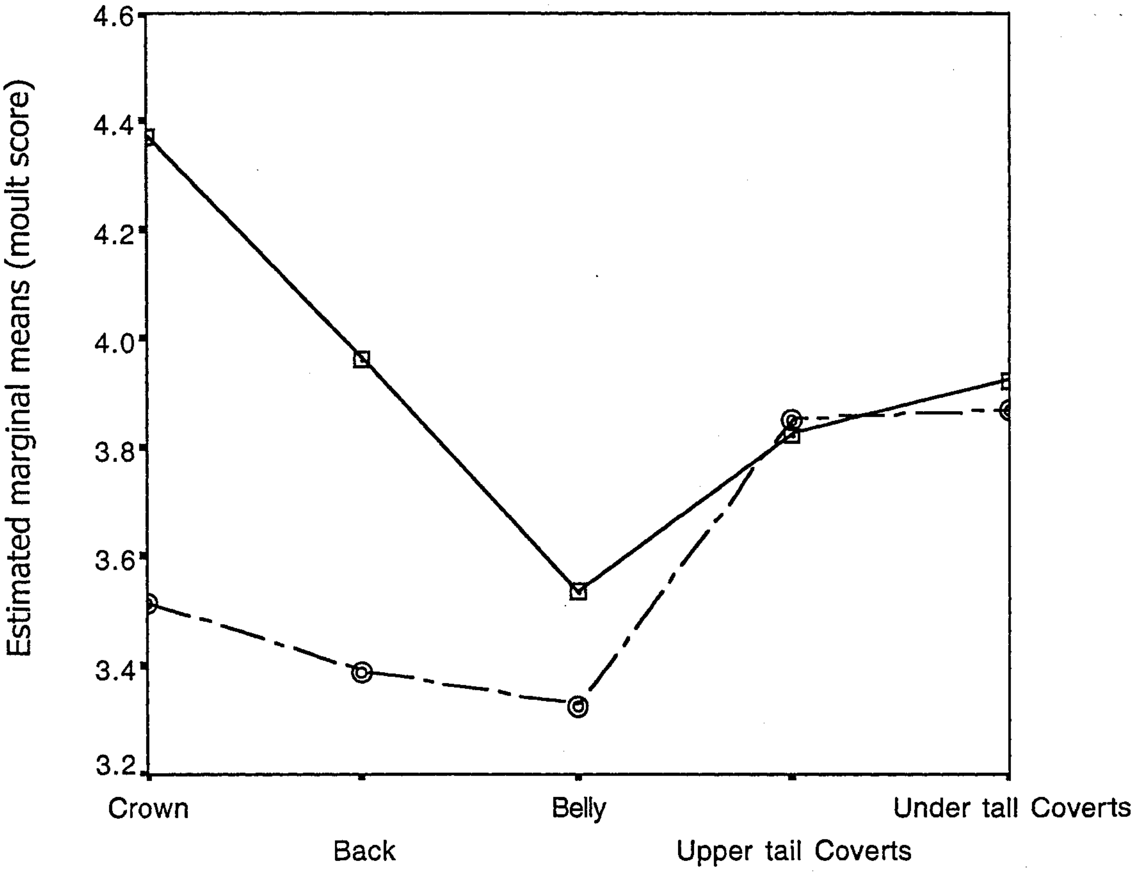


Fig. 3.9. Estimated marginal mean moult scores among body regions for HY (⊡) and AHY (◎) Yellow Warblers at IPBO.

