

# COMPARATIVE BREEDING BIOLOGY OF HARRIS' SPARROWS AND GAMBEL'S WHITE-CROWNED SPARROWS IN THE NORTHWEST TERRITORIES, CANADA<sup>1</sup>

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**Abstract.** I studied the breeding biology of Harris' Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Z. leucophrys gambelii*) in the forest-tundra ecotone of the Northwest Territories, Canada from 1989 to 1991. Adult sex ratio was 1:1 for Harris' Sparrows, and approximated 1:1 for the smaller number of White-crowned Sparrows captured. Nesting cycles of Harris' Sparrows and White-crowned Sparrows were similar, and appeared to be affected by patterns of snow melt and arthropod abundance. Adults began arriving during the last week in May; most initiated nesting during the second or third week in June, after breeding habitat was at least 60% snow-free. During all years of the study, the peak in fledging occurred just prior to maximum arthropod abundance. Clutch size and egg mass as a percentage of adult mass did not differ between the species. Only female Harris' Sparrows and White-crowned Sparrows incubated eggs and brooded nestlings, but males and females of both species fed young. Mean length of the incubation period for Harris' Sparrows (12.8 days) was shorter than previously reported. Length of the nestling period and patterns of nestling growth and development were very similar in the two species. Breeding densities of White-crowned Sparrows averaged about 30% that of Harris' Sparrows, but egg success (young fledged/eggs laid) and productivity (young fledged/pair) was higher for White-crowned Sparrows. Lower productivity for Harris' Sparrows was caused by predation on eggs and nestlings by arctic ground squirrels (*Spermophilus parryii*) and short-tailed weasels (*Mustela erminea*). Lower breeding density of White-crowned Sparrows probably was due to a lack of suitable breeding habitat, perhaps combined with a lower return rate for adult White-crowned Sparrows during some breeding seasons. I observed little evidence of interspecific competition between the species.

**Key words:** *Breeding biology; predation; Northwest Territories; Harris' Sparrow; Zonotrichia querula; White-crowned Sparrow; Zonotrichia leucophrys.*

## INTRODUCTION

Crowned sparrows (*Zonotrichia*) are among the best studied groups of passerines in the Western Hemisphere (deGraw and Kern 1990). The breeding biology of the White-crowned Sparrow (*Z. leucophrys*), White-throated Sparrow (*Z. albicollis*), and Rufous-collared Sparrow (*Z. capensis*) have been examined in detail (Miller and Miller 1968, Morton et al. 1972a, King 1973, Knapp et al. 1984, King and Mewaldt 1987, and many others), but the breeding biology of the Harris' Sparrow (*Z. querula*) has received little attention. The Harris' Sparrow is a medium-distance intracontinental migrant that winters in the midwestern United States (Root 1988) and breeds in the forest-tundra ecotone of northern Canada (Godfrey 1986). Although some descriptive information on its breeding biology has

been published (Semple and Sutton 1932, Baumgartner 1968), no comprehensive study of the species has been completed, and such basic data as length of the nesting cycle, and whether both the male and female incubate, are not available (Ehrlich et al. 1988).

In the summers of 1989, 1990, and 1991, I studied the breeding biology of the Harris' Sparrow in the Northwest Territories (NWT), Canada. Data on the Harris' Sparrow are compared to those for a sympatric population of Gambel's White-Crowned Sparrows (*Z. leucophrys gambelii*). The breeding biology of *Z. l. gambelii* has been studied extensively at latitudes in Alaska similar to that at my study site (Oakeson 1954, King et al. 1965, King and Hubbard 1981). Here I report on the nesting cycle, nestling growth and development, and effects of biotic and abiotic factors on nest success. I chose a comparative approach because comparison of life history traits among sympatric species may be useful in eval-

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uating the adaptive basis of differences in reproductive biology (e.g., Maher 1964, Lyon and Montgomerie 1987, Veiga 1990).

## STUDY AREA

The study was conducted at Warden's Grove (WG), Thelon Game Sanctuary, NWT, Canada (63°41'N, 104°26'W). The 2.0 km<sup>2</sup> study area was located adjacent to the Thelon River on a gentle, east-facing slope with an average elevation of about 200 m. The Thelon River Valley supports extensive stands of white and black spruce (*Picea glauca* and *P. mariana*) growing beyond the northern forest border. Tree islands from <0.01 ha to 12.3 ha are scattered along drainages and rocky benches throughout the area. A thick understory of mosses, dwarf birch (*Betula glandulosa*), Labrador tea (*Ledum groenlandicum* and *L. decumbens*), willow (*Salix* spp.), green alder (*Alnus crispa*), and bilberry (*Vaccinium uliginosum*) grows beneath most forest stands. [Common and scientific plant names follow Porsild and Cody (1980)]. Tree islands are typically surrounded by shrubby dwarf birch, willow, Labrador tea, bilberry, and green alder 0.3–1.5 m high. This dwarf birch community provides the primary nesting habitat for Harris' Sparrows and White-crowned Sparrows.

Extensive tundra separates tree islands from one another. Four tundra communities were recognized at WG: low *Carex* meadow, tussock muskeg, dry heath, and rockfield. Low *Carex* meadows are poorly-drained areas dominated by sedges (*Carex* spp.) and cottongrass (*Eriophorum vaginatum* and *E. angustifolium*). Tussock muskeg is characterized by cottongrass hummocks. Dry heath is dominated by lichens, scattered dwarf birch, and evergreen subshrubs, including alpine bearberry (*Arctostaphylos alpina*), alpine azalea (*Loiseleuria procumbens*), dwarf Labrador tea (*Ledum decumbens*), mountain cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*). Rockfield vegetation occurs on dry, rocky sites with <10% cover; common species include those found in dry heath, along with prickly saxifrage (*Saxifraga tricuspidata*) and mountain avens (*Dryas integrifolia*). In 1989 I ran transects through the study area to determine relative proportion of the area occupied by each plant community. The most common community was dry heath (0.28 of the study area), followed by dwarf birch (0.27), tussock muskeg (0.18), rockfield (0.12), spruce (0.10), and low

*Carex* (0.05). Detailed descriptions of plant communities of the forest-tundra ecotone are found in Larsen (1965).

The climate of the Thelon River Valley is characterized by long, cold winters, short, generally cool summers, and variable weather patterns. There are no long-term meteorological data for the area; the closest weather station is Reliance, NWT, 290 km southwest of WG. Data collected during the study represent the only records available for May–July (Table 1). The summer of 1989 was warmer and drier than in 1990 and 1991; temperatures averaged about 2°C above normal, and precipitation about 60% below normal, over much of the NWT (Environment Canada 1989). Snow melt and plant phenology were 3–5 days advanced over 1990 and 1991. The summers of 1989, 1990, and 1991 were relatively mild. Even so, violent storms may occur after the arrival of breeding migrants. During previous fieldwork in 1978, a four-day storm in mid-June brought freezing rain, snow, and winds above 110 km/hr and caused extensive mortality among breeding passerines (Norment 1985). A storm on 28–30 May 1991, with a daily minimum of –10.5°C, deposited 26 cm of snow and caused most adult *Zonotrichia* to temporarily disappear from the study area (see below).

## METHODS

I conducted fieldwork between 21 May–23 July 1989, 27 May–21 July 1990, and 24 May–17 July 1991. Previous observations were made in August and September 1977, and from 1 May–8 July 1978. Adult sparrows were caught in mist nets or Potter traps and marked with a single USFWS/CWS aluminum band and a unique combination of colored, plastic bands. Birds were weighed on a 50 g Pesola scale to the nearest 0.1 g. Tarsus length was measured to the nearest 0.1 mm with a caliper. I evaluated reproductive condition of males by examining the cloacal protuberance (CP; King and Mewaldt 1987: CP index on a scale of 0 to 3, with CP 2 and 3 indicating enlarged and turgid protuberances). I estimated the reproductive condition of females by brood patch (BP) development (King and Mewaldt 1987: BP index on a scale of 0 to 4, with BP1 and 2 occurring during egg laying, and BP2 and 3 during incubation). A scheme for determining fat classes (FC) in *Z. l. oriantha* (Morton et al. 1973) was used to describe levels of subcutaneous fat (FC index on a scale of 0 to 5, with 0

TABLE 1. Weather data recorded at Warden's Grove, Northwest Territories, 1989–1991.

	Mean ambient temperature (°C)	Mean wind speed (km/hr)	Total precipitation (mm)
1989			
May (8 days)	−3.9	11.6	5.0
June	9.7	6.5	4.6
July (23 days)	16.0	11.8	5.2
1990			
May (4 days)	5.5	14.1	0.0
June	7.5	12.3	42.1
July (20 days)	13.4	18.3	18.1
1991			
May (4 days)	−1.2	18.5	26.0
June	7.5	12.6	36.4
July (16 days)	12.5	13.7	6.6

indicating no subcutaneous fat and 5 bulging fat deposits).

Sparrow nests were located by searching breeding habitat or following birds to their nests. Population estimates were derived from a combination of known nests and repeated observation of pairs in specific areas; usually at least one member of each pair was banded. In each year the number of known nests accounted for at least 75% of the estimated Harris' Sparrow population (Table 2).

