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NESTING BIOLOGY OF THE YELLOW WARBLER AT THE NORTHERN LIMIT OF ITS RANGE

JAMES V. BRISKIE
Department of Biology
Queen's University
Kingston, Ontario K7L 3N6 Canada

Abstract.—The nesting biology of the Yellow Warbler (*Dendroica petechia*) was studied at the northern limit of its breeding range at Churchill, Canada. This region is colder and has a shorter breeding season than any in which the species was previously studied. Yellow Warblers arrived in Churchill before most deciduous vegetation had emerged and, in some instances, when snow still covered the ground. Warblers at this location built larger and better insulated nests than in southern populations, presumably as an adaptation against the cooler temperatures. Clutch size averaged 4.65 eggs and was larger than in all other populations studied so far, except those in Alaska. Nestlings grew rapidly and survivorship was similar to southern populations; only about 4% of chicks were lost through brood reduction. Males fed young more frequently than females or males in southern areas. These observations suggest that Yellow Warblers may compensate for the short subarctic summer by arriving on the breeding grounds earlier, building larger and better insulated nests, and investing more in male parental care than birds in other locations.

BIOLOGÍA DE ANIDAMIENTO DE *DENDROICA PETECHIA* EN EL LÍMITE NORTE DE SU DISTRIBUCIÓN

Sinopsis.—Se estudio la biología de anidamiento de *Dendroica petechia* en el límite norte de su distribución en Canadá. Esta región es más fría y tiene una época de reproducción más corta que cualquier otra en donde la especie haya sido estudiada. Estas aves llegan a Churchill antes de que la mayoría de la vegetación haya emergido y en ocasiones cuando la nieve aún cubre el terreno. En esta localidad estos pajarillos construyen nidos más grandes y mejor insulados que otras poblaciones más al sur, probablemente como una adaptación a las temperaturas más bajas. El tamaño promedio de la camada resultó ser de 4.65 huevos y resultó mayor que todas las otras poblaciones estudiadas, excepto la de Alaska. Los pichones crecieron rápido y la supervivencia resultó similar al de otras poblaciones más al sur; tan solo el 4% de los polluelos se perdieron. Los machos alimentaron a los polluelos con mayor frecuencia que las hembras y otros machos de poblaciones más al sur. Estas observaciones sugieren que éste pájaro podría muy bien compensar lo corto del verano subártico, llegando a las áreas de reproducción más temprano, construyendo nidos más grandes e insulados y los machos ofreciendo una mayor inversión parental que las aves de otras localidades.

The Yellow Warbler (*Dendroica petechia*) has one of the most widespread breeding ranges of any North American passerine and, apart from the Blackpoll Warbler (*D. striata*), nests farther north than any other parulid warbler (American Ornithologists' Union 1983). In this study, I describe the nesting biology of the Yellow Warbler at the northern limit of its range in the Canadian subarctic. This environment is generally characterized by short summers with cool and unpredictable weather, both of which can greatly restrict the opportunities for breeding birds (West and Norton 1975). These limitations may be offset, however, by a greater abundance of insect prey and by the increased daylength, which provides more time per day for foraging (Lack 1947). To learn how these conditions might affect the reproductive behavior of Yellow Warblers, I compared their nesting biology with populations in more temperate environ-