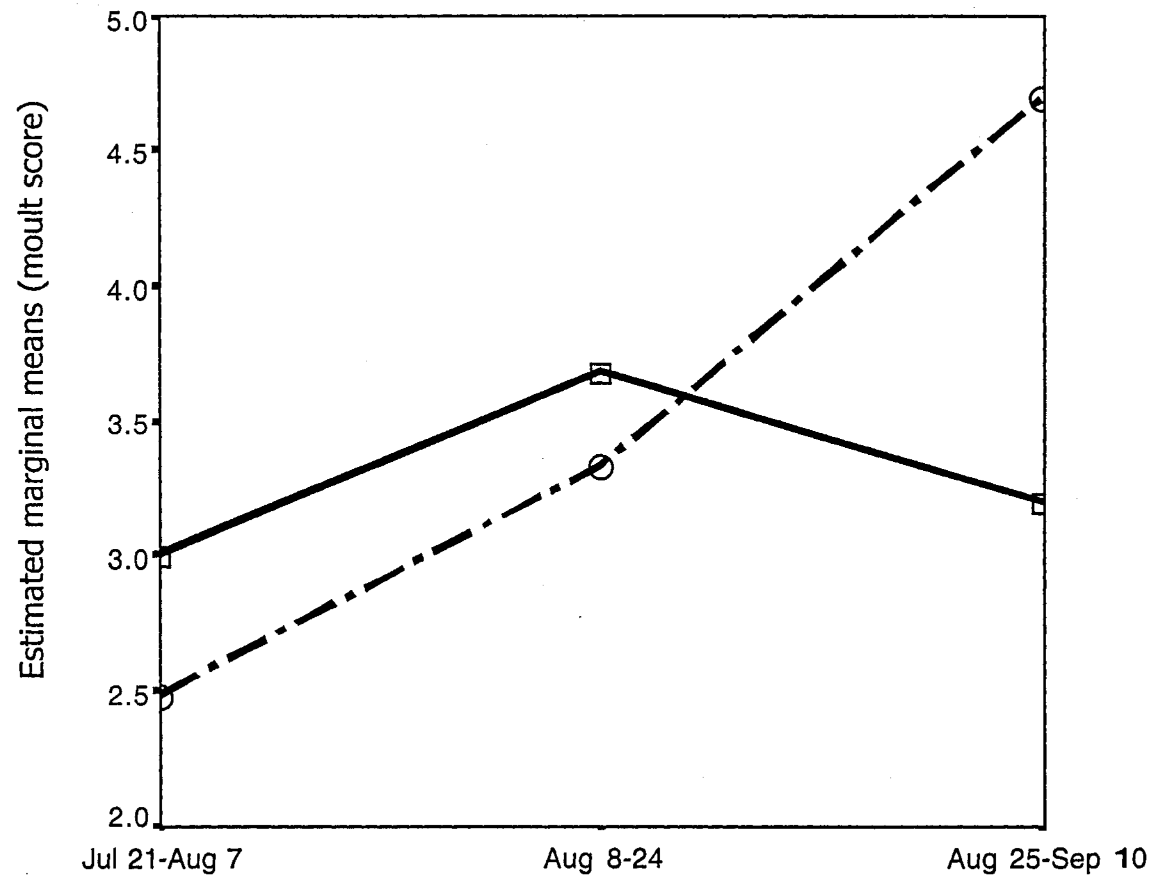


Fig. 3.10. Estimated marginal mean moult scores among time periods for HY (☐) and AHY (○) American Redstarts at TCBO.