Each nest was visited daily between 08:00 and 12:00 MST to check its condition. Once the clutch was complete, the eggs were marked, weighed to the nearest 0.05 g on a Pesola scale, and measured to the nearest 0.1 mm with a caliper; egg volumes (V) were calculated with the equation

$$V = 0.507LB^2$$

where L = maximum egg length and B = greatest egg breadth (Hoyt 1979). In most nests (about 80%/year) mass and tarsus of all nestlings were measured daily until fledging. Each year a few nests (4–6 Harris' Sparrow and 2–3 White-crowned Sparrow) were left undisturbed to determine length of the nestling phase of the nesting cycle, and to evaluate effects of repeated handling of nestlings on nest predation rates. Undisturbed nests about to fledge young were checked at 8 hr intervals to determine fledging time to within ca. 0.3 days.

Overall growth coefficients for Harris' Sparrow and White-crowned Sparrow nestlings were calculated for mass and tarsus, based on family

TABLE 2. *Zonotrichia* populations and sex ratios based on banded individuals, Warden's Grove study area, 1989–1991.

Year	Harris' Sparrow		White-crowned Sparrow	
	Population <sup>a</sup> (breeding pairs)	Male : female (n) <sup>b</sup>	Population (breeding pairs)	Male : female (n)
1989	24 (18)	1.60:1 (13)	8 (4)	1.50:1 (5)
1990	27 (23)	0.89:1 (36)	8 (4)	1.0:1 (12)
1991	27 (23)	1.12:1 (51)	7 (5)	1.0:1 (18)
Cumulative sex ratio		0.98:1 (81)		1.0:1 (32)
Cumulative capture ratio <sup>c</sup>		1.37:1 (204)		1.21:1 (62)

<sup>a</sup> Number in ( ) equals number of first nests found within the study area.

<sup>b</sup> Sex ratios based on total number of banded individuals of each sex observed on the study area; ( ) indicates sample size.

<sup>c</sup> Cumulative capture ratio based on total number of captures, including repeats.

means for all broods surviving until day 7 during all years, and a logistic growth model (Ricklefs 1968). The BMDP program AR (Dixon et al. 1990) was used to estimate K (relative growth rate, as a proportion of the asymptote/day), A (asymptote size), and I (age at inflection point, or maximum growth rate). I compared growth coefficients between species using values calculated for individual broods surviving to at least day 7 after hatching. Means for egg mass and egg volume were also based on clutch means, as values for eggs from single clutches are not independent of one another.

Nest attendance during incubation and nestling feeding was quantified by observing nests from concealed locations, or distances >25 m. Nests of marked birds were observed for periods of about 1 hr distributed throughout the active day. A detailed analysis of these observations will be given elsewhere; here I report only on general nest attendance patterns by males and females.

Between-species comparisons of egg mass and nestling size were made by expressing these parameters as a percentage of adult mass or adult tarsus length (e.g., Veiga 1990). Reference values were based on all initial captures of individuals made during the study (Harris' Sparrow: adult mass = 35.56 ± 2.17 g, n = 81; adult tarsus length = 23.27 ± 0.93 mm, n = 81; White-crowned Sparrow: adult mass = 27.61 ± 1.69 g, n = 32; adult tarsus length = 21.85 ± 0.92 mm, n = 32;  $\bar{x}$  ± SD given throughout paper). Percentages relating nestling size or egg size to adult

size or to values predicted by specific equations were arcsine square-root transformed for statistical comparisons.

Arthropod abundance was sampled with pitfall traps and sticky boards (Norment 1987). Arthropods were sampled at 24 permanent stations, each consisting of a 10 cm × 10 cm Plexiglas sticky board coated with Tanglefoot® and a 7.5 cm diameter cup containing ethylene glycol. Six stations were located 30 m apart in each major *Zonotrichia* foraging habitat: spruce forest, tussock muskeg, dry heath, and dwarf birch. Sticky boards and pitfall traps were operated simultaneously for 24 hr periods at ca. 10 day intervals. Arthropods ≥ 2 mm were counted and identified to order.

I measured temperatures with Atmospheric Environment Service Canada (AES) maximum-minimum thermometers placed 1.5 m above ground in a shaded location; rainfall was measured with an AES precipitation gauge. Wind speed was measured with a SIMS Model BTC handheld anemometer. Progression of snow melt was estimated by measuring snow cover along 1,600 m of transects placed in *Zonotrichia* nesting habitat; transects were equally divided between lines placed at the forest edge and parallel lines 50 m out on the tundra.

Statistical procedures are from Sokal and Rohlf (1981). Data were log-transformed to correct for nonnormality when appropriate.

## RESULTS AND DISCUSSION

### POPULATION AND SEX RATIO

Harris' Sparrow and White-crowned Sparrow densities were relatively constant during the three-year period (Table 2). Densities averaged 13.0 pairs/km<sup>2</sup> for Harris' Sparrows and 3.8 pairs/km<sup>2</sup> for White-crowned sparrows over the entire study area, but patches of suitable habitat supported higher numbers. In 1989 and 1990 one 12.3 ha tree island surrounded by dwarf birch had 10 nesting pairs of Harris' Sparrows (81.6 pairs/km<sup>2</sup>) and two pairs of White-crowned Sparrows (16.3 pairs/km<sup>2</sup>). There are few data on *Zonotrichia* populations in the forest-tundra ecotone of Canada. White-crowned Sparrow and Harris' Sparrow densities in a forest-edge plot at Churchill, Manitoba were 57.5 and 12.5 pairs/km<sup>2</sup>, respectively (Gillespie and Kendeigh 1982), but Harris' Sparrows are more abundant than White-crowned Sparrows in the forest-tundra zone to the north

and west of Hudson Bay (Manning 1948, Harper 1953, Mowat and Lawrie 1955, McLaren and McLaren 1981).

The adult sex ratio, based on banded individuals, was essentially 1:1 for Harris' Sparrows ( $n = 81$ ; Table 2). Relatively few adult White-crowned Sparrows ( $n = 32$ ) were banded, but the sex ratio for this species also appeared to approximate 1:1 (Table 2). Capture ratios (number of males : females captured, including all repeats) were biased towards males for both species (Table 2), although capture ratios did not differ significantly from adult sex ratios (Harris' Sparrow:  $\chi^2_{(1)} = 1.680$ ,  $P = 0.195$ ; White-crowned Sparrow:  $\chi^2_{(1)} = 0.198$ ,  $P = 0.656$ ). These results are similar to those from other *Zonotrichia* populations (Baker et al. 1981, Petrinovich and Patterson 1982). Because male White-crowned Sparrows are more likely than females to be trapped (King and Mewaldt 1987), it is difficult to conclude that the sex ratio is other than 1:1 in populations which apparently are biased towards males (Morton et al. 1972a, Hubbard 1978, King and Mewaldt 1987).

### ARRIVAL ON THE BREEDING GROUNDS

Harris' Sparrows arrived on 26 May 1978, which was a late spring (Environment Canada 1978), and 23 May 1989; White-crowned Sparrows arrived on 21 May 1978 and 26 May 1989. Poor weather in 1990 and 1991 prevented access to WG until after the first birds had arrived. Capture data between 21 May and 31 May are insufficient to allow a complete description of arrival patterns for male and female *Zonotrichia*. However, available data suggest that patterns differ between the species, with male and female Harris' Sparrows arriving on the breeding grounds at about the same time, while male White-crowned Sparrows arrive prior to most females. Sex ratios for individuals captured at WG between 1 and 3 June, the first dates for which I have adequate data, differed significantly ( $\chi^2_{(1)} = 5.926$ ,  $P = 0.0149$ ) between Harris' Sparrows (0.74:1,  $n = 33$ ) and White-crowned Sparrows (3.20:1,  $n = 21$ ). Sex ratios of birds trapped on 23–24 May 1991 at the Hoarfrost River, NWT (62°52'N, 109°16'W), about 20 km from *Zonotrichia* breeding habitat, also was less biased towards males in Harris' Sparrows (1.50:1) than in White-crowned Sparrows (3.00:1), although the difference was not significant ( $\chi^2_{(1)} = 1.082$ ,  $P = 0.2983$ ). Data from other *Zonotrichia* popula-

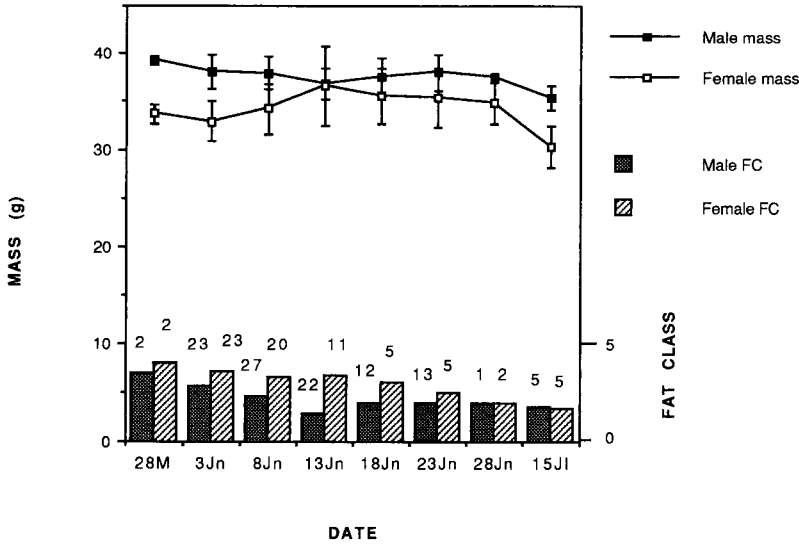


FIGURE 1. Seasonal changes in mass and fat class (FC) for male and female Harris' Sparrows in five day intervals. Vertical lines show  $\pm 1$  SD for change in mass. Dates on abscissa represent midpoints for sampling periods; data were summed and averaged for initial captures of individuals within each period from 1989 to 1991. Sample sizes are number of individuals measured within each sampling period.

tions are consistent with the observed bias towards males in early-arriving White-crowned Sparrows, but not in Harris' Sparrows. Male *Z. l. gambelii* arrive on their Alaskan breeding grounds before most females (Oakeson 1954, King et al. 1965, DeWolfe 1968a), while male and female Harris' Sparrows apparently arrive simultaneously at Churchill, Manitoba (Semple and Sutton 1932).

