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Breeding Biology and Reproductive Success of the Yellow Warbler on the Delta Beach Ridge, Manitoba

by

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BREEDING BIOLOGY AND REPRODUCTIVE SUCCESS

OF THE YELLOW WARBLER

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ABSTRACT

The breeding biology and reproductive success of a dense population of Yellow Warblers (*Dendroica petechia*) was studied during the breeding seasons of 1974 through 1976 on the forested beach ridge along the south shore of Lake Manitoba, Manitoba. Spring temperatures influenced clutch commencement. Egg laying, hatching and fledging of young occurred during periods of food abundance. Most Yellow Warblers constructed their nests in willows (*Salix* spp.), Manitoba maple (*Acer negundo* L.) and elderberry (*Sambucus pubens* Michx.). Nests were most successful, however,in hops (*Humulus lupulus* L.), elderberry and green ash (*Fraxinus pennsylvanica* Marsh.). The mean clutch size for all years was 4.5. Annual and seasonal variation in clutch size was not significant. The incubation period averaged 11.2 days; the nestling period averaged 10.4 days. Incubation prior to clutch completion resulted in asynchronous hatching and fledging. Nest success ranged from 39.8% (1976) to 63.6% (1974); it was 47.9% for all years. Higher nests were more successful than low nests. Nest success increased as the breeding season advanced. Five-egg clutches produced the most young. Predation was the major cause of nest failures. About 25% of the active Yellow Warbler nests were parasitized by the Brown-headed Cowbird (*Molothrus ater*). Cowbird parasitism decreased reproductive success.

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PART I

BREEDING BIOLOGY AND REPRODUCTIVE SUCCESS OF THE YELLOW WARBLER

INTRODUCTION

The Yellow Warbler (Dendroica petechia (Linnaeus 1766) Gray 1842) is one of the most familiar wood warblers (Griscom and Sprunt 1957). Much of the literature on this warbler has been anecdotal (Morris 1900, Dill 1902, Knight 1907, Hersey 1910, Kohler 1911, Otto 1919, Mousley 1926, Tufts 1927, Gross 1934, Smith 1943, Witschy 1958, Pittman 1960). Others have studied its behaviour (Bigglestone 1913, Ficken and Ficken 1965a), vocalizations (Morse 1966), territoriality (Kendeigh 1941, Ficken and Ficken 1965b, Frydendall 1967), feeding ecology (Frydendall 1967, Busby 1978), aspects of Brown-headed Cowbird (Molothrus ater) parasitism (McGeen 1971, 1972; Rothstein 1975) and reproductive success (Schrantz 1943, Young 1949, Batts 1961, Kammeraad 1964, 1966). However, detailed studies of its breeding biology and reproductive success are few.

A dense nesting population of Yellow Warblers on the Delta Beach Ridge, Manitoba, provided an opportunity to obtain detailed information on its breeding biology and reproductive success. This population also nests under conditions of apparently unlimited food supply (Busby 1978), thus permitting one to examine the possible influence such as food supply has on its productivity. In some species food supply directly influences clutch size (Gibb 1950, Southern 1959) and may promote a numerical response of breeding pairs to an abundant food supply (MacArthur 1958).

Part I of this study examines aspects of the breeding biology of the Yellow Warbler. This section considers its timing of breeding, nest site, clutch size, incubation and nestling period, fledging, reproductive success, mortality and second clutches. The apparent influence of food on some of these events is discussed. In Part II, consideration is given to the frequency and timing of parasitism by the Brown-headed Cowbird on this dense breeding population of Yellow Warblers. The response of the Yellow Warbler to parasitism is also discussed.

STUDY AREA

Description

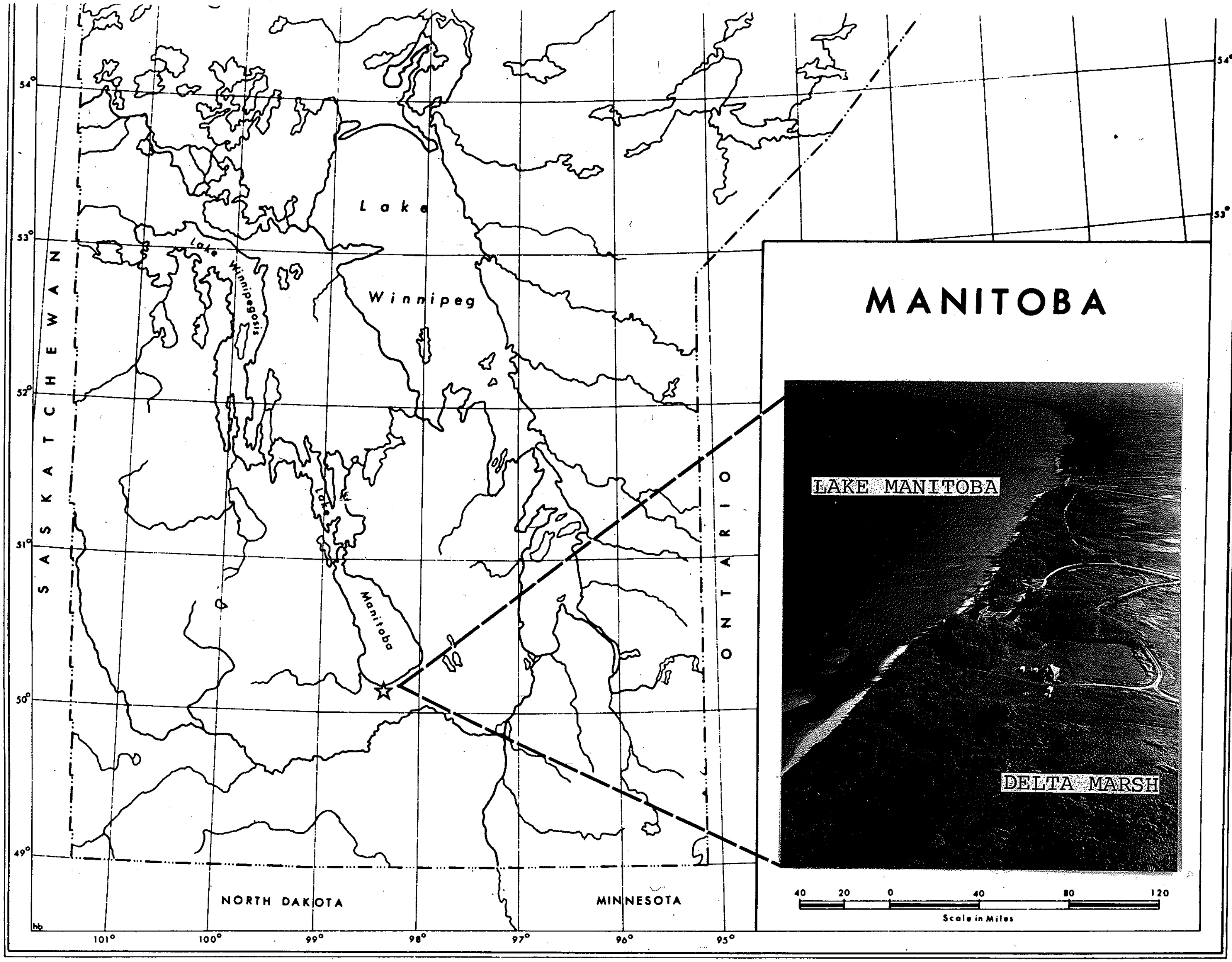
This study was conducted at the University of Manitoba Field Station (Delta Marsh) and on the adjacent property of the Portage Hunting Club. The village of Delta, Manitoba ($50^{o}11'$ $98^{o}19'$) is located approximately 4.8 km, east of the field station. The study area was located on the forested beach ridge which separates Lake Manitoba from the Delta Marsh (Fig. 1). Lake Manitoba, a remnant of glacial Lake Agassiz, is a large shallow lake extending about 185 km north and is 52 km wide at its southern end. The adjacent Delta Marsh to the south covers some 14,575 ha (Hochbaum 1944).

The broad vegetation zone, in which the Delta Marsh lies, is the grassland region. More specifically, it occurs in the prairie-aspen oak region (Ellis 1938). Information on climate,geology and soils may be found in Weir (1960), Fenton (1970) and Ellis (1938), respectively.

The formation of the beach ridge has been attributed to the action of ice, wind and waves of Lake Manitoba (Hochbaum 1944, 1967). This sandy ridge averages approximately 80 m in width (Busby 1978). The vegetation of the ridge has been described by Löve and Löve (1954), Olsen (1959) and Walker (1959).

The study area consisted of approximately 19 ha of forested beach ridge. Tree species found on the beach ridge included Manitoba maple (*Acer negundo* L.), green ash (*Fraxinus pennsylvanica* Marsh.),

Figure 1. The location of the Delta Beach Ridge and its relationship to Lake Manitoba and the Delta Marsh.


MANITOBA
LAKE MANITOBA
DELTA MARSH
Lake Winnipeg
Lake Winnipegosis
Lake Manitoba
SASKATCHEWAN
ONTARIO
NORTH DAKOTA
MINNESOTA
54°
53°
52°
51°
50°
49°
101°
100°
99°
98°
97°
96°
95°
40 20 0 40 80 120
Scale in Miles

peachleaf willow (*Salix amygdaloides* Anderss.) and eastern cottonwood (*Populus deltoides* Marsh.). The major shrubs were elderberry (*Sambucus pubens* Michx.) and sandbar willow (*Salix interior* Rowlee). Red osier (*Cornus stolonifera* Michx.) and cherry (*Prunus* sp.) occurred to a minor degree. The dominant herb was the nettle (*Urtica dioica* L.), while the main climbers were wild cucumber (*Echinocystis lobata* (Michx.) T. & G.) and hops (*Humulus lupulus* L.).