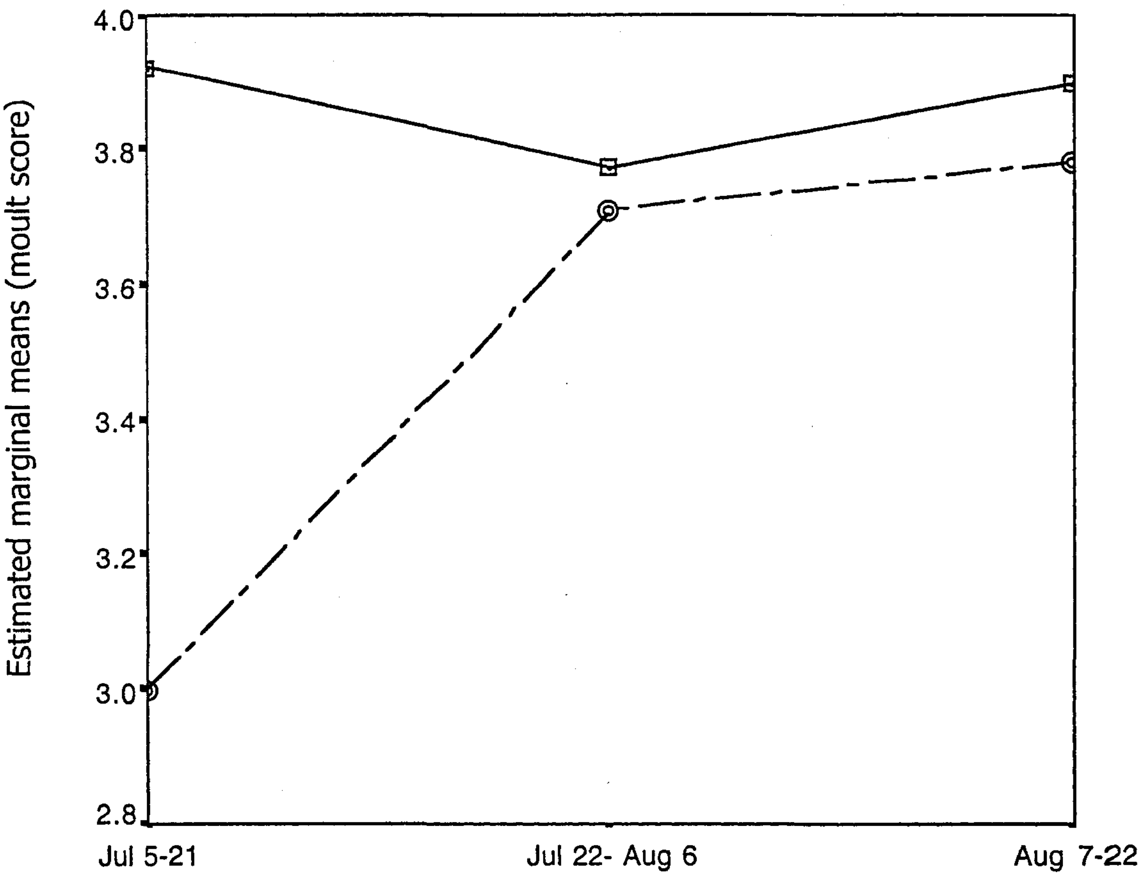


Fig. 3.11. Estimated marginal mean moult scores among time periods for HY (☐) and AHY (◎) Yellow Warblers at IPBO.

n=28; Yellow Warblers: r=0.922, p=0.001, *n*=26). Body moult occurred at approximately the same time as primary moult in both species (American Redstarts: 22 Jul to 22 Aug; Yellow Warblers: 13 Jul to 7 Aug; C. A. Debruyne et al. ms; see chapter 1; Figs. 3.12, 3.13).

Discussion

Ginn and Melville (1983) emphasized the need to examine body moult because body feathers account for more than half of the feather mass of a bird. Consequently, their replacement may lead to a greater overall energetic requirement than the moult of the flight feathers of the wing and tail. Moreover, the chronology and patterns of body moult for most North American wood-warblers has been insufficiently examined. This study compared various features of moult, such as the timing of the prebasic body moult, between age classes of two warbler species found at two locations in Ontario.

SCHEDULING OF MOULT

Moult must be precisely timed to ensure minimum energetic losses while still proving to be adequately efficient to prepare for fall migration. Moreover, a bird's annual cycle must be structured to optimally fulfill its reproductive, migratory, and moult requirements. Factors such as the timing of spring arrival on the breeding grounds for AHY warblers will set the timeline required to fulfill