#### SEASONAL CHANGES IN PHYSICAL CONDITION

Most males had functional testes when first captured; 95.8% of male Harris' Sparrows ( $n = 24$ ) and 88.2% of male White-crowned Sparrows trapped at WG before 6 June had CP scores of 2 or 3. Harris' Sparrow males collected on 7 June 1990 and 1991 had fully enlarged testes. All male *Zonotrichia* trapped on 23–24 May 1991 at the Hoarfrost River had CP scores of 0 or 1, which suggests that rapid enlargement of the seminal vesicles occurs immediately after males arrive on the breeding grounds. CP scores remained high until early July. All male Harris' Sparrows examined after 10 July ( $n = 5$ ) had CP scores of 0 or 1. Females did not develop functional brood patches until after 10 June; four of 11 female Harris' Sparrows and one of seven female White-crowned Sparrows trapped between 11–15 June

had BP 2 or 3 scores; the percent of trapped birds with functional brood patches increased to over 80% in both species after 15 June. Female Harris' Sparrows collected on 7 June 1989 and 1991 had enlarged ova, but were not in full breeding condition. All females ( $n = 5$ ) examined after 10 July had regressed brood patches.

Patterns of body mass and lipid change differed in male and female Harris' Sparrows (Fig. 1). Male mass, based on means for individuals captured in 5-day intervals, remained relatively constant until late June. Mass decreased rapidly in early July, when most pairs were feeding nestlings, just prior to initiation of postnuptial molt. Females gained mass between their arrival on the breeding grounds and mid-June, when most initiated clutches (see below); as with males, body mass decreased in July. Lipid index (FC) scores were higher for female ( $\bar{x} = 3.2$ ,  $n = 73$ ) than for male ( $\bar{x} = 2.2$ ,  $n = 105$ ) Harris' Sparrows captured within 5-day intervals (Fig. 1; Mann-Whitney  $U = 1,529.5$ ,  $P < 0.0001$ ). Comparison of FC scores for males and females within 5-day intervals indicated that females retained more body lipid than males until 20 June (Fig. 1, Mann-Whitney  $U$ -tests,  $P < 0.05$ ), after which time differences were not significant. Data for White-crowned Sparrows are too limited to depict seasonal trends, but FC scores were also higher for

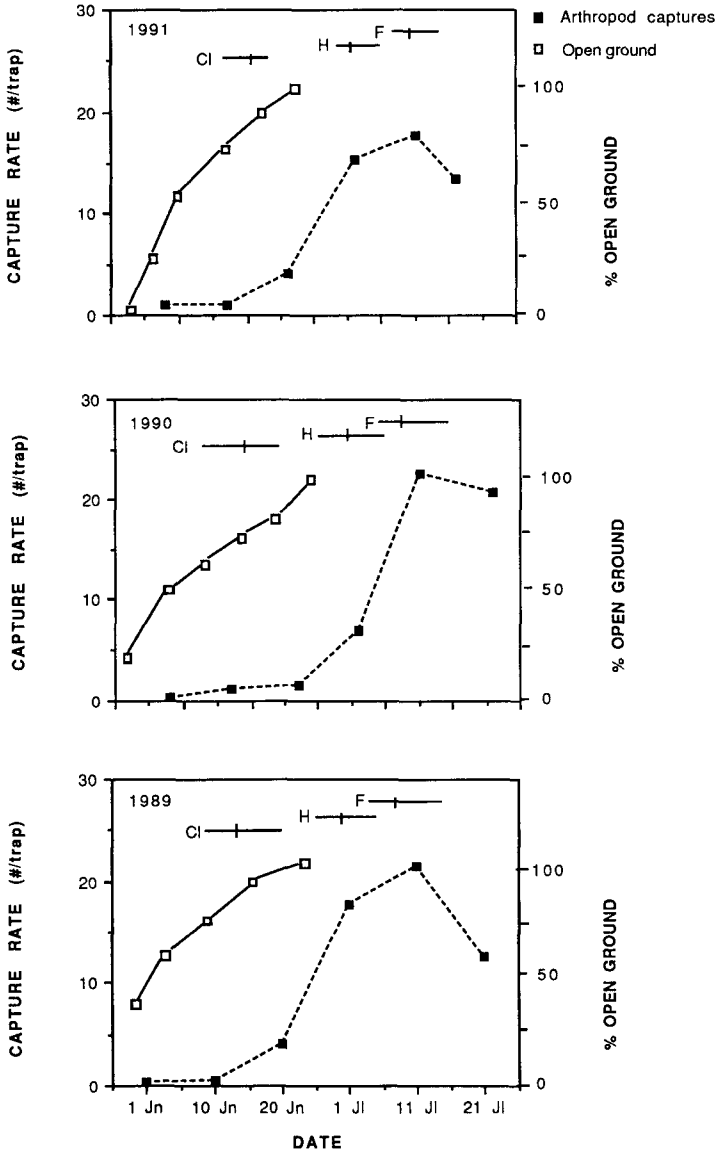


FIGURE 2. Harris' Sparrow nesting chronology, arthropod capture rates on sticky boards, and percent snow-free ground, WG study area, 1989–1991. Horizontal lines show range of dates for stages of nesting cycle; vertical lines show mean dates; CI = clutch initiation, H = hatching, F = fledging.

females ( $\bar{x} = 3.5, n = 22$ ) than for males ( $\bar{x} = 2.8, n = 21$ ) (Mann-Whitney  $U = 90.00, P = 0.0109$ ).

In Alaskan (King et al. 1965) and subalpine (Morton et al. 1973) *Z. leucophrys* populations, lipid levels also were higher in breeding females than in males. Maximum female body mass coincided with the period of maximum ovogenesis,

and male and female body mass decreased prior to the onset of postnuptial molt.

INITIATION OF BREEDING ACTIVITY

In 1989, males of both species began singing within two days of their arrival; in 1990 and 1991, males were already singing when I arrived at WG. In 1989 and 1990, paired birds were

observed by 31 May, but a late snowstorm on 28–30 May 1991 apparently disrupted pair formation. Most *Zonotrichia* temporarily disappeared from WG, and paired birds were not seen until 3 June. Intraspecific territorial chases were infrequently observed in both species; a maximum of eight per day was observed for the more common Harris' Sparrow. Territorial displays are also less frequent in Alaskan *Z. l. gambelii* than in southern *Z. leucophrys* populations (DeWolfe 1968a). The number of territorial chases/day for both species peaked between 5–13 June, the period of the nesting cycle associated with territory establishment and nest construction. Courtship activities, including precopulatory displays (Blanchard 1941), peaked between 6–12 June for Harris' Sparrows and White-crowned Sparrows. Territorial chases and singing by both species decreased in late June, when most pairs were feeding nestlings (Fig. 2). In all years few chases or complete songs were noted after 7 July.

#### NEST CONSTRUCTION AND LOCATION

All marked individuals seen with nesting material ( $n = 4$  for Harris' Sparrows) were females. Because no nests were found at the start of construction, I could not determine the time necessary for Harris' Sparrows to complete their nests. However, back-dating from the hatching of a replacement clutch laid by a female whose first nest was depredated indicated that nests are sometimes constructed in 2.5 days. There are no data available on the time necessary for Harris' Sparrows to build their nests, but nest building takes about 3 days in Alaskan *Z. l. gambelii* (Oakeson 1954). In 1990 and 1991 I checked all nest sites used during previous seasons (Harris' Sparrow:  $n = 41$ ; White-crowned Sparrow:  $n = 8$ ). In two cases, both in 1990, old nest cups were lined with fresh, dried sedges and reused by Harris' Sparrows.