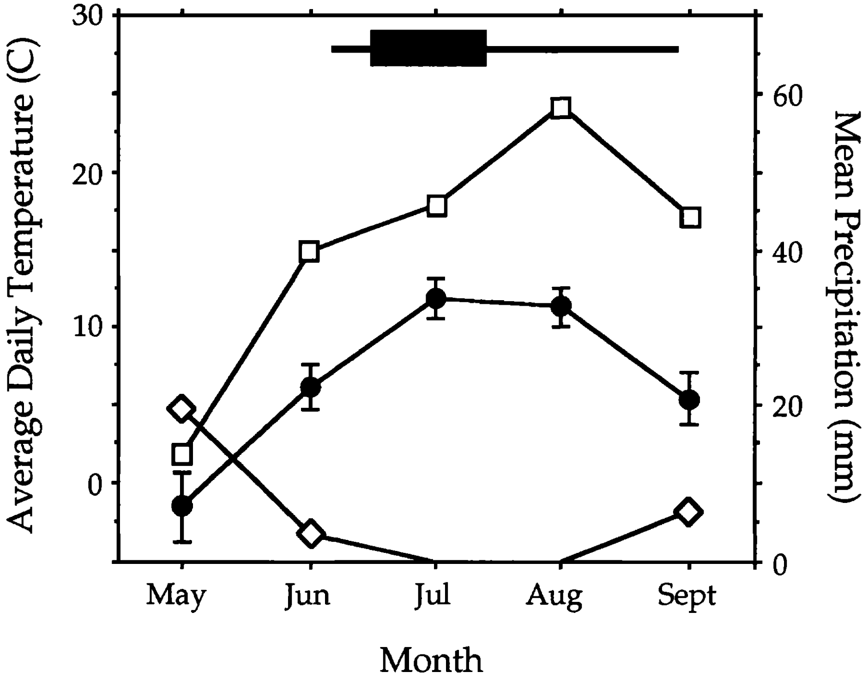

FIGURE 1. Average daily temperature (±SD, solid circles) and total mean precipitation (open squares = rain; open diamonds = snow) at Churchill, Manitoba during the Yellow Warbler breeding season. Extreme dates for arrival and departure (solid line) and clutch initiation (solid box) of Yellow Warblers on the study site are indicated at the top of the figure.

ments. My objective was to determine if warblers have evolved any specialized adaptations that permit them to compensate for the comparatively harsh conditions of the subarctic environment.

METHODS

I studied the nesting biology of Yellow Warblers near Churchill (58°40′N, 94°25′W), Manitoba, Canada, from 1987 to 1992. This region lies within the breeding range of *D. p. amnicola,* the Yellow Warbler subspecies found throughout the boreal and subarctic regions of northern North America (American Ornithologists' Union 1957). Field work began in late May or early June and continued until mid- to late July of each year; this spanned the entire period from spring arrival to fledging of young. The Churchill region is characterized by short cool summers and low rainfall (Fig. 1), and is heavily influenced by its proximity to the cold waters of Hudson Bay. The northern edge of the boreal tree-line crosses through this area, forming a mosaic of tundra and forest habitats. Snow may fall as late as the end of June and even in July the temperature averages only 11.8 C (Environment Canada 1982). The spring weather over the course of my study was typical for the area except in 1991, which was unusually early and warm, and in 1992, which was unusually late and cold.

Nests were found by searching areas where males were observed singing. Each nest was marked with flagging tape and visited every 1–5 d. Clutch size was determined only for nests found before hatching. Egg length and greatest breadth were measured with calipers and volume calculated using the formula given by Hoyt (1979: Volume = 0.51 Length × Width^2). Clutch initiation dates were determined either by direct observation or by back-dating using known laying and incubation intervals. Incubation period was defined as the number of days between the laying and hatching of the last egg (Nice 1953). Nestling period was defined as the number of days from hatching to fledging of the last-hatched chick. Nests were visited several times per day around hatching to record the time that each egg hatched. Nestlings were individually marked with felt pens and weighed daily to record their growth. Chicks were not weighed after 7 d because they fledge prematurely if handled at this age. Inner and external nest dimensions (diameter and height) were measured before hatching as nests may become compacted by nestlings. Some nests were located after clutch initiation, thus I calculated nesting success using the Mayfield (1961, 1975) method. Differences between survival probabilities of nests were tested using the techniques described by Hensler and Nichols (1981). Finally, I recorded parental feeding rates at five nests to determine the relative roles of males and females. Each nest was observed for 3 h when nestlings were 8 d old from a blind approximately 5 m from the nest.

For comparison, I used data from the literature (e.g., Schrantz 1943), particularly from a well-studied population of Yellow Warblers at Delta Marsh in southern Manitoba (Biermann and Sealy 1982; Briskie et al. 1990; Goossen 1978; Goossen and Sealy 1982; Hébert 1993; Hébert and Sealy 1993a, b; Sealy 1992). This study area is located within the northern limit of the range of *D. p. aestiva,* the subspecies found in eastern North America (American Ornithologists' Union 1957). *D. p. aestiva* and *D. p. amnicola* are similar in size (mean wing length of male *amnicola*: 62.0 ± 0.32 mm, $n = 5$; *aestiva*: 62.3 ± 0.33 mm, $n = 30$; $t = -0.41$, df = 33, $P = 0.69$; unpubl. data) but male *D. p. amnicola* have duller yellow underparts and darker chestnut breast streaks than *D. p. aestiva* males (Bent 1963).

Statistical procedures follow Sokal and Rohlf (1981) and Zar (1974). Descriptive statistics are given as mean ± 1 SE. I only made statistical comparisons between studies when it was clear that the data were collected in the same fashion and using similar methods to this study.