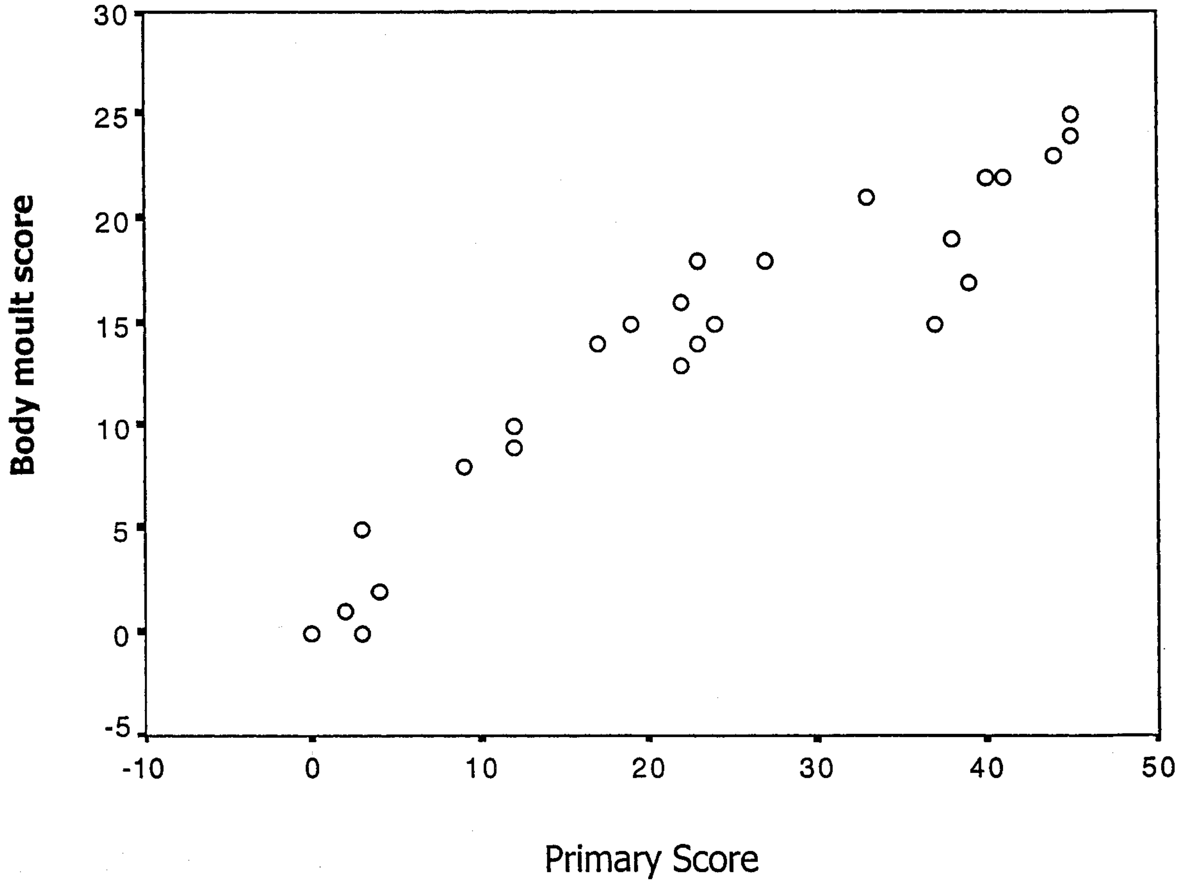


Fig. 3.12. Relationship between total body score and primary score in AHY (O) American Redstarts at TCBO.