Most *Zonotrichia* nests were placed in dwarf birch habitat at or beyond the edge of spruce islands (Table 3), as described elsewhere (Semple and Sutton 1932, Harper 1953, Rees 1973). Harris' Sparrow nests were further from the forest edge ( $27.9 \pm 38.8$  m,  $n = 64$ , range = -120 to 127 m) than White-crowned Sparrow nests ( $7.2 \pm 6.8$  m,  $n = 14$ , range = 0 to 25 m) ( $t = 3.50$ ,  $P = 0.0008$ ,  $df = 77$ ). Three Harris' Sparrow nests were found in "unusual" locations: one in the interior of a 12.3 ha forest stand, 120 m from the forest edge, and two in tussock muskeg un-

TABLE 3. Nesting habitat and nest site vegetation for *Zonotrichia* at Warden's Grove, 1989–1990.

	Number of nests (%)	
	Harris' Sparrow	White-crowned Sparrow
Nesting habitat		
Dwarf birch	58 (89.2)	12 (85.7)
Spruce	3 (4.6)	2 (14.3)
Tussock muskeg	2 (3.1)	0
Dry heath	1 (1.5)	0
Rock field	1 (1.5)	0
Main concealing plant/material		
<i>Betula glandulosa</i>	44 (67.7)	9 (64.3)
<i>Alnus crispa</i>	5 (7.7)	0
<i>Picea</i> spp.	5 (7.7)	1 (7.1)
<i>Ledum decumbens</i>	5 (7.7)	0
<i>Salix</i> spp.	2 (3.1)	1 (7.1)
<i>Vaccinium uliginosum</i>	1 (1.5)	3 (21.4)
Rock overhang	1 (1.5)	0
Turf overhang	1 (1.5)	0

protected by shrubs. Location of Harris' Sparrow nests in tundra vegetation has not been described previously, but the species sometimes nests in open spruce woods at Churchill (Semple and Sutton 1932). All nests of both species were built on the ground; most were placed beneath dwarf birch (Table 3), although White-crowned Sparrow nests were generally built in thicker, moister vegetation (Norment 1992).

#### CLUTCH INITIATION AND LAYING SCHEDULE

Average interval between nest completion and clutch initiation was  $3.8 \pm 0.7$  days ( $n = 7$ ) for Harris' Sparrows; no White-crowned Sparrow nests were found during nest building. The interval between nest completion and clutch initiation averages 1.2 days for Alaskan *Z. l. gambelii* (Oakeson 1954), but ranges from ca. 3–7 days for *Zonotrichia* at Churchill (Rees 1973). In all Harris' Sparrow nests followed from clutch initiation, eggs were laid singly on consecutive mornings, with no lapses. Back-dating for all first clutches found prior to hatching, based upon an average incubation period of 12.8 days for Harris' Sparrows and 12.0 days for White-crowned Sparrows (see below), and a 1-day laying interval, shows that the earliest Harris' Sparrow clutches were initiated on 8 June 1989 and 1990, and on 12 June 1991 (Table 4). Mean clutch initiation date was 1.5 days later in 1991, with a decreased variance and range of only 7 days (Table 4), al-

TABLE 4. Breeding calendar for *Zonotrichia* at Warden's Grove, 1989–1991. Sample sizes given in parentheses. HS = Harris' Sparrow, WCS = White-crowned Sparrow.

Event	Year					
	1989		1990		1991	
	HS	WCS	HS	WCS	HS	WCS
Clutch initiation (range)	8–20 June	11–16 June	8–19 June	11–19 June	12–18 June	14–16 June
Clutch initiation ( $\bar{x} \pm SD$ ) <sup>a</sup>	13.6 $\pm$ 2.8 (17)	14.2 $\pm$ 2.4 (4)	14.1 $\pm$ 3.4 (22)	14.5 $\pm$ 3.7 (4)	15.3 $\pm$ 1.6 (22)	15.0 $\pm$ 0.8 (5)
Incubation (range)	11 June–5 July	15 June–2 July	11 June–5 July	14 June–3 July	16 June–5 July	18 June–3 July
Incubation period (range, days)	12.0–13.0		12.0–13.0		12.0–13.5	12.0
Incubation period ( $\bar{x} \pm SD$ )	12.5 $\pm$ 0.7 (2)		12.7 $\pm$ 0.5 (4)		12.9 $\pm$ 0.6 (5)	12.0 (1)
Hatching (range)	25 June–5 July	26 June–2 July	25 June–5 July	25 June–3 July	28 June–5 July	29 June–3 July
Hatch date ( $\bar{x} \pm SD$ ) <sup>a</sup>	29.4 $\pm$ 2.4 (17)	29.8 $\pm$ 2.9 (4)	29.4 $\pm$ 3.2 (19)	28.5 $\pm$ 2.8 (3)	30.9 $\pm$ 1.8 (20)	30.1 $\pm$ 0.8 (5)
Nestlings (range) <sup>b</sup>	25 June–10 July	26 June–11 July	25 June–14 July	25 June–11 July	28 June–13 July	29 June–11 July
Fledge (range)	4–11 July	4–11 July	4–14 July	3–11 July	7–13 July	8–10 July
Fledge date ( $\bar{x} \pm SD$ ) <sup>c</sup>	7.7 $\pm$ 3.1 (13)	8.3 $\pm$ 3.6 (4)	7.4 $\pm$ 2.5 (10)	6.7 $\pm$ 4.0 (3)	9.3 $\pm$ 1.6 (16)	9.0 $\pm$ 0.8 (5)

<sup>a</sup> Days after 31 May.

<sup>b</sup> First broods only.

<sup>c</sup> Days after 30 June.



though between-year differences were not statistically significant (ANOVA,  $F_{[2,55]} = 2.07$ ,  $P = 0.1362$ ). The same between-year differences occurred in White-crowned Sparrows, with the latest mean initiation date and narrowest range in 1991 (Table 4). Mean clutch initiation dates for all nests found during the study did not differ between species ( $t = 0.22$ ,  $P = 0.8264$ ,  $df = 72$ ).

Length of the prenesting interval differs between *Z. l. gambelii* in Alaska and *Zonotrichia* at WG. Egg-laying in Alaskan *Z. l. gambelii* usually begins during the last week in May, about seven days after the first females arrive (Oakeson 1954, King et al. 1965, DeWolfe 1968a), and median clutch initiation dates occur during late May or early June (DeWolfe 1968a). The pre-laying interval for Harris' Sparrows and White-crowned Sparrows at WG is about 14 days, about the same duration as in *Z. l. oriantha* populations in California and Colorado (Morton et al. 1972a, Hubbard 1978). The prenesting interval at Churchill also approaches 14 days for both species (Semple and Sutton 1932, Rees 1973).

Early initiation of breeding means that nesting terminates by the end of June, and autumnal migration peaks in mid-August, for Alaskan *Z. l. gambelii* (Oakeson 1954, King et al. 1965, DeWolfe 1968a, Wingfield and Farner 1978). *Zonotrichia* at WG do not terminate nesting until about 10–14 July (see below), and both Harris' Sparrows and White-crowned Sparrows remain at WG until early September (Norment 1985). Arrival and departure dates are similar for *Zonotrichia* at Nueltin Lake, NWT, 450 km southeast of WG (Mowat and Lawrie 1955). Thus adult *Zonotrichia* remain on their Alaskan breeding grounds for about 14 weeks, while those breeding in the forest-tundra ecotone of the NWT begin nesting about two weeks later but are present for about the same length of time, due to a later autumnal migration.

Clutch initiation data suggest that timing of snow melt is important in determining when *Zonotrichia* initiate nest construction and laying. Assuming that nest building takes about three days (Morton 1976), and a four day interval between nest completion and clutch initiation, the earliest Harris' Sparrow nests must have been started on about 1 June in 1989 and 1990 and 5 June in 1991. In 1989 and 1990 at least 35% of the nesting habitat was snow-free by 1 June, but in 1991 the melt was delayed by about four days and <15% of the nesting habitat was snow-

TABLE 5. Mean clutch size ( $\bar{x} \pm SD$ ) and clutch-size distribution for *Zonotrichia* at Warden's Grove, 1989–1990.

Year and species	n	Clutch size			$\bar{x} \pm SD$
		3	4	5	
Harris' Sparrow					
1989 <sup>a</sup>	17	1	9	7	4.37 $\pm$ 0.62
1990	23	2	17	4	4.05 $\pm$ 0.59
1991	21	0	13	8	4.35 $\pm$ 0.49
Cumulative	61	3	39	19	4.26 $\pm$ 0.57
White-crowned Sparrow					
Cumulative	13	1	3	9	4.58 $\pm$ 0.67

<sup>a</sup> ANOVA, among-year differences in clutch size for Harris' Sparrows:  $F_{[2,58]} = 2.05$ ,  $P = 0.139$ .

free on the same date (Fig. 2). Earliest clutch initiation dates for Harris' Sparrows occurred only after the ground was 60% snow-free. Snow-free habitat is necessary for the initiation of breeding in montane *Z. l. oriantha* (Morton 1978), and snow melt influences the breeding chronology of other montane and arctic emberizines (Hussell 1972, Custer and Pitelka 1977, Smith and Andersen 1985, Fox et al. 1987).