Potential avian nest predators include the Brown-headed Cowbird, the Common Grackle (*Quiscalus quiscala*) and the House Wren (*Troglodytes aedon*). Tamsitt (1962) and Hochbaum (1971) list the mammals which occur in the Delta Marsh region. Potential mammalian nest predators include the Red Squirrel (*Tamiasciurus hudsonicus*), Longtail Weasel (*Mustela frenata*), Shorttail Weasel (*Mustela erminea*), Mink (*Mustela vison*), Striped Skunk (*Mephitis mephitis*) and possibly some of the microtines.

Weather

Weather data were obtained from the monthly weather records collected at the University of Manitoba Field Station. Table 1 presents temperature and precipitation data for May through August for each year of the study. The following summary describes the prevailing weather during the three breeding seasons of the study.

1974 May: very cool, wet; June: dry; July: normal.

1975 May: normal temperatures, wet; June: normal; July: warm.

1976 May: warm, unusually dry; June: normal except for a cool spell; July: precipitation below normal.

Table 1. Temperature and precipitation at the University of Manitoba Field Station, (Delta Marsh), Manitoba, May through August, 1974-76.

Year and month	Mean temperature (+^{o}C)	Departure from long-term mean (^{o}C)	Total precipitation (cm)	Departure from long-term mean (cm)
1974				
May	6.4	-3.6	7.2	+2.4
June	17.3	+0.6	1.0	-6.9
July	20.6	+1.8	5.4	-1.8
August	16.2	-1.7	5.9	-1.0
1975				
May	10.5	+0.5	7.7	+2.9
June	16.9	+0.2	8.0	+0.1
July	21.1	+2.3	6.8	-0.4
August	16.6	-1.3	13.9	+7.0
1976				
May	12.1	+2.1	0.5	-4.4
June	17.9	+1.2	6.9	-1.0
July	19.2	+0.4	4.4	-2.8
August	18.9	+1.0	1.9	-5.1

MATERIALS AND METHODS

This study was conducted during the breeding seasons of 1974-76. Yellow Warblers were caught in mist nets with mesh sizes 32mm and 38 mm. Upon capture, the birds were banded with numbered aluminum U. S. Fish and Wildlife Service bands. Color bands in combination with aluminum bands were used to identify individuals. Some nestlings were also banded.

Nests were located by observing females collecting nesting material or by searching potential nest site locations. Numbered flagging tape assisted in numbering and relocating nests in subsequent visits. Nests were checked almost daily in 1974 and daily in 1975 and 1976. Variation in number of nests found may not reflect population levels but may be related to the experience of the researcher in finding nests. Nest contents were recorded on each visit to determine clutch size and nest success. Nest height and plant species in which the nest was located were also recorded. Besides known cases of human disturbance, the extent to which visits aided predators in locating nests is not known. Frequent visits by an observer do not affect nesting success appreciably (Nolan 1963, Willis 1973).

The description of the breeding season was based on the dates the first egg of each clutch was laid (see Myres 1955, Seel 1968). Only parasitized and unparasitized nests of known age were used. The exact date the first egg was laid was determined in 81% of the 320 clutches initiated. Approximate dates were obtained by backdating. It was assumed that one egg was laid per day (Schrantz 1943). A period of 9 days was assigned to the interval between laying of the last egg and hatching of the first nestling, while 8 days was assigned to the interval between the hatching and the fledging of the first young. Robertson's (1973) method of determining nesting synchrony was employed to examine annual variation in the timing of breeding. Clutch initiation, however, was used rather than the date of clutch completion since this excludes variation due to different clutch sizes (Caccamise 1976).

Clutch size was determined in nests, found before the last egg had been laid, in which laying occurred on consecutive days and where there was no change in the number of eggs one day after clutch completion. Parasitized clutches and those in which a lapse of laying occurred, were omitted. Loss of eggs prior to finding a nest should not affect seasonal, annual and specific differences in clutch size (Snow 1955).

Following Skutch (1945), the incubation period was defined as the period between the laying and hatching of the last egg. Unparasitized clutches found prior to clutch initiation or clutch completion were used. Those clutches in which egg losses occurred were omitted except for 5 clutches in which loss occurred during the hatching period. These may have been young that died and were removed by the adults. The incubation period of individual eggs of unparasitized clutches was defined as the period between the laying and hatching of that egg.

The nestling period was defined as the period between the hatching of the first young and the departure of the last young in a nest. The hatching spread is thus the time interval in which an unparasitized clutch hatches. Clutch size in this latter analysis refers to eggs found per nest. About 72% of the clutches were seen prior to clutch completion. The fledging spread is the time interval in which all young of a brood leave the nest.

Reproductive success and mortality factors were determined for those nests found before clutch completion. Ideally, one should base the data on nests found before the first egg is laid (Skutch 1966). However, Nolan (1963) considered the bias resulting from nest failures during the laying period to be small. An alternative method is that of Mayfield (1960). This method permits more data to be used and attempts to compensate for the bias that occurs in calculating nest success from those nests in an advanced stage and already successful. Bias may occur in this latter method as well (see Woolfenden and Rowher 1969, Green 1977).

An active nest is one in which at least one Yellow Warbler egg was laid. A hatched nest is one in which at least one Yellow Warbler egg hatched. A successful nest is one in which at least one Yellow Warbler nestling fledged. Egg, nestling and fledgling numbers should not be taken as exact values since precise values can only be obtained if a nest is under constant observation. Both parasitized and unparasitized nests were used in the analysis of reproductive success. Only unparasitized nests were used in determining the relationship between clutch size and nest success.

Data from renests and second clutches were analyzed together with data from first nests. Statistical tests used include linear regression, analysis of vaiance, chi-square and z-test. The level of significance used was $P < .05$. Nomenclature of plants follows Scoggan (1957) while scientific names of birds and mammals follows the American Ornithologists' Union check-lists (1957, 1976) and Burt and Grossenheider (1964), respectively.

STATUS OF THE YELLOW WARBLER ON THE DELTA BEACH RIDGE

A dense population of Yellow Warblers breeds on the forested ridge (Hochbaum 1944). Up to 12 nesting pairs per 0.4 ha (or about 29.6 pairs/ha) have been reported (Hochbaum 1971). A 1.7 ha plot on the study area was estimated to have supported 33 pairs during the breeding season or 19.1 pairs per ha. The nesting density on the Delta Beach Ridge exceeds that of populations reported in other localities (see Table 2). Densities vary along the ridge possibly in relation to plant species composition, food resources and territorial requirements of Yellow Warblers.

Table 2. Yellow Warbler breeding densities at 8 localities.

Location	Density (prs/ha)	Study
Michigan	0.2	Batts (1961)
Michigan	2.1[1]	McGeen (1972)
Wisconsin	3.5	Young (1949)
Minnesota	5.0[1]	Fashingbauer _et al_.(1957)
Utah	5.5 - 8.2[1]	Frydendall (1967)
Iowa	6.1[1]	Kendeigh (1941)
Minnesota	8.2[1]	Beer _et al_. (1956)
Delta Beach Ridge	19.1	This study
Delta Beach Ridge	29.6	Hochbaum(1971)

[1]Values from Busby 1978.

RESULTS

Spring Arrival

Yellow Warblers were first observed on the study area during the second or third week of May (Table 3). Males returned first. These first arrivals probably were migrants since banded resident males were noted after these initial sightings. Males spent most of their time singing and foraging before most of the females had returned. Intraspecific aggression between males increased after the females arrived.

Timing of breeding

The breeding season extended from late May or early June until early July (Fig. 2). The period in which clutches were initiated varied from 24-42 days (mean = 34.3 days) (Table 4). Using the extreme clutch initiation dates, the potential clutch initiation period is from 26 May to 7 July or 43 days.

Nesting synchrony and length of laying period were dependent upon weather conditions prior to the egg laying period. In the late spring of 1974, 50% of the clutches were initiated in 2 days and egg laying extended over 24 days. Both 1975 and 1976 data reflect favourable spring conditions promoting less synchrony within the population and a longer laying period (Table 4). Annual differences in the laying date of the first egg was 14 days (1974 and 1976), however, annual variation in the initiation of the last clutch was only 5 days (1974 and 1975).

Table 3. Spring arrival of the Yellow Warbler on the Delta Beach Ridge, 1974-76.

	Male		Female	
Year	Arrival	Resident Arrival[1]	Arrival	Resident Arrival
1974	15 May[2]	-	-	-
1975	13 May	19 May	16 May	23-24 May[3]
1976	9 May[3]	15 May	12 May	15 May

[1]Based on behaviour, influx or a banded individual

[2]Sex unknown - Yellow Warbler singing 14 May

[3]D. G. Busby (pers. comm.)

Figure 2. Clutch initiation by the Yellow Warbler on the Delta Beach Ridge in 1974, 1975 and 1976. Arrows indicate mean date of clutch initiation.