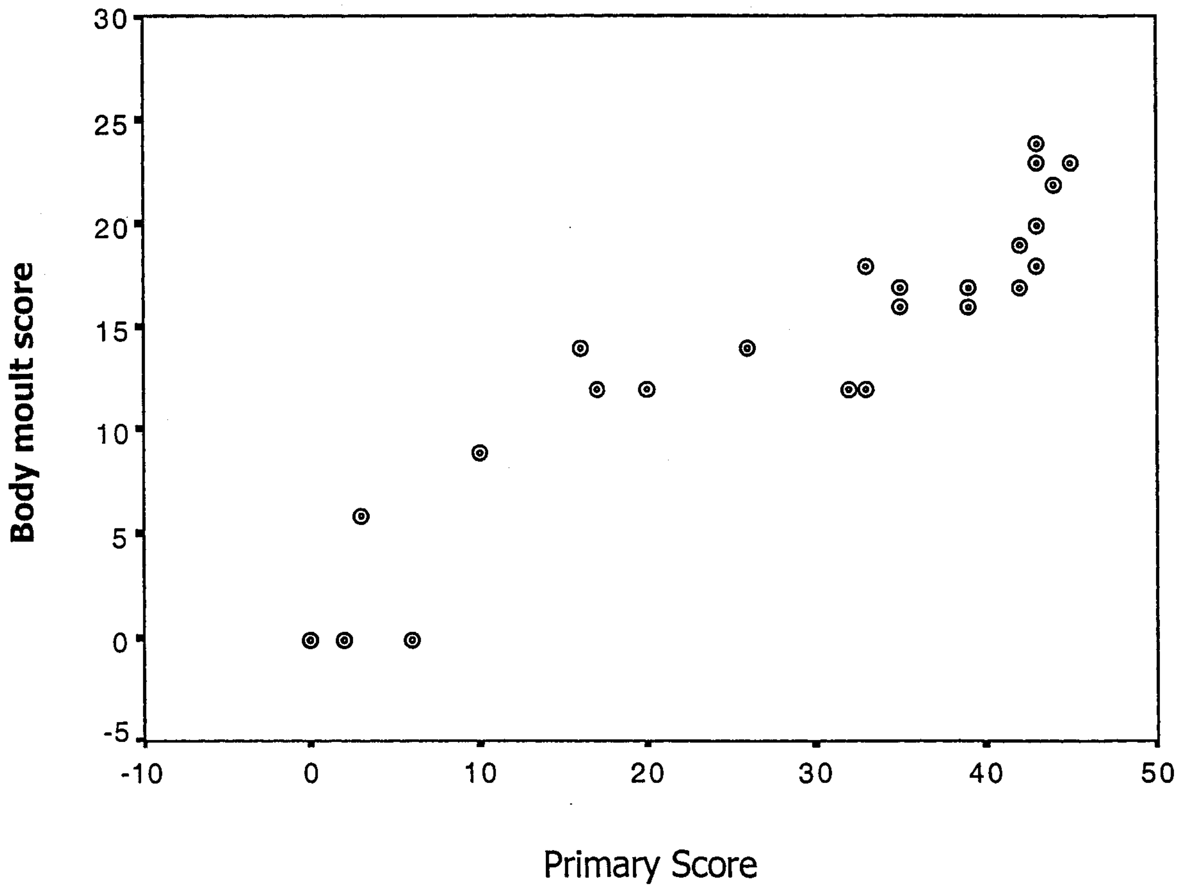


Fig. 3.13. Relationship between total body score and primary score in AHY (⊚) Yellow Warblers at IPBO.

all of the tasks associated with breeding and raising young. On the other hand, the timeline of moult for HY birds is probably established by their hatch dates, with factors, such as the amount of nutritional provisions from adults at the nest, determining the optimal physiological conditions for moult.

I found that body moult for both HY and AHY American Redstarts occurred at the same time for all body regions from mid-July through early September. Similarly, Jackson et. al. (1992) found that both Hermit and Townsend's Warblers displayed no differences in the timing of body moult between age groups. In addition, Northern Rough-winged Swallows (Yuri and Rohwer 1997), Purple Martins (Niles 1972), Reed Buntings (*Emberiza schoeniclus*; Bell 1970), and Andean Sparrows (*Zonotrichia capensis*; Miller 1961) also showed no differences between timing of body moult between juvenile and adult birds.

Furthermore, my findings are consistent with nest records for American Redstarts in Ontario that ranged from the end of May through to the end of July, peaking in mid-June (Peck and James 1987), which suggest that HY birds typically undergo prebasic moult soon after they have fledged the nest. Likewise, HY Golden-winged Warblers (*Vermivora chrysoptera*; Faxon 1911) and HY Orange-crowned Warblers (*Vermivora celata*; Foster 1967) were found to begin prebasic moult within one month of leaving the nest.

In addition, my findings indicate that the onset of body moult in AHY American Redstarts may overlap with the end of the breeding period –

particularly during the time young leave the nest – which suggests that adult birds have sufficient energetic requirements to complete their parental duties concurrently with the onset of moult. Vega Rivera et al. (1998) suggested that the Wood Thrush (*Hylocichla mustelina*) are able to overlap moult with fledgling care because their young are relatively independent at this time and could, therefore, procure some of their own food; thus, reducing parental demands. Furthermore, Bent (1953) noted that American Redstarts consume berries and fruits in addition to their insectivorous diet in late summer, which may provide additional nutrients needed to fulfill the energetic requirements of moult while caring for young.