RESULTS

Arrival.—Male Yellow Warblers were first spotted on 9 Jun. 1987, 3 Jun. 1988, 8 Jun. 1989 and 9 Jun. 1992 (mean = 7 June) but were already present upon my arrival in 1990 (14 June) and 1991 (4 June). Females were first noted either on the same day (1988) or within 2 d (1987, 1989, 1992; mean = 9 June) after the arrival of males. These dates average 3–4 wk later than for birds arriving in southern Manitoba (arrival date at Delta Marsh: 10–20 May; S. G. Sealy, pers. comm.). A later arrival at Churchill is expected because this area is almost 1000 km north of Delta Marsh. Nonetheless, warblers at Churchill arrive there at an earlier phenological stage relative to snow melt and bud emergence than in southern Manitoba, appearing well before leaves on deciduous shrubs emerge and, in some years, when snow still partly covers the ground. For example, in 1988 snow covered all but the topmost twigs of the willow thickets (i.e., >1 m drifts) when the first male warblers arrived; one male was even observed singing from an exposed branch on an otherwise completely snow-buried territory. In temperate parts of their range, the first Yellow Warblers do not typically arrive until after the first leaves have emerged (pers, obs.; S. G. Sealy, pers. comm.).

Nesting habitat and breeding density.—Yellow Warbler nests were confined to the small patches of willow scrub that lined the rivers, streams and lake margins in the area. *Salix planifolia, S. pedicellaris,* and *Betula glandulosa* were the dominant shrub species and formed a canopy averaging 1–2 m in height. In physiognomy, this habitat was similar to old-field and forest edge habitats where Yellow Warblers nest in temperate regions.

The breeding density of Yellow Warblers at Churchill was relatively low. In 1991, I located seven nests in a 10.4-ha patch of suitable habitat (approx. 0.7 pairs/ha). This density appeared typical of other local populations but lower than that reported elsewhere (e.g., 3.4 pairs/ha reported in Wisconsin; Young 1949) and much lower than the 19.1 pairs/ha recorded at Delta Marsh in southern Manitoba (Goossen and Sealy 1982).

Nest-site characteristics.—Yellow Warbler nests were found exclusively in deciduous shrubs. *S. planifolia* was the most frequently used nest-tree species (69.2%, n = 39), followed by *S. pedicellaris* (15.4%), *S. candida* (7.7%), *B. glandulosa* (5.1%) and *S. lanata* (2.6%). Nest height averaged 62.4 ± 3.3 cm (n = 45) and ranged 24–120 cm, or one-third of that in southern Manitoba (mean = 1.72 m; MacKenzie et al. 1982). Although trees are small at Churchill, nest-trees averaged 191.9 ± 12.0 cm (range = 100–333 cm); the relative height of nests (nest height/nest-tree height) averaged 0.43 ± 0.03 (range = 0.20–0.77) or about half way up the height of the nest-tree. Relative nest-height was similar to that in southern Manitoba (mean = 0.46; MacKenzie et al. 1982). Nest position within the available nesting habitat was not quantified, but most nests were built in the largest shrubs in or near the center of a willow patch.

Nest construction and size.—Nests were typically constructed before most leaves had emerged on the willow bushes, thus they were visible and exposed until well into incubation. Nest construction required an average of 6.2 ± 1.1 d (range = 4–10 d, n = 5). This is longer than the 4 d reported by Schrantz (1943), but resulted from one female that required

TABLE 1. Dimensions of Yellow Warbler nests at Churchill (subarctic population) and Delta Marsh, Manitoba (temperate population). Values are mean ± SE. Sample size is 30 nests for each population.

Dimension (cm)	Churchill	Delta marsh[1]
External diameter[2]	8.7 ± 0.17	7.3 ± 0.14
External height[2]	7.6 ± 0.26	6.6 ± 0.18
Inner diameter	4.7 ± 0.09	4.7 ± 0.08
Inner height	3.8 ± 0.08	4.0 ± 0.09

[1] From S. G. Sealy, pers. comm.
[2] t-test: $P < 0.05$.

10 d to construct her nest. If this female is excluded then the construction period (5.3 d) is similar to that for Yellow Warblers in temperate populations. Nests were constructed from fine grasses and down from willow catkins and fireweed (*Epilobium* spp.) seed capsules, and lined with feathers (mainly from Willow Ptarmigan, *Lagopus lagopus* and Canada Goose, *Branta canadensis*) and down.