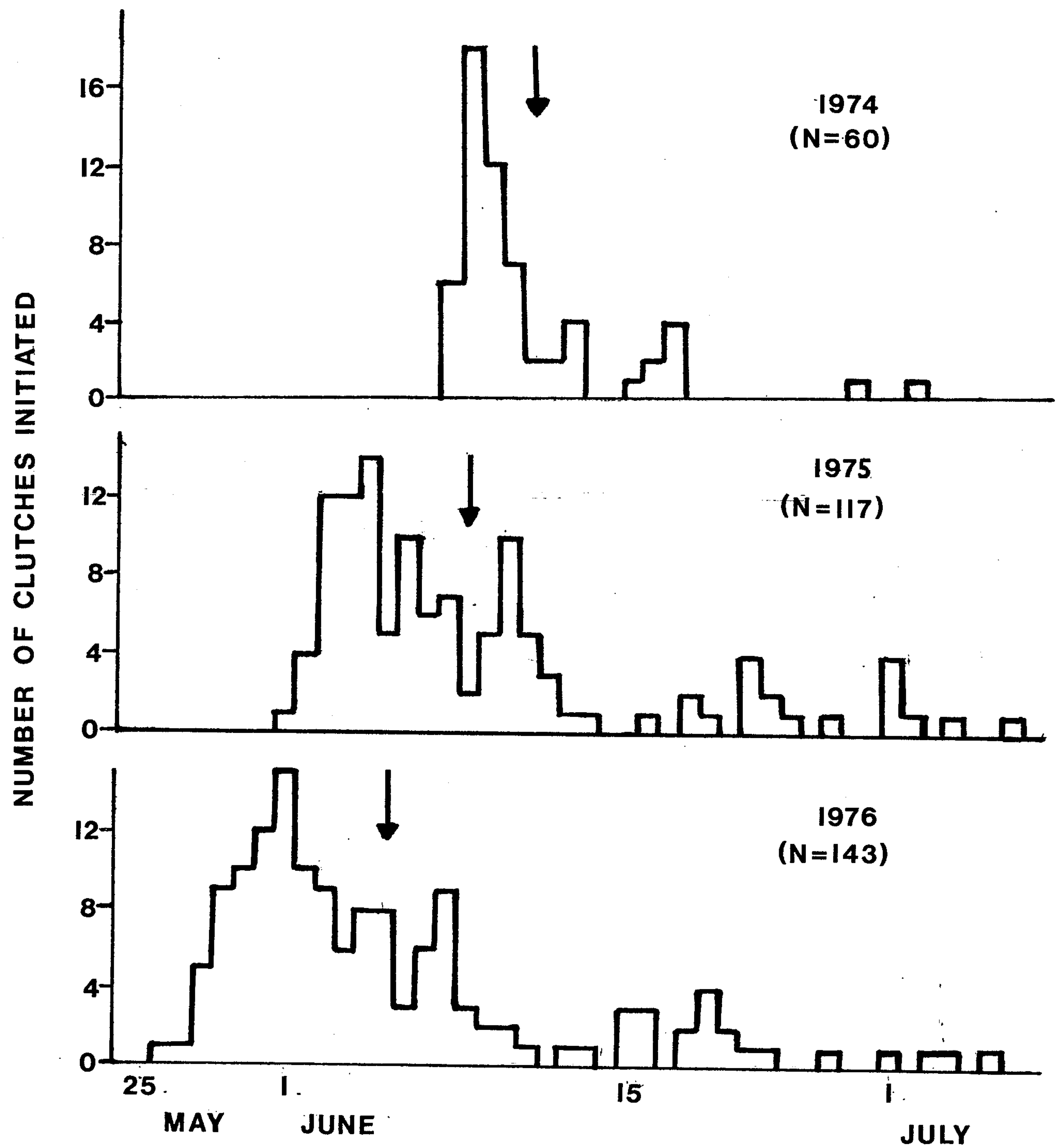

NUMBER OF CLUTCHES INITIATED
1974
(N=60)
1975
(N=117)
1976
(N=143)
0
4
8
12
16
25
1
15
MAY
JUNE
JULY

Table 4. The breeding season of the Yellow Warbler on the Delta Beach Ridge.

	1974	1975	1976
Total no. of active nests	66	119	148
Total no. of clutches initiated	71	128	158
Date of first clutch initiation	9 June	1 June	26 May
Date of last clutch initiation	2 July	7 July	6 July
Clutch initiation period (days)	24	37	42
Dates including 50% of clutches initiated	10-11 June	3-8 June	28 May-4 June
Duration of this period	2	6	8

The beginning of the laying period is directly influenced by temperature prior to the onset of laying. A negative correlation ($r = -0.99$) was found between the warmth sum and the date the first egg of the season was laid (Fig. 3). Rainfall during May was positively correlated with the date the first egg was laid ($r = 0.78$). The correlation of the warmth sum and rainfall with the laying of the first egg of the season was statistically not significant ($P > .05$).

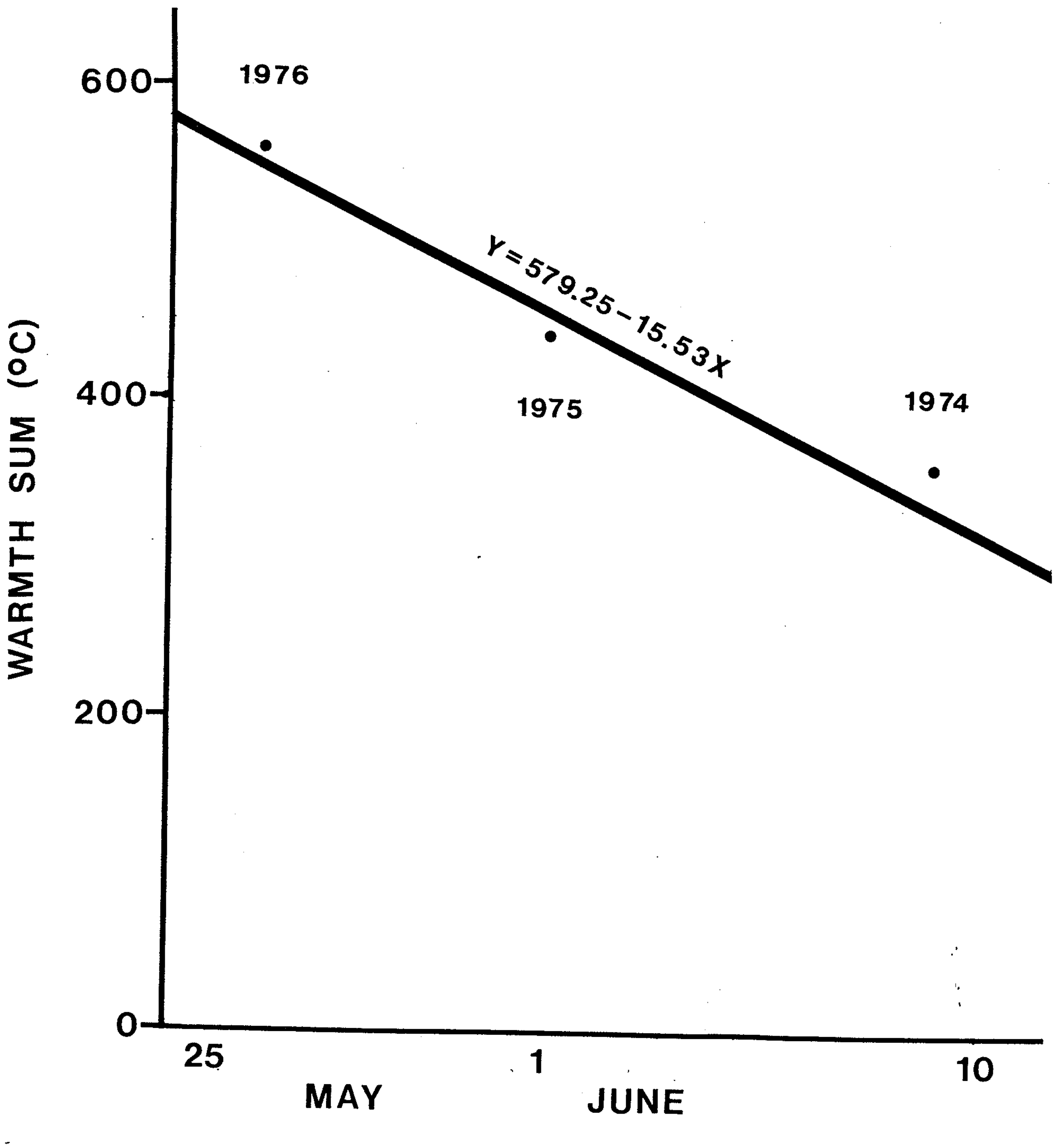
Egg laying, hatching and fledging occurred during periods of food abundance (Fig. 4, data from Busby 1978). The first peak of food abundance occurred on 6 June 1975 and 1 June 1976. At least 50% of the clutches initiated coincided with this peak in both years. Young began fledging prior to the second major peak in 1975 while in 1976 fledging began before the third peak of food abundance.

Nest site

Nest sites chosen were herbs, vines, shrubs and trees (Table 5). *Salix* spp. comprised 30% of the nest sites selected. *Acer negundo* and *Sambucus pubens* were the second and third most common nest sites, respectively. This frequency of the 3 main nest sites selected, prevailed in 1975 and 1976. In 1974, after a late spring the order was reversed. *Sambucus pubens* was selected most frequently followed by *Acer negundo* and *Salix* spp., respectively.