Thus differences in length of the prenesting period and timing of the nesting cycle between Alaskan *Z. l. gambelii* and *Zonotrichia* at WG may be due mainly to differences in the timing of snow melt in the two areas. Much of the breeding habitat in Alaska is snow-free by mid-May (Oakeson 1954), while at WG most *Zonotrichia* breeding habitat remains snow-covered until after 1 June.

#### CLUTCH SIZE AND EGG TRAITS

Clutch size was  $4.58 \pm 0.67$  ( $n = 13$ ) for White-crowned Sparrows and  $4.26 \pm 0.57$  ( $n = 61$ ) for Harris' Sparrows; this difference approached statistical significance ( $t = 1.80$ ,  $P = 0.0770$ ,  $df = 72$ ). Modal clutch size was four for Harris' Sparrows and five for White-crowned Sparrows (Table 5). Mean clutch size for White-crowned Sparrows was similar to *Z. l. gambelii* clutch size at Fairbanks (DeWolfe 1968a: 4.56; Morton 1976: 4.89). Clutch size increases with latitude in *Z. leucophrys* (Morton 1976), and appears to do so in Harris' Sparrows. Harris' Sparrow clutches at WG had a higher proportion of five-egg clutches and a significantly greater mean clutch size than at Churchill (58°45'N) or Herchmer (57°30'N), Manitoba (Table 6; Tukey-Kramer procedure,  $P < 0.05$  for pairwise comparisons).

Mean Harris' Sparrow clutch size was smaller

TABLE 6. Mean clutch size ( $\bar{x} \pm SD$ ) and clutch-size distribution for Harris' Sparrows at three breeding localities.

Locality	n	Clutch size			$\bar{x} \pm SD$	Sources
		3	4	5		
Herchmer, Manitoba (57°30'N)	10	5	5	0	3.50 ± 0.53	Egg records, National Museums of Natural Sciences, Ottawa
Churchill, Manitoba (58°45'N)	84	10	64	10	4.00 ± 0.49	Semple and Sutton (1932), Jehl and Smith (1970), Rees (1973), egg records
Warden's Grove, NWT (63°41'N)	61	3	39	19	4.26 ± 0.57	Present study

in 1990 than in 1989 and 1991, although differences were not statistically significant (ANOVA; Table 5). Fewer five-egg Harris' Sparrow clutches also were found in 1990 than in 1989 or 1991, but clutch size distribution did not differ between years ( $\chi^2_{[2]} = 3.299$ ,  $P = 0.192$ ). White-crowned Sparrow sample sizes are small, but the smallest mean clutch size also occurred in 1990 (1989: 4.75 eggs; 1990: 4.0 eggs; 1991: 5.0 eggs). Although between-year differences in Harris' Sparrow clutch size were not statistically significant, the relative lack of five-egg clutches in 1990 suggests that environmental factors influence *Zonotrichia* clutch size. Clutch size of arctic passerines is generally smaller in years with delayed snow melt, due in part to a seasonal decline in clutch size through the nesting season (Williamson and Emison 1971, Hussell 1972, Custer and Pitelka 1977, Fox et al. 1987). However, the 1990 nesting season at WG was not delayed relative to 1989 or 1991 (Fig. 2). Food availability and weather during the prelaying and laying periods of the nesting cycle also could influence *Zonotrichia* clutch size through effects on the energy budgets of breeding females (see Murphy and Haukioja 1986). However, this hypothesis cannot be tested without detailed data on time and energy budgets of female *Zonotrichia*.

Egg mass averaged  $3.09 \pm 0.26$  g/egg ( $n = 58$  clutches) for Harris' Sparrows and  $2.48 \pm 0.13$  g/egg ( $n = 12$  clutches) for White-crowned Sparrows. Egg volume averaged  $3,073 \pm 277$  mm<sup>3</sup>/egg ( $n = 45$  clutches) for Harris' Sparrows and  $2,546 \pm 100$  mm<sup>3</sup>/egg ( $n = 12$  clutches) for White-crowned Sparrows. I compared egg mass of Harris' Sparrows and White-crowned Sparrows by calculating the average egg mass for each clutch as the percentage of the equation

$$E = aW^{0.67},$$

where E = egg mass, W = adult body mass, and a = a constant for each order or family (Rahn et al. 1975, Veiga 1990). The difference between species was significant (Harris' Sparrow:  $86.2 \pm 7.1\%$  of expected egg mass,  $n = 58$ ; White-crowned Sparrow:  $81.2 \pm 4.3\%$  of expected egg mass,  $n = 12$ ; separate *t*-test for unequal variances,  $t = 2.63$ ,  $P = 0.013$ ,  $df = 30.7$ ). Thus Harris' Sparrows lay a relatively larger egg than do White-crowned Sparrows. These results should be interpreted cautiously because I did not correct for loss of egg mass during incubation. White-crowned Sparrow eggs lose 18% of their mass during incubation (King and Hubbard 1981), and mass loss averaged  $11.5 \pm 4.1\%$  ( $n = 10$  clutches) for Harris' Sparrow eggs in clutches weighed on day 0 and day 12 of incubation. Additionally, egg mass as a simple percentage of adult mass did not differ between species (Harris' Sparrow:  $8.7 \pm 0.7\%$ ,  $n = 58$ ; White-crowned Sparrow:  $9.0 \pm 0.5\%$ ,  $n = 12$ ; separate *t*-test for unequal variances,  $t = 1.51$ ,  $P = 0.1367$ ,  $df = 23.5$ ).

#### INCUBATION

Only female Harris' Sparrows and White-crowned Sparrows incubated eggs. Incubation period, defined as the interval between laying of the last egg in a clutch and the day the last egg hatched, was  $12.8 \pm 0.5$  days ( $n = 11$ , range = 12.0–13.5 days) for Harris' Sparrow nests found with incomplete clutches. Reported length of the incubation period for three Harris' Sparrow nests at Churchill were 13.5, 13.5, and 15.0 days (Jehl and Hussell 1966a, Rees 1973). These lengths may be atypical; the 15.0 day period may have been caused by inclement weather (Rees 1973) and the 13.5 day periods equal the maximum at WG. A single White-crowned Sparrow clutch found before completion had an incubation period of 12.0 days, which is the average length of

incubation for the species over its geographical range (Morton 1976). The longer incubation period in Harris' Sparrows relative to White-crowned Sparrows is to be expected, as incubation length decreases as egg mass declines (Rahn and Ar 1974).

The 1989 sample size for Harris' Sparrow incubation period was too small to allow comparison with other years, but the range of values was similar in all three years, and 1990 and 1991 incubation periods did not differ (Table 4;  $t = 0.377$ ,  $P > 0.05$ ,  $df = 7$ ). Female *Zonotrichia* did not begin incubation until after 10 June in all years of the study, but by 5 July all eggs in first nests had hatched (Table 4).

#### HATCHING SYNCHRONY AND THE NESTLING PERIOD

Hatching synchrony was similar for Harris' Sparrows and White-crowned Sparrows; 84.7% of Harris' Sparrow eggs ( $n = 204$ ) hatched on day 0 (the first day in which one or more of the eggs in a clutch hatched), 14.8% on day 1, and 0.5% on day 2. In White-crowned Sparrows ( $n = 40$ ), 80% of the eggs hatched on day 0, and 20% on day 1. The percentage of Harris' Sparrow clutches with asynchronous hatching did not differ between five-egg clutches (58.8%,  $n = 17$ ) and three- and four-egg clutches (40.0%,  $n = 35$ ) ( $\chi^2_{(1)} = 2.18$ ,  $P = 0.139$ ). Other *Z. leucophrys* populations also showed no consistent differences in synchrony between clutches of different sizes (King and Hubbard 1981).

Average length of the nestling period for undisturbed nests, based on nest means, was  $9.26 \pm 0.48$  days (range = 8.5–10.0 days,  $n = 9$ ) for Harris' Sparrows and  $9.08 \pm 0.63$  days for White-crowned Sparrows (range = 8.0–10.0 days,  $n = 3$ ). Nestling period decreases with latitude in *Z. leucophrys*, and averages ca. 8–9 days for undisturbed nests in Alaska (Morton 1976, King and Hubbard 1981). Mean nestling periods at Churchill are ca. 8.7 days for White-crowned Sparrows and 8.9 days for Harris' Sparrows (Rees 1973). Some nestling *Zonotrichia* left the nest on day 8 if disturbed, while almost all did so if handled on day 9. Consequently, mean fledging date for disturbed nests was about 0.5 days earlier (Harris' Sparrow:  $8.8 \pm 0.8$  days,  $n = 26$ ; White-crowned Sparrow:  $8.6 \pm 0.7$  days,  $n = 9$ ; these differences were not significant for either species;  $t$ -tests,  $P > 0.05$ ). Only female *Zonotrichia* brooded, and males and females of both species fed nestlings.

Timing of the nestling phase for Harris' Sparrows was similar in 1989 and 1990, but was delayed by about two days in 1991 (Table 4). The first eggs hatched on 25 June in 1989 and 1990, and on 28 June in 1991; mean hatch date was 1.5 days later in 1991 than in the two previous years. Fledging peaked on 7 July in both 1989 and 1990, and 9 July 1991 (Fig. 3, Table 4). Annual differences in hatching and timing of the nestling phase and fledging were similar for White-crowned Sparrows (Table 4); ranges were smaller, probably due to smaller sample sizes.