Nests were significantly larger (19.2% wider, 15.2% higher) than those in southern Manitoba (Table 1). The larger size of nests was due to a 54% increase in the thickness of the nest-wall (2.0 cm vs. 1.3 cm) and not to a larger cup.

Breeding season.—The earliest clutch initiation was on 14 June (in the early spring of 1991) and the latest on 10 July (in the late spring of 1992), a period spanning 27 d (Fig. 2). This period is less than the 42-d clutch-initiation period reported by Goossen and Sealy (1982) and Briskie et al. (1990) from southern Manitoba. I had only enough data to determine the duration of the clutch-initiation period for 1988 and 1989: clutch initiation spanned 12 d in 1988 (21 June–3 July, n = 12 nests) and 14 d in 1989 (21 June–5 July, n = 26). Most clutches were initiated during the last week of June (Fig. 2) and coincided with the rapid increase in spring temperature (Fig. 1).

Excluding 1992, clutch initiation began 12–18 d (mean = 14.3, n = 3 years) after males first arrived on the breeding grounds. In the late spring of 1992, the first clutch initiation did not occur until 30 d after males first arrived on the breeding grounds and many birds did not attempt to breed; only four nesting attempts were observed, two of which were abandoned before clutch completion. The period between arrival and clutch initiation has not been quantified in detail elsewhere, but is about 2 wk in southern Manitoba (S. G. Sealy, pers. comm.).

Clutch and egg size.—Yellow Warblers at Churchill laid clutches of either four or five eggs (mean = 4.65 ± 0.07, n = 54). Clutch size increases with latitude (Fig. 3) and warblers at Churchill laid clutches at a size expected for birds nesting this far north; only warblers in Alaska laid larger clutches (Kessel 1989).

Mean egg length averaged 17.08 ± 0.18 mm (n = 12 clutches) and mean width 13.07 ± 0.10 mm. Calculated egg volume averaged 1.49 ±

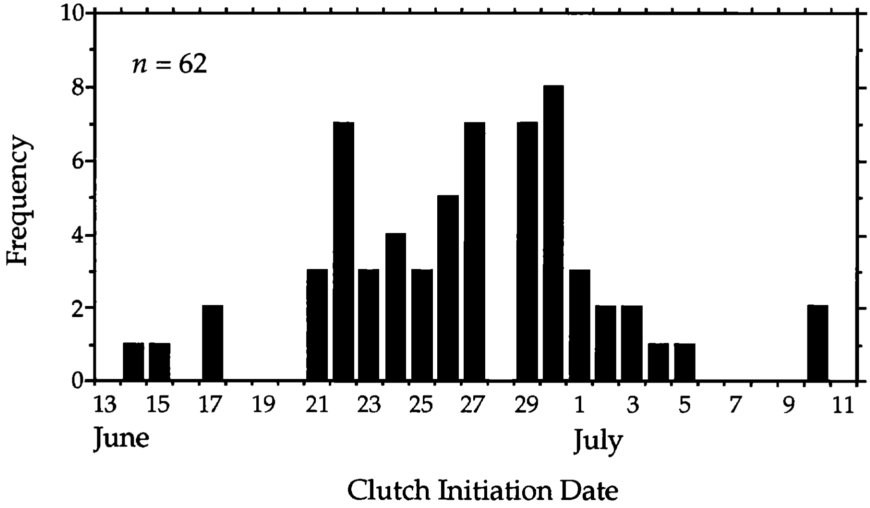

FIGURE 2. Timing of clutch initiation by Yellow Warblers at Churchill, Manitoba. Data from 1987 to 1992 combined in this figure.

0.03 cm^3. Egg length and width at Churchill was not significantly different than egg length (17.33 ± 0.22; $t = -0.89$, df = 18, $P = 0.39$) and egg breadth (13.28 ± 0.14; $t = -1.29$, $P = 0.22$) reported by Schrantz (1943) for clutches in Iowa. Egg length at Churchill was also not significantly different from egg length at Delta Marsh (16.80 ± 0.08; $t = 1.26$, df = 95, $P > 0.05$); however, eggs at Churchill were significantly wider than those from Delta Marsh (12.60 ± 0.04; $t = 4.20$, $P < 0.05$; Sealy 1992).