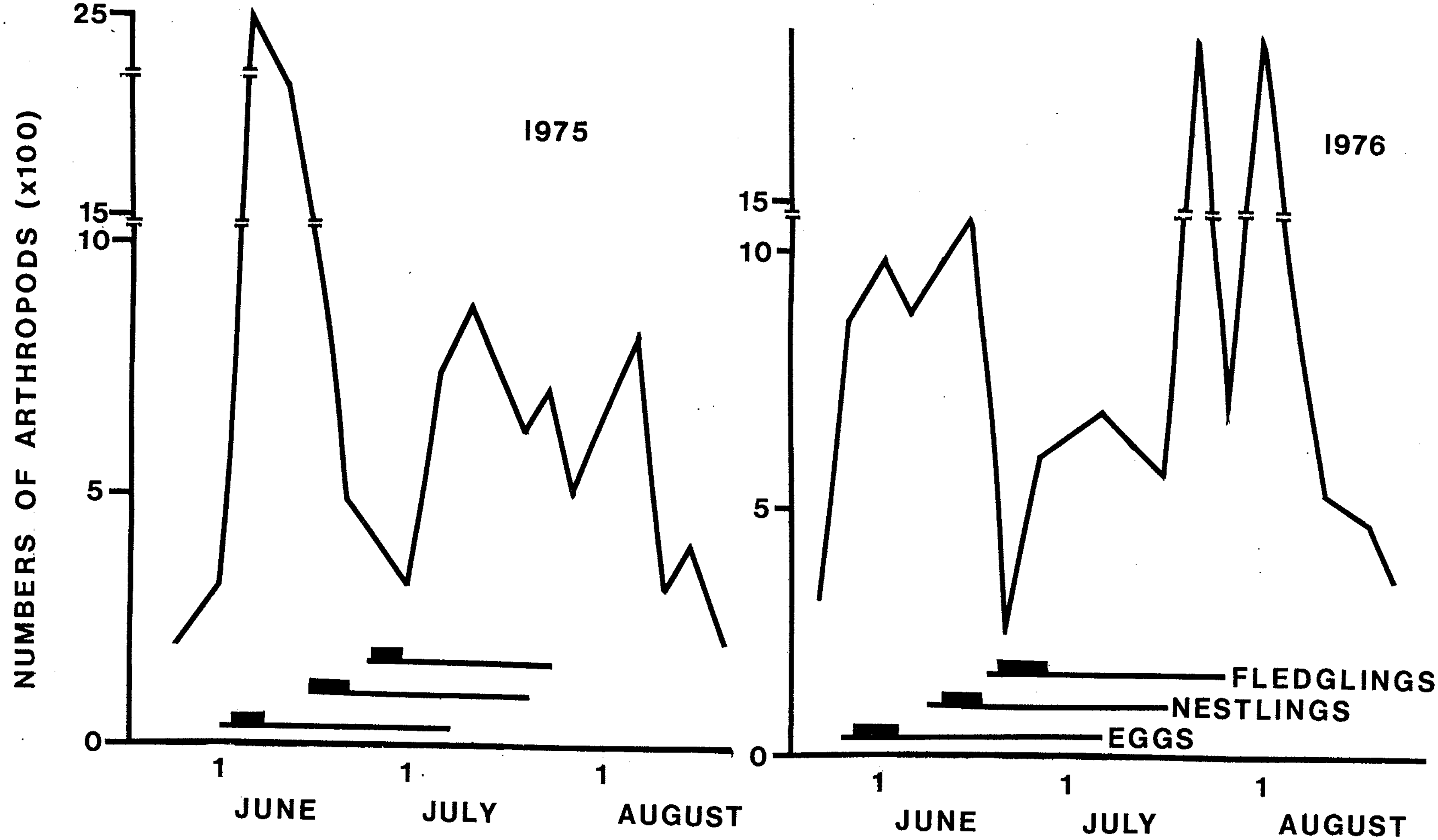
The mean nest height for 320 active nests was 178.1 cm with a range of 21 to 854 cm (Table 6). Annual differences were statistically significant (analysis of variance, $P < .05$) with the

Figure 3. Relationship between temperature and the date of the first egg laid by the Yellow Warbler on the Delta Beach Ridge. Warmth sum is the sum of degrees ^{o}C above freezing of the mean daily temperature for 1 May to 9 June.



600
400
200
0
WARMTH SUM (°C)
1976
1975
1974
Y = 579.25 − 15.53X
25
1
10
MAY
JUNE

Figure 4. Chronology of the Yellow Warbler nesting cycle on the Delta Beach Ridge in relation to the abundance of foliage arthropods (data from Busby 1978). Nest stages are expressed in terms of the first egg laid, the first egg hatched and the first nestling fledged of clutches initiated. Bars indicate 50% of each nest stage.



NUMBERS OF ARTHROPODS (x100)
25
15
10
5
0
1975
1
JUNE
1
JULY
1
AUGUST
1976
15
10
5
0
FLEDGLINGS
NESTLINGS
EGGS
1
JUNE
1
JULY
1
AUGUST

Table 5. Frequency of plant species use by Yellow Warblers as nest sites, 1974-76.

Species	1974 Active Nests	1975 Active Nests	1976 Active Nests	Total Active Nests	Total Percent
Salix spp.	11	44	41	96	30.0
Acer negundo	18	25	38	81	25.0
Sambucus pubens	23	19	23	65	20.0
Fraxinus pennsylvanica	3	10	11	24	7.0
Humulus lupulus	-	2	16	18	6.0
Rubus idaeus L.	1	7	9	17	5.0
Ribes sp.	-	4	4	8	2.0
Cornus stolonifera	1	2	1	4	1.0
Rosa sp.	2	-	-	2	1.0
Prunus sp.	-	-	2	2	1.0
Symphoricarpos sp.	-	1	-	1	0.5
Urtica dioica	-	-	1	1	0.5
Populus deltoides	-	-	1	1	0.5
Convolvulus sp.	-	-	1	1	0.5
Total	59	114	148	321	100.0

Table 6. Nest height (cm) of active Yellow Warbler nests during 1974-76.

Year	N	Mean $\pm$ S. E.	Range
1974	58	155.8 $\pm$ 18.16	21.0 - 702.5
1975	114	148.5 $\pm$ 10.50	25.0 - 476.0
1976	148	209.6 $\pm$ 14.43	26.0 - 854.0
Total	320	178.1 $\pm$ 8.45	21.0 - 854.0

highest mean occurring in 1976.

Clutch Size

One egg is laid per day until the clutch is completed. Occasionally a day may be skipped. Of 144 completed clutches, clutch size ranged from 3-5 eggs with a mean of 4.5 (Table 7). Fifty percent of the clutches contained 5 eggs, 46.9% contained 4 eggs while 3.5% contained 3 eggs. Annual variation in clutch size was not significant (analysis of variance, $P > .05$). Clutch size decreased as the breeding season progressed (Table 8), however, the difference was not significant (analysis of variance $P > .05$). Five-egg clutches were the most common from 25 May to 7 June; 4-egg clutches predominated from 8 June to 5 July. Reduced clutch sizes were possibly due to renesting.

Incubation

Only the female incubated. The interval between laying of the last egg and hatching of the first young was 9.4 days with a range of 8-11 days (Table 9). This interval decreased as clutch size increased suggesting that incubation was initiated prior to clutch completion. Further evidence for this was found when the period between laying and hatching of individual eggs was examined. The incubation period for 101 individual eggs ranged from 11 to 14 days (Table 10). The incubation period decreased from egg #1 to #5 in a clutch. Incubation periods greater than 12 days were characteristic only of eggs #1 to #3 with only one 13-day period occurring

Table 7. Clutch size of the Yellow Warbler on the Delta Beach Ridge, 1974-76.

	Number of eggs					
Year	3	4	5	Total	Mean	S. E.
1974	1	15	17	33	4.5	0.10
1975	0	27	25	52	4.5	0.07
1976	4	25	30	59	4.4	0.08
Total	5	67	72	144	4.5	0.05

Table 8. Seasonal variation in clutch size of the Yellow Warbler.

Time interval	Number of eggs 3	4	5	Mean	S. E.
25 May - 7 June	0	19	46	4.7	0.06
8 - 21 June	1	38	26	4.4	0.06
22 June - 5 July	4	10	0	3.7	0.13

Table 9. Incubation periods of the Yellow Warbler.

Clutch Size	(a) Period (days) between laying of last egg and hatching of first young			(b) Incubation period (days) of each clutch. Last egg laid to last egg hatched			Difference between mean periods for (a) and (b)
	No. of Clutches	Mean (days)	S.E.	No. of Clutches	Mean (days)	S.E.	
3	2	10.5	0.50	1	12.0	0.00	1.5
4	39	9.6	0.11	31	11.2	0.07	1.6
5	43	9.2	0.10	29	11.2	0.09	2.0
Total	84	9.4	0.08	61	11.2	0.06	

Table 10. Incubation period (days) of individual Yellow Warbler eggs.

Egg	N	Mean	Range
1	23	12.8	11 - 14
2	24	12.1	11 - 13
3	22	11.7	11 - 13
4	20	11.4	11 - 12
5	12	11.3	11 - 12
All last eggs	22	11.3	11 - 12

for egg #3. These data suggest that incubation does occur before clutch completion and may begin by the third egg. The small range for incubation periods of individual eggs reflects little variation in the incubation constancy. The incubation period was 11.2 days (Table 9). Incubation periods were the same for clutches of 4 and 5. Annual variation in the incubation period was small (Table 11).

Nestling period

The hatching of the first egg occurred between 8 and 22 June for the 3 breeding seasons (Table 12). The major factor attributed to the variation in mean hatch date for the three years was the weather conditions prior to clutch initiation. This is also reflected in the time it took for 50% of the clutches to start hatching. Fifty % of the clutches began hatching within 2 days in the late spring of 1974 while this period was extended to 7 days in the favourable springs of 1975 and 1976.

Incubation prior to clutch completion resulted in asynchronous hatching. The average hatching spread of 74 clutches was 2.8 days with a range of 1 to 5 days (Table 13). The hatching spread interval for clutches of 3 and 4 were similar, however, 5-egg clutches averaged a little longer. The difference in hatching spread between the 3 clutch sizes was not significant (analysis of variance, $P > .05$).

The mean nestling period for 59 broods was 10.4 days with a range of 9 to 13 days (Table 14). Nestling periods of 10 days were most common and represented 37% of the nestling periods. The duration of the nestling period increased as the brood size increased.

Table 11. Annual variation in the incubation period of the Yellow Warbler, 1974-76.

Year	No. of Clutches	Incubation Period
1974	11	11.1 days
1975	23	11.2 days
1976	27	11.3 days
Total	61	11.2 days

Table 12. Hatching dates of first Yellow Warbler young, 1974-76.

Year	No. of clutches	Mean hatch date	50% hatch	No. of days	Extreme dates
1974	48	25 June	23-24 June	2	22 June-11 July
1975	78	24 June	15-21 June	7	15 June-19 July
1976	108	20 June	11-17 June	7	8 June-17 July

Table 13. Hatching spread of Yellow Warbler clutches.