Hatching of Harris' Sparrows and White-crowned Sparrows began shortly after arthropod abundance, as measured with pitfall traps and sticky boards, began to increase from very low numbers in early and mid-June (Table 7, Fig. 2). Fledging peaks during the second week in July occurred just prior to arthropod abundance peaks during all three years of the study (Fig. 2). The only exception was in 1991, when large numbers of spiders were captured in pitfall traps on 21 June (Table 7). Sticky boards capture mostly emergent adult tundra arthropods (MacLean and Pitelka 1971, Custer and Pitelka 1977); thus the nestling phase of the *Zonotrichia* breeding cycle should coincide with an earlier peak in larval abundance. Pitfall trap data support this prediction, as summed totals for larvae captured during all three years showed a broad peak between 1 July and 10 July (Norment, unpubl. data).

Fine temporal adjustment of reproductive function and breeding cycle in birds is controlled by complex interactions between many environmental factors (Wingfield 1980). In arctic and montane habitats, snow melt may be the most important proximal cue influencing when birds begin breeding (see references cited above), as snow cover influences nest site availability. Progression of snow melt may also be a reliable predictive cue for arthropod abundance during the critical nestling and fledgling phases of the nesting cycle, as thaw, along with climatic factors, influences patterns of arthropod abundance and emergence in tundra habitats (MacLean and Pitelka 1971, Custer and Pitelka 1977, Tolbert et al. 1977, Hågvar et al. 1978).

Birds breeding in relatively harsh environments should produce young when food for nestlings is near maximal (Geisel 1976), and timing of reproduction may be adjusted from year to year to coincide with peak insect biomass in montane populations of Dark-eyed Juncos (*Juncos hyemalis*; Smith and Andersen 1982, 1985)

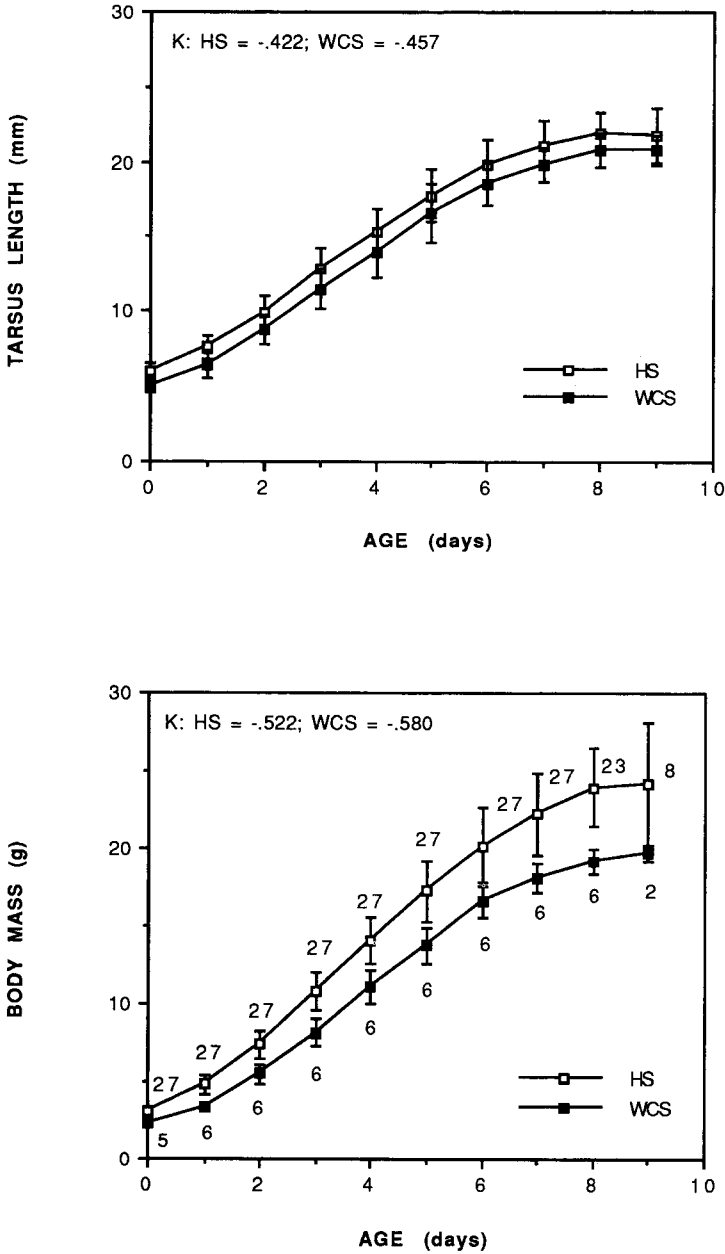


FIGURE 3. Growth curves for tarsus length (top) and mass (bottom) of Harris' Sparrow (HS) and White-crowned Sparrow (WCS) nestlings. Family means for all broods measured from 1989 to 1991 are shown. Vertical lines show  $\pm 1$  SD; sample sizes in bottom graph are number of broods measured.

and White-crowned Sparrows (Morton et al. 1972a). Between-year differences in timing of breeding for *Zonotrichia* at WG did occur, but these differences were relatively slight (ca. 2 days). In many arctic-breeding species year-to-year ad-

justment of breeding chronologies may be limited by synchronization of breeding cycles with long-term, "expected" peaks in arthropod abundance (Holmes 1966, Bunnell et al. 1975, Seastedt and MacLean 1979), which will ensure that

TABLE 7. Number of arthropods captured/trap ( $\bar{x} \pm SD$ ) for pitfall traps and sticky boards, Warden's Grove, 1989-1991;  $n = 24$  for all dates.

Date <sup>a</sup>	1989		1990		1991	
	PF <sup>b</sup>	SB <sup>c</sup>	PF	SB	PF	SB
1-3 June	1.2 ± 1.4	0.4 ± 0.7	1.1 ± 1.1	0.4 ± 0.6	1.0 ± 1.1	1.1 ± 1.0
9-12 June	1.3 ± 1.1	0.5 ± 0.7	1.3 ± 1.2	1.2 ± 1.5	1.1 ± 1.9	1.1 ± 1.2
20-22 June	1.5 ± 1.3	4.0 ± 4.3	2.7 ± 2.1	1.5 ± 1.9	7.4 ± 7.3	4.1 ± 4.0
1 July	2.7 ± 2.9	17.7 ± 17.3	2.0 ± 1.6	7.0 ± 9.4	3.2 ± 2.0	15.4 ± 14.8
9-11 July	2.3 ± 1.5	21.5 ± 15.2	3.5 ± 2.5	22.5 ± 15.6	2.7 ± 2.0	17.7 ± 9.1
16-22 July	1.5 ± 1.6	12.5 ± 8.5	2.8 ± 2.4	20.6 ± 11.4	2.5 ± 1.3	13.5 ± 8.4

<sup>a</sup> Range of trapping dates, 1989-1990.

<sup>b</sup> PF = pitfall trap.

<sup>c</sup> SB = sticky board.

young reach independence before the end of adult insect emergence (Custer and Pitelka 1977), and with sufficient time to complete necessary development before migration.

#### NESTLING GROWTH AND DEVELOPMENT

Growth curves for nestling body mass and tarsus length (Fig. 3), based upon family means for all broods surviving until day 7, were similar for Harris' Sparrows and White-crowned Sparrows. Growth constants (K) for body mass and tarsus length were higher for White-crowned Sparrows than for Harris' Sparrows, although differences were not statistically significant (Table 8). A smaller growth constant for Harris' Sparrows is as expected, as K-values decrease with increasing body mass (Ricklefs 1968). In both species K-values for tarsus were significantly less than for mass (Table 8;  $t$ -tests,  $P < 0.05$ ), as observed in Sage Sparrows (*Amphispiza belli*) and Brewer's Sparrows (*Spizella breweri*) (Petersen et al. 1986). K-values for White-crowned Sparrow and Harris' Sparrow nestlings were similar to values for other emberizines, including *Z. leucophrys* (Ricklefs 1968, Hubbard 1978, Petersen et al. 1986). Inflection points (I) for body mass and tarsus length did not differ between species (Ta-

ble 8), indicating that White-crowned Sparrow and Harris' Sparrow nestlings achieved maximum growth rates at about the same time.

Day 0 nestling tarsus length, expressed as a percentage of adult size, was smaller for White-crowned Sparrow than for Harris' Sparrow nestlings ( $t$ -test,  $P < 0.05$ , Table 9). Day 0 nestling mass did not differ significantly between the species, although the mean was less for White-crowned Sparrows (Table 9). Asymptotes (A) for Harris' Sparrow nestlings were significantly larger than for White-crowned Sparrows (Table 8). However, day 8 nestling mass and tarsus length, expressed as a percentage of adult size, did not differ between the species, and  $R$ -values (ratio of asymptote to adult size; Ricklefs 1968) also were similar (Table 9). These results indicate that although White-crowned Sparrows hatched at a relatively smaller size than Harris' Sparrows, they tended to grow more quickly, and nestlings of the two species fledged at similar sizes relative to adult mass and tarsus length.