Incubation period.—The incubation period of Yellow Warblers at Churchill ranged 11–13 d (mean = 11.7 ± 0.21 d, $n = 15$). This period is significantly longer than the 11.3 ± 0.10 d ($n = 22$) reported by Goossen (1978) in southern Manitoba ($t = 2.23$, df = 35, $P = 0.032$).

Hatching success.—The number of hatchlings in nests that survived to hatching averaged 3.9 ± 0.10 (range = 3–4, $n = 10$ nests) for clutches of four and 4.64 ± 0.11 (range = 4–5, $n = 22$ nests) for clutches of five eggs. The proportion of all eggs that hatched was 97.5% for clutches of four ($n = 40$ eggs) and 92.7% for clutches of five ($n = 110$ eggs). For all nests that survived to hatching, hatching success was 94.0% ($n = 150$). In southern Manitoba, 89.8% of Yellow Warbler eggs ($n = 428$) hatched successfully (calculated from Goossen and Sealy 1982); this difference was not significant ($G_{adj} = 3.09$, df = 1, $P > 0.05$).

Hatching asynchrony.—Most warbler clutches hatched within 24 h. Hatching spread (time from first- to last-hatched egg within a nest) averaged 1.3 ± 0.21 d (range = 1–2 d, $n = 6$) for clutches of four and 1.2 ± 0.09 d (range = 1–2 d; $n = 20$) for clutches of five. For all clutches combined, 77% of clutches ($n = 26$) hatched within 24 h. Hatching spread for clutches of four at Churchill (1.3 d) did not differ significantly

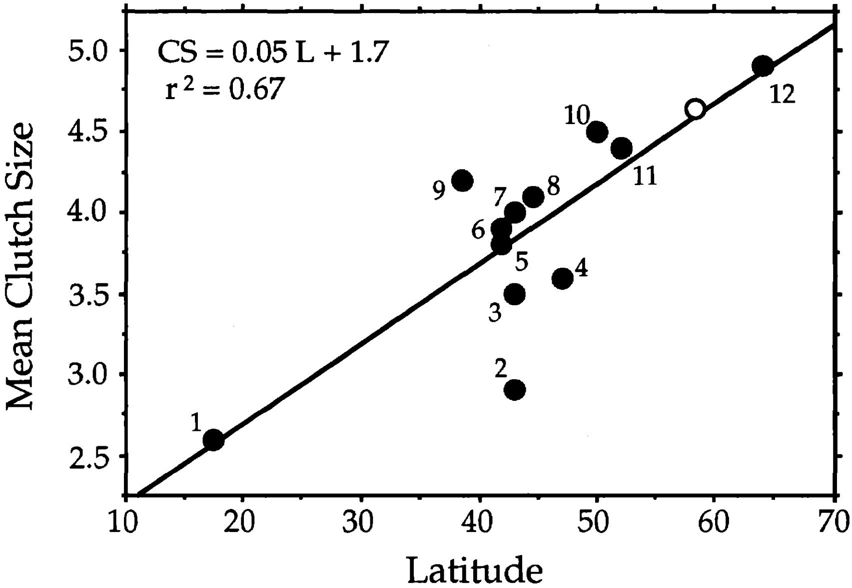

FIGURE 3. Relation between latitude (°N) and mean clutch size in the Yellow Warbler. Mean clutch size at Churchill, Manitoba given by open circle. Numbers by solid circles refer to following populations: 1, Puerto Rico (Cruz et al. 1985); 2, Michigan (McGeen 1972); 3, Wisconsin (Young 1949); 4, North Dakota (Stewart 1975); 5, Michigan (Batts 1961); 6, Utah (Frydendall 1967); 7, Iowa (Schrantz 1943); 8, Ontario (Clark and Robertson 1981); 9, Kansas (Johnston 1964); 10, Delta Marsh, Manitoba (Goossen and Sealy 1982); 11, Canadian Prairie Provinces (Prairie Nest Records Scheme; calculated by Goossen and Sealy 1982); 12, Alaska (Kessel 1989).

from the 1.4 ± 0.07 d (n = 33) reported for four-egg clutches in southern Manitoba (t = 0.01, df = 31, $P > 0.05$; Hébert 1993a). Clutches of five eggs, however, hatched significantly more synchronously at Churchill (1.2 d) than in southern Manitoba (1.9 ± 0.07 d, n = 28 [Hébert 1993a]; t = 6.52, df = 46, $P < 0.005$).