Although the total number of Yellow Warblers of each age group moulting in each body region was similar to that of American Redstarts, AHY Yellow Warblers began moult later than HY individuals; with body moult in HY Yellow Warblers likely beginning in late June to early July. Moreover, nest record dates in Ontario for Yellow Warblers ranged from mid-May through the end of July, peaking during the first two weeks in June (Peck and James 1987), suggesting that HY birds may begin body moult while still in the nest. This is consistent with Stewart (1952) who found that the final stages of juvenal feather growth overlapped slightly with the onset of the first prebasic moult in HY Common Yellowthroats (*Geothlypis trichas*). This suggests that birds with an early prebasic moult relative to their dates of births spend little time in juvenal plumage. However, the scheduling of body moult may vary geographically. For example, King (1972) found that the prebasic moult of HY Rufous-collared Sparrows (*Zonotrichia capensis*) began approximately five days after completion of juvenal plumage in Columbia, but noted that HY birds from Argentinean populations started prebasic moult a few months after fledging. Furthermore, the timing of prebasic moult in HY birds may be dependent on their hatch dates. Newton (1966) noted that juvenile Bullfinches (*Pyrrhula pyrrhula*), which hatched late in the breeding season, began prebasic moult a few days after leaving the nest only having nearly completed juvenile plumage growth, compared to juvenile Bullfinches that hatched at an earlier date. He concluded that even if later birds retained juvenile feathers, instead of replacing them quickly, the energetic benefits would be trivial since juvenile feathers weigh very little.

Factors such as the energetic requirements of parental duties during the breeding period might delay the onset of body moult in AHY Yellow Warblers so both processes do not greatly overlap. Although Rimmer (1988) found that the prebasic moult of adult Yellow Warblers in the James Bay region, Ontario typically overlapped with breeding, it was primarily during the fledgling stage when the time and energetic demands of parental care were decreasing substantially.

INTENSITY OF MOULT

Although body moult occurred at the same time for HY and AHY American Redstarts at TCBO, the intensity of moult in each region differed between the age classes, with HY birds displaying a more intense moult overall particularly in the undertail covert region. Yellow Warblers at IPBO also displayed differences in moult scores between HY and AHY among body regions, with HY birds having, on average, higher moult scores in all body regions particularly on the head and back. Similarly, Stewart (1952) found differences in moult sequences among feather tracts between HY and AHY Common Yellowthroats, particularly in the ventral, caudal, and alar feather tracts. Likewise, Yuri and Rohwer (1997) found differences in intensity of moult among body regions for Eastern Rough-winged Swallows, with juveniles moulting fewer crown and chin feathers overall. They suggested that this might be because Rough-winged Swallows undergo a partial spring moult that is limited almost entirely to feathers of those regions. In addition, Hubbard (1980) noted similarities in moult patterns between the first prebasic and the prealternate moult in Yellow-rumped Warblers, which suggests that HY warblers may balance feather replacement in specific body regions by changing moult intensities with each moult period. However, the prealternate moult may be more variable among parulids than the other moult periods (Foster 1967). Therefore, the prealternate moult patterns may not necessarily explain variations in moult intensity observed in the two warbler species that I examined.

Furthermore, the progression of body moult differed between age classes for both American Redstarts and Yellow Warblers. Body moult scores for American Redstarts greatly differed between HY and AHY individuals during the August 25 to September 10 time period, whereas, for Yellow Warblers differences in moult scores between HY and AHY birds were observed from July 10 to July 21. These findings may be associated with the overall scheduling of body moult seen for each species. Similar scheduling of body moult for HY and AHY American Redstarts could explain similarities in moult intensity during the first month of the moult period. In addition, observed differences towards the end of the moult period might be due to an increase in moult intensity in AHY birds since breeding duties have terminated, allowing for more energy to be allocated to the moulting process.