Clutch Size	Days 1	2	3	4	5	Total	Mean
3	0	1	2	0	0	3	2.7
4	1	15	20	3	0	39	2.6
5	0	7	20	4	1	32	3.0
Total	1	23	42	7	1	74	2.8

Table 14. Length of nestling period of the Yellow Warbler.

Brood Size	Days 9	10	11	12	13	Total	Mean
1	1	0	0	0	0	1	9.0
2	1	3	0	0	0	4	9.8
3	5	6	5	2	1	19	10.4
4	2	9	10	2	0	23	10.5
5	1	4	6	1	0	12	10.6
Total	10	22	21	5	1	59	10.4

Fledging

Fledging of young began in the fourth week of June in 1975 and the third week of June in 1976 (Table 15). In both years, the last fledgling left during the fourth week of July. The difference in the time it took for 50% of the young to fledge may be attributed to the early spring in 1976. Other factors involved are renesting and cowbird parasitism.

Most first nestlings fledge at 9 days of age (Table 16); the range was 8 to 11 days. The nestling period of the first fledgling in a nest decreased as brood size increased. This may be related to the crowding factor of larger broods.

Asynchronous hatching resulted in asynchronous fledging in 74% of 54 broods (Table 17). Young warblers fledged over 1 to 5 days averaging 2.2 days. The fledging spread increased with increasing brood size.

Reproductive success

Nest success. - When all mortality factors are considered, annual nest success of active nests found before the last egg was laid varied from 39.8% in 1976 to 63.6% in 1974 (Table 18). The combined nest success for the three seasons was 47.7%. The difference between those active nests found before the last egg laid and those found after the last egg was only 1.1%. The overall nest success for all active nests was 47.9%.

Egg success. - Of the 974 eggs from 227 active nests, annual hatching

Table 15. Fledging dates of first Yellow Warblers, 1975-76.

Year	No. of broods	Mean fledging date	50% fledge	No. of days	Extreme dates
1975	51	2 July	25-29 June	5	24 June-23 July
1976	52	30 June	20-28 June	9	18 June-26 July

Table 16. Age of fledging of first Yellow Warbler nestlings.

Brood Size	Days 8	9	10	11	Total	Mean
1	0	1	0	0	1	9.0
2	0	2	2	0	4	9.5
3	0	11	5	1	17	9.4
4	3	13	5	0	21	9.1
5	2	6	4	0	12	9.2
Total	5	33	16	1	55	9.2

Table 17. Fledging spread of Yellow Warbler broods.

Brood Size	Days 1	2	3	4	5	Total	Mean
1	0	0	0	0	0	0	0.0
2	3	1	0	0	0	4	1.3
3	6	7	3	1	0	17	1.9
4	3	7	9	2	0	21	2.5
5	2	5	4	0	1	12	2.4
Total	14	20	16	3	1	54	2.2

Table 18. Yellow Warbler nest success, 1974-76.

	1974			1975			1976			Total		
	No. of active nests	No. of successful nests	% successful	No. of active nests	No. of successful nests	% successful	No. of active nests	No. of successful nests	% successful	No. of active nests	No. of successful nests	% successful
Nests found before last egg laid	44	28	63.6	98	47	48.0	93	37	39.8	235	112	47.7
Nests found after last egg laid	7	3	42.9	20	9	45.0	53	27	50.9	80	39	48.8
All active nests	51	31	60.8	118	56	47.5	146	64	43.8	315	151	47.9

success varied slightly with a combined success of 56.1% (Table 19). The success of eggs laid which fledged young varied from 26.7% in 1976 to 41.7% in 1974. The overall fledging success of eggs was 34.9%.

Nestling success. - Nestling survival from hatching to fledging varied from 47.8% in 1976 to 74.7% in 1974 (Table 19). The overall fledging success of eggs that hatched was 62.3%.

Clutch success in relation to season. - Table 20 illustrates the clutch success in biweekly intervals for clutches found before the last egg was laid. Clutches used were not necessarily complete, since some failed before the full complement of eggs had been laid. For the three breeding seasons, clutch success increased fom 36.7% during the 25 May to 7 June period to 55.6% during 22 June to 5 July. The difference in clutch success was not significant (chi-square, $P > .05$).

Nest success in relation to nest site. - Of the plant species used 10 or more times as a nest site, nest success and the number of young fledged per active nest were greatest in Humulus lupulus followed by Sambucus pubens and Fraxinus pennsylvanica (Table 21).

Nest success in relation to nest height. - Three categories of nest height were recognized (Table 22). They reflect the herb, shrub and tree strata of the vegetation on the ridge, respectively. Nest success was greatest in the tree layer and lowest in the shrub layer

Table 19. Egg and nestling success of active Yellow Warbler nests found before the last egg was laid, 1974-76.

	1974	1975	1976	Total
No. of active nests	36	98	93	227
No. of hatched nests	23	60	65	148
No. of successful nests	20	47	37	104
No. of eggs laid	156	402	416	974
No. of eggs hatched	87	227	232	546
Average number of eggs per active nest	4.3	4.1	4.5	4.3
Percent eggs laid that hatched	55.8	56.5	55.8	56.1
No. of fledglings	65	164	111	340
Percent eggs hatched that fledged young	74.7	72.2	47.8	62.3
Percent eggs laid that fledged young	41.7	40.8	26.7	34.9
Average no. of fledglings per active nest	1.8	1.7	1.2	1.5
Average no. of fledglings per hatched nest	2.8	2.7	1.7	2.3
Average no. of fledglings per successful nest	3.3	3.5	3.0	3.3

Table 20. Success of Yellow Warbler clutches in relation to the season, 1974-76.

Year	25 May - 7 June	8 - 21 June	22 June - 5 July
1974	-	57.9% (22/38)	-
1975	45.3% (24/53)	45.5% (15/33)	45.5% (5/11)
1976	29.9% (20/67)	40.9% (9/22)	71.4% (5/7)
1974-76	36.7% (44/120)	49.5% (46/93)	55.6% (10/18)[1]

[1]Includes one clutch after 5 July, 1975.

Table 21. Success of active Yellow Warbler nests, found before the last egg was laid, in relation to nest-supporting plant, 1974-76.

Species	Active nests	Successful nests	Percent successful	Young fledged per active nest
Humulus lupulus	10	6	60.0	1.9
Sambucus pubens	41	23	56.1	1.9
Fraxinus pennsylvanica	17	8	47.1	1.6
Salix spp.	61	27	44.3	1.3
Acer negundo	57	25	43.9	1.6
Symphoricarpos sp.	1	1	100.0	5.0
Ribes sp.	5	4	80.0	2.2
Cornus stolonifera	3	1	33.3	1.0
Rubus idaeus	9	2	22.2	0.7
Rosa sp.	1	0	0.0	0.0
Prunus sp.	1	0	0.0	0.0

Table 22. Success of active Yellow Warbler nests found before the last egg was laid, in relation to nest height.

	Nest height		
	≤ 1 m	> 1 m ≤ 3 m	> 3 m
Active nests	84	90	33
Successful nests	43	35	19
Percent successful	51.2	38.9	57.6
Young fledged per active nest	1.9	1.1	1.9

Differences in nest success for high nests ($>$ 3 m) and low nests ($\leq$3 m), as well as for the three vegetation strata, were not significant (chi-square, $P > .05$).

Nest success in relation to clutch size. - Table 23 illustrates 10 parameters showing the relationship between clutch size and nest for 117 active nests and 118 clutches. In comparing large (5 eggs) clutches with small (3 and 4 eggs) clutches, no significant differences were found for the parameters examined (chi-square and analysis of variance, $P > .05$). The number of young fledged per active nest increased with increasing clutch size.

Nest success in relation to cowbird parasitism. - The incidence of parasitism in active nests for the three breeding seasons was about 25% (see Part II). Unparasitized nests were more successful in all respects than parasitized nests (Table 24). Significant differences were found for the proportion of eggs laid that hatched, eggs that fledged (chi-square, $P < .05$), fledglings per active nest and fledglings per hatched nest (analysis of variance, $P < .05$). No significant differences were found for eggs laid per active nest and fledglings per successful nest (analysis of variance, $P > .05$).

Mortality

Nest failures. - Of the 227 active parasitized and unparasitized nests, 123 (54.2%) were unsuccessful. The major factor was pre-

Table 23. Clutch size and nest success of the Yellow Warbler.

	Clutch Size 3	4	5	Mean
Number of active nests	4	55	59	4.5
Percent of active nests with hatchlings	100	82	80	81
Percent of hatched nests with fledglings	75	69	68	69
Percent of active nests with fledglings	75	56	54	56
Percent of eggs hatched	83	70	68	69
Number of eggs hatched per active nest	2.5	2.8	3.4	3.1
Number of eggs hatched per hatched nest	2.5	3.4	4.3	3.8
Percent of eggs that produced fledglings	58	47	42	44
Percent of nestlings that fledged	70	67	61	64
Number of fledglings per hatched nest	1.8	2.3	2.6	2.4
Number of fledglings per active nest	1.8	1.9	2.1	2.0

Table 24. Egg and nestling success for parasitized and unparasitized Yellow Warbler nests found before the last egg was laid, 1974-76.

	Parasitized	Unparasitized
No. of active nests	58	169
No. of hatched nests	27	121
No. of successful nests	14	90
No. of eggs laid	235	739
No. of eggs hatched	95	451
Average no. of eggs per active nest[1]	4.1	4.4
Percent eggs laid that hatched[2]	40.4	61.0
No. of fledglings	39	301
Percent eggs hatched that fledged[2]	41.1	66.7
Percent eggs laid that fledged[2]	16.6	40.7
Average no. of fledglings per active nest[2]	.7	1.8
Average no. of fledglings per hatched nest[2]	1.4	2.5
Average no. of fledglings per successful nest[1]	2.8	3.3

[1]Not significant ($P > .05$)

[2]Significant ($P < .05$)

dation, which accounted for 62.6% (77/123) of the nest failures (Table 25). Desertion was the second major factor accounting for 15.4% (19/123) of the failures. Of the 19 deserted nests, 9 (47.4%) were deserted because of cowbird parasitism. Nest failure attributed to the cowbird was 8.9% (11/123).