Growth.—Mean mass of nestlings did not differ significantly between broods of four and five at any age ($P > 0.05$; Fig. 4). Although several authors have reported growth of warblers in other populations, none of their results are in a form that permits statistical comparison. The mean mass of warbler nestlings at Churchill at 7 d after hatching (broods of four: 9.12 ± 0.10 g, n = 32; broods of five: 9.40 ± 0.09 g, n = 30), however, is greater than that reported by Schrantz (1943) for 7-d-old nestlings in Iowa (8.78 g; SE and sample size not reported).

Nestling period and nest success.—Nestlings fledged an average of 8.5 ± 0.17 d after hatching (range = 8–10 d, n = 14). This result is not significantly different from the 8.2 ± 0.23 d (n = 12) for warblers in southern Manitoba (t = 1.17, df = 24, $P > 0.05$; data calculated from Goossen 1978).

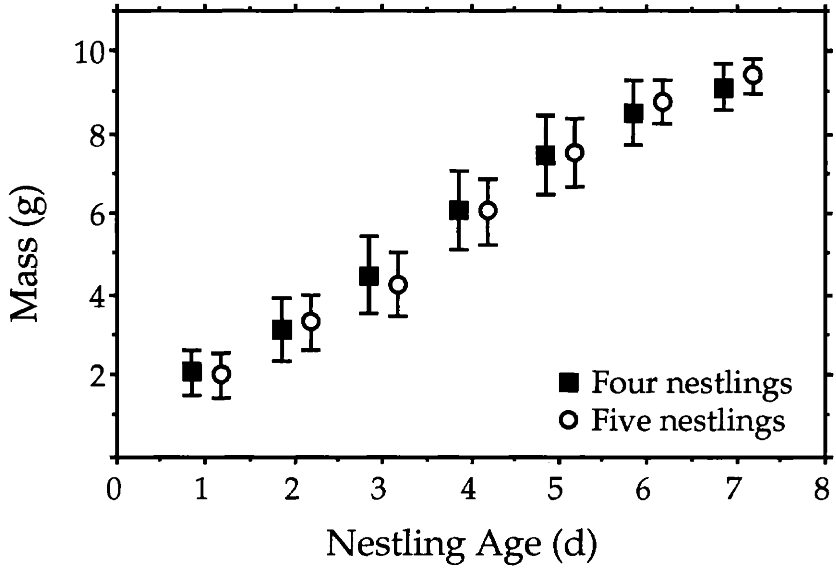

FIGURE 4. Growth in mass of Yellow Warbler nestlings at Churchill, Manitoba in broods of four and five young. Sample size is 32 nestlings for broods of four and 30 nestlings for broods of five. Figures are mean ± 1 SD.

The daily probability of survival of Yellow Warbler nests at Churchill calculated using the Mayfield (1961, 1975) method was 0.969 ± 0.001 for clutches of eggs (n = 61 nests) and 0.974 ± 0.002 for broods of nestlings (n = 36 nests). This difference was not significant (z = 0.388, P = 0.70). Assuming an average of 15.4 d for laying and incubation (this study), nests had a 61.7% probability of surviving from clutch initiation to hatching. Once hatched, 79.9% of nests survived the average 8.5-d period to fledging. Overall, warbler nests had a 49.3% chance of survival from clutch initiation to fledging. This figure is similar to the 54.8% success calculated from Hébert and Sealy (1993a), and the 47.9% by Goossen and Sealy (1982) for Yellow Warblers in southern Manitoba. Although not calculated in exactly the same way, nest success at Churchill was also similar to that observed in Iowa (54.2%) by Schrantz (1943).

The main cause of nest failure was predation. Of 24 failed nests, 22 (91.7%) were destroyed by predators before young could have fledged safely. Although no acts of predation were observed, the most likely predators in the area were weasels (*Mustela* spp.), foxes (*Vulpes fulva* and *Alopex lagopus*), Gray Jays (*Perisoreus canadensis*) and American Crows (*Corvus brachyrhynchos*). No nests were destroyed by wind but two nests failed when deserted during a prolonged period of cold and snowy weather.

For broods that survived to fledging, chick loss during the nestling period was rare. Partial brood loss (likely from starvation) occurred in only two (11.1%, n = 18) nests. The number of young fledging from broods of four averaged 3.89 ± 0.11 (range = 3–4; n = 9) while the mean number fledging from broods of five was 4.78 ± 0.22 (range = 3–5; n = 9). Overall, only 3.7% (n = 81) of chicks were lost due to starvation or exposure in nests that fledged at least one offspring. Starvation of young was also uncommon at Delta Marsh, where only 2% of nestling deaths were attributed to starvation (Goossen and Sealy 1982).