Similarly, differences in body moult schedules in Yellow Warblers could explain differences in moult intensity over time. Although body moult may overlap slightly with the end of the breeding period in AHY birds, they may compensate with a less intensive moult during this period. Hahn et al. (1992) indicated that the timing and rate of prebasic moult in birds could be adjusted in response to environmental cues such as nutritional resource availability. In White-crowned Sparrows (*Zonotrichia leucophrys*), for example, the intensity of feather replacement varied throughout the moult process in concordance to nutritional availability (Murphy and King 1984a, b).

BODY MOULT IN RELATION TO PRIMARY MOULT IN AHY BIRDS

Body moult occurred during the same time period as the primary moult for both AHY American Redstarts and Yellow Warblers. Rimmer (1988) also determined that body moult progressed concurrently with the period of flight feather moult in Yellow Warblers. Similarly, Nolan (1978) found concurrent body moult in specific feather tracts, such as the dorsal and sternal regions, during primary moult in Prairie Warblers (*Dendroica discolor*) in the southern United States. These findings suggest that warblers can undergo moult in all of these regions concomitantly. Both physiological and behavioural changes in warblers might occur to minimize the energetic costs of moult. For example, studies have demonstrated increases in metabolic rates during moult (e.g., Koch and deBont 1944, Wallgren 1954, Lindström et. al. 1993), but have suggested factors such as diet and body mass may also need to be accountable when calculating the energetic costs of feather synthesis. In addition, Newton (1966) found that moulting Bullfinches were less active and rested most of the day, and suggested they did so to conserve energy. Likewise, Ginn and Melville (1983) noted that passerines tend to be more secretive when moulting. Thus, a combination of behavioural and physiological factors might allow concurrent body and primary moult observed in the Yellow Warblers and American Redstarts.

MOULT IN RELATION TO MIGRATION

The timing of body moult for HY and AHY American Redstarts at TCBO appears to be consistent with the timing of fall migration (median migration date 27 Aug ± 9 days). Additionally, both age classes arrived synchronously at banding stations at LPBO, and at the Allegheny Front Migration Observatory in northern West Virginia (Hall 1981, Woodrey and Chandler 1997). This supports additionally my findings of no age class differences in timing of prebasic moult for this species. Jackson et al. (1992) noted that male Hermit Warblers (*Dendroica occidentalis*) and Townsend's (*Dendroica townsendi*) Warblers complete most of their prebasic moult on their breeding grounds prior to migration, and suggested that their breeding areas provided sufficient food resources to allow birds to moult before departure. Sherry and Holmes (1997) observed that American Redstarts also preferred productive moist woodlands located near water, which might explain similarities in moult scheduling among these species.

On the other hand, both HY and AHY Yellow Warblers at IPBO may begin migrating while undergoing the final stages of body moult. This corresponds with Rimmer (1998) who found that migration peaks in mid-August for HY Yellow Warblers and late August for AHY individuals in the James Bay region; which may, in turn, explain the slightly earlier body moult period in HY birds. Similarly I found that HY Yellow Warblers began moulting in late June to early July and AHYs started in early July. Southern populations of Yellow Warblers appear to migrate earlier than those in the north (Lowther et al. 1999). In addition, Rimmer (1988) noted that the AHY Yellow Warblers in the James Bay region began migrating during the final stages of moult (final stages of growth of last two primaries) and suggested that the energetic costs associated with this incomplete stage of moult were small enough to do so. This may also be the case for the Yellow Warblers at IPBO. Rimmer also found a decrease in body weight of these warblers during the later stages of moult because individuals departed without the typical accumulation of premigratory fat. Consequently, he suggested that migration might be regulated to flight efficiency rather than physiological readiness to adhere to their migration schedule. Further study of the energetics of moult in warblers would provide invaluable information in this regard.

This study provides a foundation for future research of body moult in two wood-warbler species found throughout eastern North America. External factors, including food availability and geographical distribution, and internal factors, such as physiological status, may provide some explanation for body moult scheduling. Continued examination of the many biological and environmental aspects of moult and migration in birds will contribute to a better understanding of body moult patterns in wood-warblers.

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