Of 121 active nests found before the last egg was laid, 93 (76/9%) failed after the laying period (Table 26). Of the three categories (laying, incubating and nestling periods) the most nest failures occurred during incubation.

Egg mortality. - The major factor was predation. Although 21.5% (92/428) of egg mortality was attributed to predation, another 28.0% (120/428) disappeared for no apparent reason (Table 27). Some of the latter group may have been predated or taken by the cowbird.

Nestling mortality. - The major factor was predation. Although 17.5% (36/206) of the nestling mortality was attributed to predation another 50.5% (104/206) of the nestlings disappeared (Table 28). Some of the latter group may have been eggs or dead nestlings which were thrown out by the adults during hatching. Weather accounted for 7.3% (15/206) of the nestling mortality. Most of this mortality occurred in 1976 when a cold spell occurred in June. The cowbird accounted for 6.8% (14/206) of the nestling mortality. Because of the smaller size of Yellow Warbler nestlings, they are crowded out of the nest, starve in the nest or are crowded to death. Loss of young may also occur because of overt cowbird

Table 25. Causes of nest failure in active Yellow Warbler nests found before the last egg was laid, 1974-76.

Factors	Parasitized	Unparasitized	Total	Percent
Predation	15	62	77	62.6
Desertion	13	6	19	15.4
Cowbird	10	1	11	8.9
Weather	1	6	7	5.7
Unknown	3	0	3	2.4
Human disturbance	0	2	2	1.6
Nest position	2	0	2	1.6
Poor nest construction	0	1	1	0.8
Starvation	0	1	1	0.8
Total	44	79	123	99.8

Table 26. Frequency of Yellow Warbler nesting failures compared with stage of nesting cycle.

Nesting Stage	Parasitized	Unparasitized	Total	Percent
Laying	12	16	28	23.1
Incubation	18	31	49	40.5
Nestling	13	31	44	36.4
Total	43	78	121	100.0

Table 27. Factors contributing to egg mortality in active Yellow Warbler nests found before the last egg was laid.

Factor	Parasitized	Unparasitized	Total	Percent
Disappeared	16	104	120	28.0
Predation	26	66	92	21.5
Deserted	32	33	65	15.2
Unhatched	10	38	48	11.2
Cowbird	31	2	33	7.7
Weather	2	19	21	4.9
Human Disturbance	2	12	14	3.3
On ground	5	8	13	3.0
Buried	13	0	13	3.0
Poor nest construction	0	5	5	1.2
Damaged in nest	2	0	2	0.5
Nest position	1	1	2	0.5
Total	140	288	428	100.0

Table 28. Factors contributing to nestling mortality in active Yellow Warbler nests found before the last egg was laid.

Factor	Parasitized	Unparasitized	Total	Percent
Disappeared	25	79	104	50.5
Predation	2	34	36	17.5
Weather	1	14	15	7.3
Cowbird	14	0	14	6.8
On ground	2	7	9	4.4
Human disturbance	2	6	8	3.9
Dead in nest	4	2	6	2.9
Starvation	0	5	5	2.4
Nest position	3	2	5	2.4
Deserted	3	0	3	1.5
Caught in nest	0	1	1	0.5
Total	56	150	206	100.1

predation.

Second clutches

In both 1975 and 1976, there was evidence of the Yellow Warbler attempting to raise a second brood following the success of the first one. At least 6 such cases were observed. In 3 of these cases, the females were color banded. Four of the females laid their second clutches in the original nests. Second clutches were smaller than first clutches (5 eggs→ 4 eggs N=4); 4 eggs→ 2 eggs N=1) in all but one case where the same number of eggs (4) were laid for both clutches. Only one of those second clutch attempts was successful.

DISCUSSION

The apparently unlimited food conditions on the Delta Beach Ridge may directly influence the density and productivity of Yellow Warblers. Ample food resources not only sustain this population but may also permit more eggs to be produced. Thus, with a dense breeding population and a large clutch size, one would expect the total number of young fledged to be greater than in areas where conditions are reversed. This discussion examines whether the dense nesting population of Yellow Warblers on the Delta Beach Ridge produce more young when compared with populations of lower density and smaller clutch size. Factors influencing the timing of breeding and reproductive success are also discussed.

Timing of breeding

Variations in the annual onset of breeding are related to proximate factors (for review see Immelmann 1971). It has been established that in late springs breeding is delayed while in early springs breeding begins sooner than it normally would (Marshall 1951, Goodacre and Lack 1959). This is clearly illustrated by the Yellow Warbler in this study. The springs of 1974, 1975 and 1976 may be described as late, normal and early, respectively. The strong negative correlation between the warmth sum and the first egg date reveals that the breeding season is initiated sooner than normal in warm early springs, while it is hindered by late cool springs. The synchrony in laying for the three seasons also reflected the spring conditions (see Table 4).

Food may be a proximate factor influencing the timing of nesting as may be the case with the Tri-colored Blackbird (*Agelaius tricolor*) (Payne 1969) and the House Martin (*Delichon urbica*) (Bryant 1975). For the Yellow Warbler on the Delta Beach Ridge, a proximate stimulus to the onset of breeding may be the emergence of the Chironomidae (Diptera). Although quantitative data are lacking, the first emergence of adult chironomids that settled on the ridge in 1974 was on 9 June. This was also the date of the first egg laid of the breeding season. In 1975, no chironomids were found in the 25 May arthropod sample (Fig. 4 in Busby 1978), however, in the 1 June sample, they were present. Again, this coincides with the date of the first egg laid of the 1975 season. In 1976, chironomids were present in the 22 May sample (Fig. 5 in Busby 1978) and the first egg was laid on the 26 May. Although there are no data in Fig. 4 for the period prior to 25 May 1975 and 22 May 1976 (before egg laying started), the data suggest that food supplies were low. Food may then be limiting the start of breeding to the period when food supplies are sufficient for the formation of eggs (Lack 1966).

Food is also an ultimate factor which influences bird breeding seasons (Lack 1954, Snow and Snow 1964). Studies have shown that nesting generally coincides with an abundance of food (Gibb 1950, Davis 1971, Bryant 1975). For the Yellow Warbler on the Delta Beach Ridge, the timing of nesting occurs when food is in abundance (Fig.4). The major portion of the food supply consisted of the Chironomidae making up 64% (1975) and 52% (1976) of the arthropods available (Busby 1978).

Correspondingly, chironomids were also the major food item in the diet of the Yellow Warbler (Busby 1978). Chironomids were also an important food item for juveniles. A sample of 7 fledglings in 1975 revealed that 78% (111/143) of the arthropods eaten were chironomids, while in 1976 the value was 71% (164/232) for a sample of 13 fledglings (Busby, unpublished data). The chironomids are then an important food item in the food supply, providing nutrients for both the egg-laying female Yellow Warblers and the survival of the fledglings.

Clutch size

The clutch size of the Yellow Warbler is generally considered to be 4 or 5 eggs (Knight 1907, Stoner 1932, Bent 1953, Tufts 1961). However, two-egg (Schrantz 1943) and 6-egg clutches (Chapman 1907, Smith 1943, Bent 1953) have been reported. The mean clutch size in the present study was higher than that found elsewhere (Table 29). It is possible that unlimited food on the Delta Beach Ridge permits the Yellow Warbler to produce more eggs. Increased clutch size associated with abundant food resources has been reported in other parulids (MacArthur 1958, Zach and Falls 1975) and other species (Gibbs 1950, Southern 1959). Five-egg clutches were the most productive (Table 23). Most 5-egg clutches were produced during the early part of the egg-laying period when the food supply was abundant.

An inverse relationship between clutch size and breeding density has been noted in passerines (Johnston 1956, Perrins 1965, Balen 1973). It appears that for the Yellow Warbler, clutch size is directly related to breeding density (Table 29). This apparent relationship may be the result of two other contributing factors. Variation in food supply in

Table 29. Clutch size in relation to breeding density and location.

Location	Latitude	Density (prs/ha)	Clutch Size	Reference
Michigan	43	2.1[1]	2.9	McGeen (1972)
Wisconsin	43	3.5	3.5	Young (1949)
North Dakota	46-49	-	3.6	Stewart (1975)
Michigan	42	0.2	3.8	Batts (1961)
Utah	42	5.5-8.2[1]	3.9	Frydendall (1967)
Alberta	49-60	-	4.0	Salt (1973)
Iowa	43	-	4.0	Schrantz (1943)
Manitoba	50	19.1	4.5	This study

[1]Values from Busby 1978.

those studies listed may affect the clutch size and the latitude (Lack 1954) may also contribute to the size of clutches laid. Clutch size in those studies above 45^{0} latitude was greater (4.0) than in those below 45^{0} (3.6).

Although the onset of laying varied annually because of spring weather conditions, differences in food supply were small (approximately 8% smaller in 1976 than in 1975) (Busby 1978). Annual variation in clutch size of the Yellow Warbler is not greatly influenced by proximate environmental factors.

Asynchronous hatching

Reproductive success is influenced by patterns of hatching (Howe 1976). An asynchronous hatching pattern may result in the elimination of the youngest nestling through starvation (Willson 1966, Dyrcz 1974) although this is not always the case (Best 1977). Reasons why the phenomenon of asynchronous hatching is considered adaptive are (1) the feeding responsibilities of the parents are eased, (2) incubation is initiated prior to clutch completion thereby reducing the time the eggs are exposed (Lill 1974), (3) mortality in high predation situations is reduced (Hussell 1972), and (4) the brood size is adjusted to the food supply (Lack 1947, 1954, 1966).