Because Harris' Sparrows and White-crowned Sparrows are congeners and use similar suites of ground-foraging behaviors (Norment 1992), growth patterns and relative sizes of nestlings at fledging in the two species should closely resem-

TABLE 8. Growth coefficients ( $\bar{x} \pm SD$ ) for mass and tarsus length in *Zonotrichia* nestlings; K = relative growth rate, A = asymptote, and I = point of maximum growth in days after hatching. Means and standard deviations based upon calculation of growth coefficients for individual broods reaching at least day 7 after hatching. Sample size = 27 broods for Harris' Sparrows (HS) and six broods for White-crowned Sparrows (WCS).

	Mass			Tarsus		
	K	ASYMP	I	K	ASYMP	I
HS	-0.522 ± 0.084	26.98 ± 2.90	3.99 ± 0.75	-0.422 ± 0.065	25.05 ± 1.45	2.96 ± 0.60
WCS	-0.580 ± 0.064	23.02 ± 5.08	3.86 ± 0.43	-0.457 ± 0.074	23.67 ± 2.17	3.17 ± 0.93
$P^a$	0.1170	0.0143	0.6670	0.2360	0.0412	0.4830

<sup>a</sup>  $t$ -tests.

TABLE 9. Nestling measurements for Harris' Sparrows (HS) and White-crowned Sparrows (WCS). Day 0 and day 8 values expressed as percentages of adult measurements; *R*-values are the ratios of nestling growth asymptotes/adult size (Ricklefs 1968). Means based on means for individual nests and backtransformed from arcsine square root values. Sample sizes: Harris' Sparrow: *n* = 36 (day 0) and 24 (day 8); White-crowned Sparrow: *n* = 6 (day 0 and day 8).

	Day 0		Day 8		<i>R</i> -values	
	Mass	Tarsus	Mass	Tarsus	Mass	Tarsus
HS	8.6 ± 0.9	26.3 ± 2.5	67.4 ± 7.1	94.2 ± 5.9	0.76:1	1.08:1
WCS	8.1 ± 0.7	23.4 ± 2.0	69.7 ± 3.0	95.2 ± 5.2	0.76:1	1.08:1
<i>P</i> <sup>a</sup>	0.244	0.012	0.496	0.706		

<sup>a</sup> *t*-tests.

ble one another (see Ricklefs 1968, 1973a, 1984). *R*-values for mass of ground-foraging birds are usually less than 1 (Ricklefs 1968); *R*-values < 1 also have been reported for tarsus length of ground-foraging Sage and Brewer's Sparrows, which suggests the importance of pedal locomotion (Petersen et al. 1986).

Development of nestling White-crowned Sparrows was similar to that found elsewhere (Blanchard 1941, Banks 1959, Morton et al. 1972b) and will not be described here. However, nestling Harris' Sparrow development has not been described in detail; the following account is based on individuals from nests observed during all years of the study. On hatching day (day 0), sparse gray down was about 10 mm long in the humeral, femoral, alar, capital, and spinal (back only) feather tracts. Eyes were closed and nestlings gaped silently; body movements were feeble and uncoordinated. The mouth lining was red and surrounded by a yellow rim on the beak. By day 2 all tracts had darkened; darkening was least developed in the ventral and crural tracts. On day 3 the eyes began to open, and the sheaths of primary feathers began to penetrate the skin of some chicks. Some individuals 'peeped' faintly when gaping. By day 4 ensheathed feathers were emerging from all feather tracts. On day 5 all nestlings had open eyes, and gaped and oriented towards the nest entrance. Feather tips were beginning to emerge in the ventral, crural, humeral, and spinal tracts. By day 6 remiges and rectrices had emerged from their sheaths; nestlings generally crouched silently and did not gape if handled. By day 7 nestlings could perch unassisted. On day 8 some nestlings gave a sharp distress call, struggled, and tried to leave the nest if handled. Day 9 nestlings generally abandoned the nest after being handled, although they could

not fly. Harris' Sparrow nestlings could fly short distances (< 10 m) four days after fledging.

#### REPLACEMENT NESTING

I observed one instance of replacement nesting (in 1990) for Harris' Sparrows and none for White-crowned Sparrows. The Harris' Sparrow replacement nest involved a pair whose first clutch was depredated on 18 June 1990. A second nest was built 16 m from the first nest and a clutch initiated on 21 June. Late clutch dates (after 20 June) and occasional mate guarding and precopulatory displays when most pairs were feeding nestlings suggested that replacement nesting also occurred in 1989 and 1991. Montane *Z. l. oriantha* lay replacement clutches following loss of a clutch (Morton et al. 1972a, Hubbard 1978, King and Mewaldt 1987), and late nesting dates suggest that Harris' Sparrows and White-crowned Sparrows also do so at Churchill (Jehl and Hussell 1966b, Rees 1973).

#### MORTALITY AND NEST SUCCESS

Overall hatching rate was 76.1% for Harris' Sparrows and 81.2% for White-crowned Sparrows (Table 10). Major causes of egg loss for Harris' Sparrows, as a percentage of eggs laid, were hatching failure (10.8%) and predation (10.0%); abandonment (10.9%) and hatching failure (7.3%) accounted for all White-crowned Sparrow egg losses. Overall fledging rate was 62.6% for Harris' Sparrows and 86.7% for White-crowned Sparrows (Table 10). Major cause of nestling loss for Harris' Sparrows, as a percentage of nestlings hatched, was predation (26.3%); 9.3% of all Harris' Sparrow nestlings and 11.1% of White-crowned Sparrow nestlings vanished from nests with healthy nestlings and were presumed to have died, causes unknown. Overall egg success

TABLE 10. Causes of nesting mortality\* in Harris' Sparrows and White-crowned Sparrows, Warden's Grove, 1989-1991. Percentages given in parentheses.

	Harris' Sparrow			Total	White-crowned Sparrow
	1989	1990	1991		Total
Eggs laid	74	94	92	260	55
Losses					
Hatching failure	7 (9.5)	16 (17.0)	5 (5.4)	28 (10.8)	4 (7.3)
Predation	0 (0.0)	14 (14.9)	12 (13.0)	26 (10.0)	0 (0.0)
Abandonment	0 (0.0)	4 (4.3)	4 (4.4)	8 (3.1)	6 (10.9)
Young hatched	67 (90.5)	60 (63.8)	71 (77.2)	198 (76.1)	45 (81.2)
Nestlings	67	60	71	198	45
Losses					
Predation	17 (25.4)	23 (38.3)	12 (16.9)	52 (26.3)	0 (0.0)
Exposure	0 (0.0)	0 (0.0)	3 (4.2)	3 (1.5)	0 (0.0)
Starvation	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (2.2)
Unknown cause	7 (10.4)	4 (6.7)	8 (11.3)	19 (9.6)	5 (11.1)
Young fledged	43 (64.2)	33 (55.0)	48 (67.6)	124 (62.6)	39 (86.7)
Egg success	0.581	0.351	0.487	0.476	0.704

\* Values based upon nests found prior to hatching of eggs.

[(hatching rate)(fledging rate), Mayfield 1975] was higher for White-crowned Sparrows [ $0.704 = (0.812)(0.867)$ ] than for Harris' Sparrows [ $0.476 = (0.761)(0.626)$ ]. I also calculated egg success using the Mayfield (1975) method to account for differences in the length of time known nests were exposed to predators and other mortality factors. Because few nests were found after nestlings hatched, values for egg success calculated by the Mayfield method were only slightly lower than values obtained by tabulating all egg and nestling losses: 0.439 for Harris' Sparrows and 0.647 for White-crowned Sparrows.

Difference in egg success between Harris' Sparrows and White-crowned Sparrows was due mainly to higher predation rates on Harris' Sparrow nests. Thirty percent (78/260) of all Harris' Sparrow eggs and nestlings, and 34.4% of all nests (22/64) were lost to predation, but none of the White-crowned Sparrow nests were depredated (Table 10). Predation was most severe in 1990, when 14.9% of all Harris' Sparrow eggs, 38.3% of all nestlings, and 50% (12/24) of all nests were depredated. Known nest predators in the study area included arctic ground squirrels (*Spermophilus parryii*) and short-tailed weasels (*Mustela erminea*). Ground squirrels appeared to be the most common and important nest predator. I observed two incidents of predation by ground squirrels; in both cases, the squirrels appeared to

locate the nest during a random search. Both nestlings and eggs were consumed, and the lining was pulled partly out of the surrounding cup of lichens and twigs. Ground squirrel sightings were higher in 1990 ( $n = 31$ ) than in 1989 ( $n = 19$ ) or 1991 ( $n = 15$ ). No direct observation of nest predation by weasels was observed. However, three dead nestlings, all with numerous hematomas, were found scattered around a Harris' Sparrow nest. The attack was attributed to weasels because surplus killing is characteristic of weasels, and the nest was >500 m from the nearest ground squirrel den. Other potential nest predators included red squirrels (*Tamiasciurus hudsonicus*) and Gray Jays (*Perisoreus canadensis*); adult Harris' Sparrows became nervous and gave repeated alarm calls when either species was present.