Feeding and division of labor.—Both sexes fed nestlings at all five nests watched. At 8 d after first hatch, males made an average of 11.1 ± 1.5 feeding visits per hour (range = 8.3–16.3) and females 8.3 ± 1.2 visits per hour (range = 4.3–11.3; n = 15 h) to the nest. The number of feeding visits differed significantly between males and females ($z = -2.03$, $P = 0.04$). The percentage of feeding trips made by males averaged 59.3% (range = 51.4–71.0%); this division of labor was slightly less equitable than in southern Manitoba where males made about 53% of feeding trips (8.4–10.4 trips per hour) to nests with 8-d-old young (Biermann and Sealy 1982); however, these differences cannot be compared statistically.

Cowbird parasitism.—At Churchill, Yellow Warblers breed beyond the northern limit of the Brown-headed Cowbird (*Molothrus ater*), and unlike populations sympatric with cowbirds, no rejection behavior (e.g., egg burial, nest desertion) could be induced through the experimental introduction of cowbird eggs (Briskie et al. 1992). Moreover, adult warblers did not respond aggressively to the presence of a female cowbird model placed near their nests (Briskie et al. 1992).

Renests and second broods.—Birds were unbanded in my study; thus I could not be sure of the identity of individuals at suspected re-nests nor of the frequency of renesting. On the basis of the appearance of new nests shortly after the loss of a nearby nest, however, it was likely that renesting occurs if nests are lost during early incubation.

There was no evidence of double-brooding and it is unlikely to occur. In the average year, even the earliest nests do not fledge young before late July and any second brood would require birds to remain in the area well past the end of the short subarctic summer.

Fall migration.—I left the study area before fall migration commenced; Jehl and Smith (1970) summarized a few observations suggesting most Yellow Warblers leave the Churchill region by mid-August to early September. As a consequence, as few as 9–10 wk may elapse between spring arrival and fall departure. This period is approximately 3–4 wk shorter than that spent by Yellow Warblers on the breeding grounds in southern Manitoba (S. G. Sealy, pers. comm.).

DISCUSSION

Yellow Warblers in Churchill have only a short period in which to nest. As a result, nesting is highly synchronized relative to that observed in temperate populations; clutch initiation spanned only about 2 wk, compared to more than double this period in temperate populations. The short subarctic summer also means that only a single brood can be raised per season. In some years, even this is not possible and some birds may forego breeding altogether. Faced with this severe limitation, how has the nesting biology of Yellow Warblers been modified to cope with the relatively harsh subarctic environment?

The most direct way to compensate for limited time is to accelerate the reproductive cycle and thereby shorten the total time required to raise a brood. The duration of the nestling period was similar to that in temperate populations, however, and the length of the incubation period was actually longer in Churchill. This suggests that these features of warbler life history may be invariant or relatively difficult to change (perhaps because of physiological limits). Nonetheless, by arriving before the vegetation has emerged, warblers in Churchill initiate clutches much earlier in the spring than warblers in temperate populations and thereby raise their young without having to shorten any subsequent period of parental care prior to the southward migration.

Arriving earlier in the spring necessarily means encountering conditions far more severe than that faced by birds in temperate regions. For example, many territories were still snow-covered when males arrived and nest sites remained exposed for several weeks. To compensate, warblers in Churchill select nest sites in the center of willow patches, which offer better protection from weather and predators. To reduce heat loss, nest-walls were also about 50% thicker than in southern Manitoba. These thicker and better insulated nests should retain heat longer and reduce heat loss to wind. As the nest cup was not different in size from that found in temperate populations, the larger nests at Churchill were not simply a consequence of the larger clutches laid by birds in this area. Instead, the increase in nest size and nest-wall thickness appear to be designed to insulate the eggs and young from the more severe climate encountered by birds in the subarctic.

Unlike southern Manitoba, Yellow Warblers in Churchill hatched their clutches very synchronously, often in periods of less than 24 h for a clutch of five eggs. The adaptive significance of hatching asynchrony is widely debated (see Magrath 1990 for a review) and there are several possible explanations for the greater synchrony in Churchill warblers. As few warbler nestlings were lost through starvation, high synchrony could be an adaptation to low levels of brood reduction. That is, if brood reduction is seldom necessary, there should be no advantage to hatching eggs asynchronously. Alternatively, greater synchrony could result from an inability of females to both produce and incubate eggs simultaneously. If resources are more limiting during clutch initiation in the subarctic (as may be the case, based on spring arrival), then females may be unable to gather enough energy to produce eggs and initiate incubation concurrently. Cool temperatures during laying may also chill the eggs more quickly during absences and take greater energy and time to re-warm. The result will be a delay in the onset of incubation, and greater hatching synchrony. Whether hatching synchrony by Yellow Warblers in the subarctic is a consequence of environmental constraints or a life history adaptation will, however, require further study.