Asynchronous hatching has been reported for the Yellow Warbler (Gross 1934, Schrantz 1943, Kammeraad 1964) and its occurrence on the Delta Beach Ridge was due to incubation prior to clutch completion. Young that died in the nest possibly due to starvation in 1976 may have done so because of inclement weather conditions. The food supply appeared to be abundant (Busby 1978) and therefore starvation of the youngest sibling because of asynchronous hatching need not occur.

With high predation rates on the ridge, it is adaptive for Yellow Warblers to commence incubation prior to clutch completion thereby concealing the eggs from predators. Asynchronous fledging provides a better opportunity for some of the young to survive than having all the young at the same developmental stage. With an adequate food supply, spreading out of the parental feeding duties may not be important on the ridge. With easily accessible food resources, time used in foraging may be reduced and the effect of asynchronous hatching on parental feeding tasks may be cancelled out.

Reproductive success

Nest success of the Yellow Warbler ranges from 42% to 75% (Table 30). Success of nests in the present study (48%) falls within the range of these studies. Nest success in open-nesting altricial birds ranges from 38% to 77% with an average of 49% (Nice 1957). These figures must be viewed with caution since the procedures were not outlined in 17 of 35 studies and may include nests found after clutch completion which would bias them toward success (Woolfenden and Rowher 1969). There are several studies of parulids which have attempted to minimize the bias toward success. Mayfield (1960) found nest success to be about 45% for the Kirtland's Warbler (*D. kirtlandii*), while for the Yellow-breasted Chat (*Icteria virens*) and Prairie Warbler (*D. discolor*) it was 22% (Thompson and Nolan 1973) and 15% (Nolan 1963) respectively. Both hatching success and fledging success of eggs laid in the present study were the second lowest value when compared to those studies cited in Table 30. However, fledging success of nestlings in

Table 30. Reproductive success of the Yellow Warbler.

No. of nests	Hatching Success (%)	Fledgling Success (%) (Eggs)	Fledgling Success (%) (Nestlings)	Nest Success	Productivity[1]	Source
41	71	54	76	-	2.2	Schrantz (1943)
12	48	33	70	42	2.8	Young (1949)
16	-	-	-	75	-	Kendeigh (1941)
20	57	39	67	45	1.5	Batts (1961)
15[2]	84	-	-	-	-	Salt (1973)
262	-	38	-	-	-	McGeen (1972)
29	-	-	-	69	-	Kendeigh (1942)
227	56	35	62	48[3]	1.5	This study

[1] Young fledged per nest

[2] Data from Prairie Nest Records Scheme

[3] Based on 235 active nests found before the last egg was laid

this study was the lowest value compared to the other studies. Productivity (young fledged per nest) in this study shared the lowest value with that of Batts' (1961) value. It is evident from these comparisons that the reproductive success of the Yellow Warbler on the Delta Beach Ridge is not unusually high. In fact, it is lower than most studies. A superabundant food supply does not necessarily guarantee a high fledging success since predation and cowbird parasitism reduce the potential reproductive success. Predation was the major cause of nest failures (Table 25) and may be the main factor which prevents the Yellow Warbler from producing more young on the ridge. However, with a dense breeding population and a low productivity, more young will be fledged per unit of habitat than at low population levels. Thus the dense population of Yellow Warblers on the Delta Beach Ridge does not produce more young per nest as a result of an unlimited food supply but rather nests in high numbers to produce more young at a low productivity rate. Green (1977) has shown that in an increasing breeding population of birds, the number of young produced can increase even though the apparent value decreases. Breeding at high densities as compared to low may result in increased reproductive success. Robertson and Norman (1977) found at Delta, Manitoba that most passerine hosts to the cowbird including the Yellow Warbler, had higher fledging success at high nest densities compared to low. They attributed this difference to host mobbing in high density situations, thereby reducing the frequency of parasitism.

Nest success has been reported to increase with the advance of the breeding season (Longcore and Jones 1969, Roseberry and Klimstra 1970, Thompson and Nolan 1973, this study). This may be attributed to the development of vegetation cover as the season progresses, increased nestling attention by adults because of the smaller clutch sizes of renests (Longcore and Jones 1969) and changes in the diets, activities, numbers or species of predators (Nolan 1963). In the present study, nest success was lower in an early breeding season (1976) than in the later season of 1974 (Table 18). It is suggested that some of the factors which influence nest success over a season also affect annual nest success, depending upon when the breeding season was initiated.

It has been shown that nest success increases (Holcomb 1969) or decreases with nest height (Longcore and Jones 1969, Holcomb 1972). Although not significant, Yellow Warbler nest success on the Delta Beach Ridge was lower in nests below 3 m than in nests that were higher. One factor which decreased nest success, especially those nests less than 3 m, was cowbird parasitism. With the mean height of parasitized nests being 1.1 m (Part II), nests less than 3 m have a greater probability of being parasitized and unsuccessful. High nests are less susceptible to parasitism and enjoy a greater probability of success. Nest success relative to height may be influenced by the limit of height at which predators are active. Defoliation of vegetation by the Forest Tent Caterpillar (*Malacosoma disstria*) in 1976 may have aided predators in locating nests, however, Fashingbauer *et al*. (1957) found that nest success was actually greater in a defoliated plot than in a control (undefoliated) plot. Higher nest heights in 1976 may be explained by the fact that defoliation may have rendered nests and activities of Yellow Warblers more visible than in the previous two years.

One way in which a bird can contribute to increasing its reproductive potential is by raising a second brood (Marshall and Balda 1974). However, the occurrence of second broods is dependent upon the earliness of breeding while the food supply may determine their frequency (Dunnet 1955). There is evidence that at least some Yellow Warblers on the Delta Beach Ridge attempt to raise a second brood. This reproductive strategy contributes to maximize Yellow Warbler productivity in a region where productivity is low.

PART II

COWBIRD PARASITISM ON THE YELLOW WARBLER

INTRODUCTION

The Yellow Warbler (Dendroica petechia) is a frequent host of the Brown-headed Cowbird (Molothrus ater) (Bent 1953, Friedmann 1963). Since parasitism decreases the number of young fledged by the host (Mayfield 1960, Hill 1976), it therefore influences the host's reproductive success. Aspects of cowbird parasitism of the Yellow Warbler have been examined by McGeen and McGeen (1968) and McGeen (1971, 1972). Rothstein (1975) and Robertson and Norman (1976, 1977) have examined its response as a host. In this paper, I examine aspects of cowbird parasitism of a dense population of Yellow Warblers.

STUDY AREA AND METHODS

This investigation was carried out during the breeding seasons of 1974-76 on the forested beach ridge between Lake Manitoba and the Delta Marsh, Manitoba ($50^{\circ}11'$ $98^{\circ}19'$). Nests were checked almost daily, the regularity of daily inspection increasing with each season. Only active nests were considered in this analysis. In determining the timing of cowbird egg laying, it was assumed that the Yellow Warbler had laid at least a 4-egg clutch. Further information on the study area and methods may be found in Part I.

RESULTS

The cowbird's laying season for the 3 years of the study began in the fourth week of May and extended to the second week in July (Fig. 1). Cowbirds laid from 1 to 3 eggs per active nest (Table 1). One cowbird egg laid per active nest occurred in 85% of the 82 nests. The annual difference for the mean number of cowbird eggs laid per season was small with a pooled mean of 1.2 eggs per active nest. Parasitism was 23.6% to 26.1% with an average of 24.8% in 331 active nests in the study. Cowbirds laid their eggs during the early stages of Yellow Warbler nest activities (Table 2). Cowbird eggs laid before incubation (incubation defined as after the last or fourth egg was laid) comprised 83% of all cowbird eggs laid. Parasitism was most frequent (58.3%) during the laying period of the host.

Yellow Warblers responded to parasitism in two ways. They either accepted or rejected the cowbird egg. Rejection resulted in nest desertion or burial of the cowbird egg; a new floor was then added to the nest. Of 72 cowbird eggs laid in active nests, 40% were accepted and 60% were rejected (Table 3). Most rejected eggs were buried.

Those nests higher than 4.91 m were not parasitized (Table 4). The mean height of unparasitized nests was almost twice that of parasitized nests (z test, $P < .05$).

Figure 1. Exact dates for cowbird eggs laid in active Yellow Warbler nests. Arrows indicate mean clutch initiation date of the Yellow Warbler.

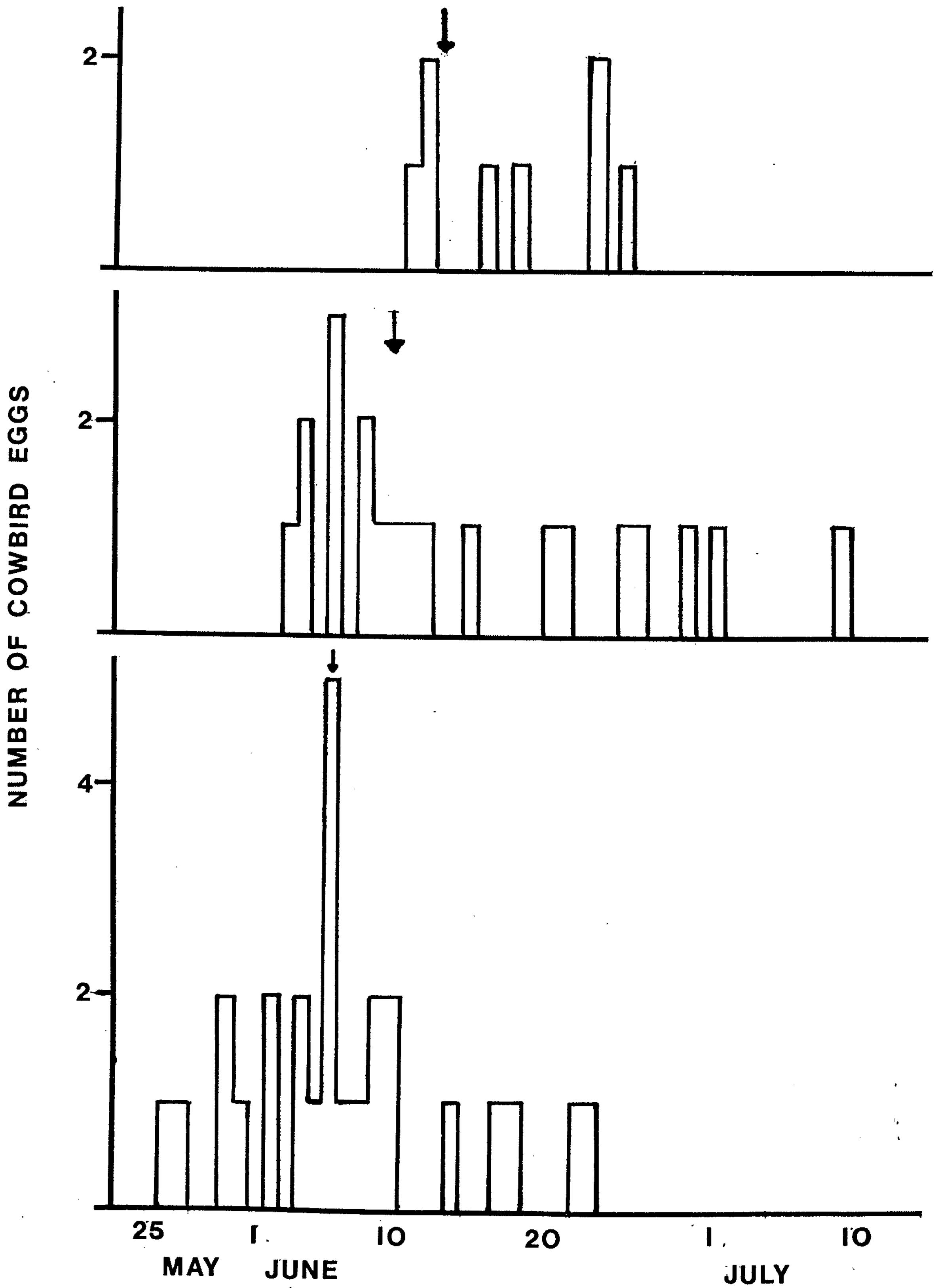

NUMBER OF COWBIRD EGGS
2
2
4
2
25
1
10
20
1
10
MAY
JUNE
JULY

Table 1. Frequency of cowbird parasitism on the Yellow Warbler, 1974-76 .

Year	No. of cowbird eggs laid per active nest			Mean	No. of active nests	Percent parasitism
	1	2	3			
1974	12	3	1	1.3	64	25.0
1975	27	4	0	1.1	119	26.1
1976	31	3	1	1.1	148	23.6
Total	70	10	2	1.2	331	Mean 24.8

Table 2. Timing of cowbird egg deposition in active Yellow Warbler nests, 1974-76.

Nest stage	1974	1975	1976	Total	Percent
Prelaying	5	6	4	15	25.0
Laying	5	14	16	35	58.3
Incubation	2	2	4	8	13.3
Nestling period	1	0	1	2	3.3
Total	13	22	25	60	99.9

Table 3. Response of the Yellow Warbler to cowbird parasitism, 1974-76.

	Number of cowbird eggs				
Response	1974	1975	1976	Total	Percent
Accepted	4	11	14	29	40.3
Buried	13	9	9	31	43.1
Deserted	1	4	7	12	16.7
Total	18	24	30	72	100.1

Table 4. Comparison of nest height (cm) of active unparasitized nests and all parasitized nests.

	N	Mean and S. E.	Range
Unparasitized	242	200.1 ± 10.32	27.0 - 854.0
Parasitized	77	109.7 ± 10.26	21.0 - 491.0

DISCUSSION

Several studies have examined the incidence of cowbird parasitism on the Yellow Warbler. Hicks (1934) found 62 of 142 (42%) nests in Ohio were parasitized. Parasitism rates as high as 65% (14 nests) and 70% (10 nests) have been reported for London, Ontario (Scott 1977). Robertson and Norman (1977) found parasitism in Ontario was 30.0% of 484 nests. Parasitism in this study was 24.8%, slightly higher than that reported by Robertson and Norman (1977) who found cowbird parasitism to be 20.6% (102 nests) in Manitoba. Variation in cowbird breeding densities may explain this difference (see Elliott 1978). Mayfield (1965) considered parasitism to be moderate at the 10-30 percent level.

For the Delta Marsh region, Robertson and Norman (1977) showed that in high host nest densities ($\geq$ 24 nests per ha) parasitism was significantly lower than in low nest densities ($<$ 24 nests per ha). They attributed this difference to the host's mobbing response to cowbird intrusions. Several host species were involved, including Yellow Warblers. Aggression in the Yellow Warbler at a high nest density was greater than at a low nest density. It was suggested that aggressive host behaviour acts as an antiparasite adaptation only in host populations of high density.

The range of cowbird eggs per parasitized nest in the present study is smaller than that found by Scott (1977) where the range was 2 to 7 eggs with a mean of 3.9 (in 1969) and 2.7 (1960-68). Young (1963) summarized several studies and found the mean to be 1.5 eggs.

Berger (1951) reported a range of 1-3 eggs in parasitized Yellow Warbler nests and the mean calculated from his data was found to be 1.8. It has been suggested that if nests are limited, a cowbird will lay more eggs than the usual 1 egg per nest (Hann 1941). Since there is a dense breeding population of Yellow Warblers on the Delta Beach Ridge, the cowbird has numerous opportunities to parasitize their nests. The expected result, a low to moderate incidence of parasitism with each parasitized nest receiving 1 cowbird egg, was found in the present study.

Cowbirds generally lay their eggs in nests during the host's laying period (Hann 1941). Norris (1947) found that cowbird's eggs would be accepted if they were laid in singles and not prior to the laying of the host's eggs. The Yellow Warbler is considered to be a poor host since multiple eggs are infrequently accepted and eggs which are not synchronized with its laying period are not tolerated (McGeen 1971). Synchronization, in McGeen's study, was 42.5% with a desertion or burial rate of 86.5%. In the present study, synchronization differed only slightly from rejection (58.3% and 59.7%, respectively). Variables promoting the differences found in McGeen's and this study may include the densities of Yellow Warbler and cowbird populations as well as their historical exposure to each other.

Host species of the cowbird are divided into two groups: rejectors and acceptors. The Yellow Warbler is considered an acceptor species by Rothstein (1975). He found that in 16 cases of parasitism, with real and artificial eggs, all were accepted by the Yellow Warbler.

He contends that egg burial and nest desertion are not antiparasite adaptations. He suggests that desertion may be the result of researcher visits to the nest, alteration of clutch size by the cowbird (therefore interfering with the normal stimulus of incubation) or the host's discovery of the cowbird at the nest. Egg burial is equated with the bird's response to a strange object in the nest. He suggests that the delay caused by egg burial may result in nest stages (nest building and laying) occurring simultaneously rather than consecutively as is the usual pattern. This would, therefore, explain why host eggs may also be buried.

In the present study, frequency of nest desertion was about 4 times greater for parasitized nests (29.5%) than for unparasitized nests (7.6%). At least 20.5% of the desertion in parasitized nests were attributed directly to the cowbird. This would mean that parasitized nests still were deserted about 3 times as often as unparasitized nests. Since both types of nests were visited by the author, the frequency of desertion because of human disturbance should be the same. These data suggest desertion due to researcher visits should be minimal. The normal stimulus to incubation is not necessarily affected by an increase in surface area of eggs since Yellow Warblers incubated up to 5 eggs plus a cowbird egg. The third argument can not be refuted since the Yellow Warblers' response to the cowbird at the time of parasitism was not observed.

Egg burial was more frequent than desertion. Of 72 cowbird eggs, 31 (43.1%) were buried while 12 eggs (16.7%) were deserted. Rothstein (1975) suggested that to show whether egg burial is indeed a response to the presence of the cowbird egg, parasitized nests should result in egg burial of the cowbird egg and host egg(s) while egg burial should not occur in unparasitized nests. During 1976, Yellow Warblers buried cowbird eggs along with their own eggs. A single case of egg burial in an unparasitized nest was recorded in 1976. Predation was probably responsible for this behaviour. The evidence suggests that egg burial is a common event in parasitized nests. Experiments comparing the response to strange items and cowbird eggs are needed to show conclusively whether Yellow Warblers respond specifically to the cowbird egg or whether they respond generally to any strange object in the nest. Until further data clarify the response of the Yellow Warbler to the cowbird eggs, nest desertion and egg burial should be considered as potential antiparasite adaptations for this species.

Studies by Wiens (1963) and Nolan (1963) have shown no preferred nest height at which parasitism occurs. In the present study, parasitized nests were significantly lower than unparasitized nests. The explanation may be found when examining the historical habitat and habits of the cowbird. Historically, cowbirds inhabited grassy prairies (Mayfield 1965). Mayfield suggests that grassland hosts are less tolerant of the cowbird because of the long exposure to it,while hosts in forested regions tolerate it more because of less exposure to the cowbird. Since cowbirds originally would have parasitized hosts which nested on the ground or close to it, they would, therefore, select low host nests in forested regions. There is ample opportunity for nest parasitism on the Delta Beach

Ridge because of the dense passerine population. Cowbirds, therefore, have no difficulty in selecting their preferred low nest height.

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