Male Yellow Warblers feed young in all populations but males feed at a slightly higher rate than do females in Churchill and possibly than do males in southern Manitoba. A greater investment by males in the subarctic might be expected for several reasons. First, northern birds should require greater investment in parental care simply because of the larger brood sizes, and this increased demand may be taken up proportionately more by males. Such a situation may result if females are already investing the maximum effort possible into parental care and any further increase has to be provided by the male (which does not brood and therefore may have more time available in which to forage). The need for greater male parental care is further exacerbated by greater hatching synchrony, which reduces the size hierarchy among the nestlings and thereby increases sibling competition and the overlap in peak food demands by the young (Hébert and Sealy 1993b). Lastly, the short breeding season, high synchrony of clutch initiations, and low density of conspecifics may mean that the opportunities for males to seek additional mates or extra-pair copulations may be more limited than in temperate populations. Thus, the only avenue open for males to increase reproductive success may be to invest proportionately more in parental care than in mate attraction. More data are required on paternity and the role of males in parental care in both northern and southern populations, however, before this idea can be tested thoroughly.

The ability of the Yellow Warbler to survive and breed in the subarctic appears to involve the modification of several pre-existing behavioral patterns rather than the evolution of altogether new strategies or behaviors. For example, by shifting arrival and clutch initiation to earlier in the spring, warblers can compensate for the short summer without having to reduce time allocated to incubation or nestling care. By building larger and better insulated nests, and by placing nests in more sheltered areas, warblers are able to withstand the cooler conditions associated with earlier clutch initiations. Nesting in the subarctic may nonetheless impose several constraints. The relatively short summers impose strict time limits on the timing and frequency of nesting attempts. The high degree of synchrony in clutch initiations and the low density of conspecifics may also limit the ability of males to increase their reproductive success through mate attraction and instead may favor a greater commitment to parental care. Together these small differences in investment and timing of the reproductive cycle may have allowed the Yellow Warbler to expand its range north into the subarctic.

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FROM THE EDITOR

I began my tenure as Editor of the *Journal of Field Ornithology* 5 yr ago with a letter (62[1]:18) to our readers, so it seems appropriate to end my tenure with another. First, I sincerely thank many people: John Smallwood and Bob Beason, who edited the Recent Literature sections; Greg Butcher, Robert Marshall and Jim Lowe, who edited the Bird Count Supplements; Jed Burtt, Greg Butcher and George Mock of the Association of Field Ornithologists; Sharon Kindall and Nancy Owen of Allen Press; Raúl Pérez-Rivera, Enrique Hernández and Bob Black, who did the Spanish translations; and most especially Teresa Holevas, who was my editorial assistant. Second, I thank the authors who submitted manuscripts for publication in the *Journal of Field Ornithology*. With remarkably few exceptions, my interactions with authors, whether or not their manuscripts were accepted for publication, were professional and pleasant. Any credit for the quality of this journal goes to the authors of the papers that have been published. Third, I wish my successor, C. Ray Chander, well in his position as Editor. The transition seems to have been a smooth one, and I have every confidence in Ray's editorial ability.

My first issue began with an unusual paper (62[1]:1–18), so it seems only fitting to end my last issue with an unusual paper. As Nisbet et al. explain, their paper was written in response to a critique by Bertram Murray, Jr. of their work on Blackpoll Warbler migration. I had intended to publish these two papers back-to-back in this issue, but Murray withdrew his manuscript. After considerable deliberation, I decided to publish the Nisbet et al. reply to Murray's critique. Readers will no doubt detect the intensity of feeling among the protagonists in this controversy. I have always been drawn to controversies in biology, and I have found the "blackpoll debate" to be a fascinating example of the sociology of science. Interested readers might want to contact Bert Murray for a copy of his manuscript.

I have thoroughly enjoyed my tenure as Editor. Working with authors was tremendously rewarding for me, and although I look forward to my "retirement," I urge others with the inclination to take up the editor's pen. You will not regret it.