Belding's ground squirrels (*Spermophilus beldingi*) and least chipmunks (*Eutamias quadrivittatus*) may take significant numbers of *Z. l. oriantha* eggs and nestlings (Morton et al. 1972a, Hubbard 1978). However, although arctic ground squirrels may kill collared lemmings (*Dicrostonyx kilangmiutak*), consumption of bird eggs and young by the species has not been reported (see Boonstra et al. 1990). Weasels (*Mustela* spp.) also are important predators on *Z. l. oriantha* nests (Morton et al. 1972a, Hubbard 1978) and on ground-nesting arctic passerines (Hussell and

Holroyd 1974, Custer and Pitelka 1977, Lyon and Montgomerie 1987).

Known predators on adult Harris' Sparrows were Northern Shrikes (*Lanius excubitor*) and Gray Jays; other possible predators included Merlins (*Falco columbaris*), Parasitic Jaegers (*Stercorarius parasiticus*), and short-tailed weasels. Of these species, the Northern Shrike is probably most important. A pair of shrikes nested on the study area in 1991, and bands and tarsi from three female Harris' Sparrows were found in a shrike cache; a fourth female disappeared while a shrike was hunting near her nest. Shrike predation on Harris' Sparrows also occurs during the winter (Baumgartner 1968). Although Gray Jays are probably incapable of killing a healthy adult Harris' Sparrow under normal circumstances, one female caught in a mist net was killed by a Gray Jay in 1989. Merlins and Parasitic Jaegers were observed attacking other passerines on the study area, but were never seen pursuing Harris' Sparrows or White-crowned Sparrows.

Three Harris' Sparrow nests and two White-crowned Sparrow nests with eggs or nestlings were abandoned during the study. It is likely that predation on adults was responsible for all cases of abandonment by Harris' Sparrows, but for neither case of abandonment by White-crowned Sparrows. In all three cases of suspected predation, marked birds comprised one or both members of the nesting pair and were not observed after nest abandonment occurred. One female Harris' Sparrow incubating eggs was killed by a shrike, while another female feeding day 6 nestlings probably also was killed by a shrike.

Repeated visits to nests can increase nest predation (Major 1990). However, no White-crowned Sparrow nests in which nestlings were handled were depredated, and success rates for disturbed (28/40) and undisturbed Harris' Sparrow nests (11/15) did not differ ( $\chi^2_{(1)} = 0.007$ ,  $P = 0.935$ ). Data on the effects of nest disturbance on predation rates in other studies of *Zonotrichia* are equivocal. Banding of nestlings did not affect nest predation in *Z. l. nuttalli* (Petrinovich and Patterson 1983), but nest visitation did increase predation rates on *Z. l. oriantha* nestlings (Mead and Morton 1985).

Inclement weather may cause significant nesting failure in some *Zonotrichia* populations (Jehl and Hussell 1966b, Morton et al. 1972a, Hubbard 1978, King and Mewaldt 1987), but storms had little effect on mortality of *Zonotrichia* at

WG. Only one brood of Harris' Sparrow nestlings died of exposure, and these were from a nest in which the female disappeared. A severe storm in 1978 caused territorial adults of several primarily insectivorous species to disappear from the study area (Norment 1985), but spot map censuses conducted before and after the storm showed no loss of territorial *Zonotrichia* pairs (Norment, unpubl. data).

#### EGG SUCCESS IN OTHER *ZONOTRICHIA* POPULATIONS

Egg success for Harris' Sparrows (0.476) was similar to values calculated from the ratio of fledglings to eggs laid in other North American *Zonotrichia* populations, which range from ca. 0.30 (Petrinovich and Patterson 1983) to 0.67 (Hubbard 1978). There are few comparative data on egg success in arctic- or subarctic-breeding *Zonotrichia*. Egg success was 0.53 for *Z. l. gambelii* at Cape Thompson, Alaska (Williamson et al. 1966). Hatching success at Churchill was 0.89 for Harris' Sparrows and 0.69 for White-crowned Sparrows (Jehl 1972); values at WG were 0.76 and 0.81, respectively. The low value for White-crowned Sparrows at Churchill was due to a severe storm in one year; few White-crowned Sparrow or Harris' Sparrow eggs were lost to predators (Jehl 1972). Ricklefs (1969) proposed that egg success for open-nesting arctic passerines should generally be at least 60%, due to lower rates of nest predation than in temperate or tropical areas. However, data collected since 1969, including those from the present study, show that predation rates may exceed 40% of nests or eggs and young of ground-nesting arctic passerines in some years (Williamson and Emison 1971, Hussell and Holroyd 1974, Custer and Pitelka 1977, Lyon and Montgomerie 1987).

Egg success for White-crowned Sparrows at WG (0.704) was higher than for Harris' Sparrows, and higher than in most other studies of *Z. leucophrys*, where predation rates on eggs and young range from 34% (Morton et al. 1972a) to 72% (King and Mewaldt 1987). The complete absence of predation is unusual, and has been reported in only one other study of *Zonotrichia*. Oakeson (1954) did not calculate egg success for *Z. l. gambelii* in Alaska, but mentions that all nests ( $n = 8$ ) fledged at least one nestling. However, most potential predators in her study area had been removed by trapping. Decreased predation on White-crowned Sparrow nests at WG,



TABLE 11. Productivity<sup>a</sup> of Harris' Sparrows and White-crowned Sparrows nesting at Warden's Grove, 1989–1990.

	Harris' Sparrow				White-crowned Sparrow
	1989	1990	1991	Cumulative	Cumulative
Number of nests	17	23	21	61	12
Mean clutch size	4.35	4.09	4.35	4.26	4.62
Hatching success (%)	90.5	63.8	77.2	76.1	81.2
Fledging success (%)	64.2	55.0	67.6	62.6	86.7
Egg success (%)	58.1	35.1	48.7	47.6	70.4
Number of pairs	17	22	21	60	12
Number fledged/pair	2.53	1.50	2.23	2.07	3.25

<sup>a</sup> Values based upon nests found prior to hatching of eggs.

where there are many predators, may be due, at least in part, to nest placement. White-crowned Sparrows placed nests in significantly thicker vegetation than did Harris' Sparrows (Norment 1992).

#### PRODUCTIVITY

Harris' Sparrow nest productivity (number of young fledged/nest) ranged from 1.50 in 1990 to 2.53 in 1989 (Table 11). Cumulative productivity, based on nests found prior to hatching, was 2.07. The main cause of between-year differences in productivity was increased nest predation in 1990. Productivity for Harris' Sparrows at WG is similar to values reported for temperate *Z. leucophrys* populations, which range from 1.71 fledglings/pair (Morton et al. 1972a) to about 2.5 fledglings/pair (Petrinovich and Patterson 1983), although King and Mewaldt (1987) calculated a productivity of 0.99 fledglings/pair in 1975 for *Z. l. oriantha* at Hart Mountain, Oregon using the Mayfield method. Cumulative productivity for White-crowned Sparrows was 3.25 young/nest, 157% of the value for Harris' Sparrows (Table 11), and higher than productivity reported for other *Zonotrichia* populations.

#### INTERSPECIFIC INTERACTIONS

There is no evidence for interspecific competition between Harris' Sparrows and White-crowned Sparrows at WG. I observed only four interspecific chases involving both species, other than those occurring at trapping stations baited with grain. All chases were initiated by male Harris' Sparrows; however, Harris' Sparrows also occasionally chased American Tree Sparrows (*Spizella arborea*) and Lapland Longspurs (*Calcarius lapponicus*), and the two species of *Zonotrichia* generally appeared to ignore one another.

Males of the two species sometimes sang simultaneously from the same tree, and in 1989 a pair of White-crowned Sparrows and a pair of Harris' Sparrows nested within 10 m of one another. I did not map territorial boundaries, but repeated sightings of marked birds and nest locations indicated that substantial territorial overlap occurred between the two species. Interspecific agonistic interactions between Harris' Sparrows and White-crowned Sparrows also was observed at Churchill (Rees 1973, Shackleton et al. 1991). However, levels of interspecific aggression at Churchill appear to be low, there is extensive territorial overlap, and levels of response to songs of the other species are generally low (Rees 1973).

#### CONCLUSIONS

In general, the breeding biology of Harris' Sparrows and White-crowned Sparrows at WG was very similar. Sex ratios and nesting cycles were almost identical, and males and females of the two species showed similar patterns of change in body mass and lipid stores. Both species exhibited low levels of intra- and interspecific agonistic interactions. Only female White-crowned Sparrows (DeWolfe 1968b) and Harris' Sparrows built nests, incubated, and brooded young, while both males and females fed nestlings. General patterns of nestling development also were quite similar in the two species, and their nestlings fledged at the same size relative to adults. Several small differences that did exist, such as lengths of the incubation and nestling periods and growth rates, were statistically nonsignificant, and conformed to trends predicted by the White-crowned Sparrow's smaller body size.

The most important differences between the breeding biology of the two species involved the

lower population density, and higher egg success and productivity, of White-crowned Sparrows at WG. Increased egg success and productivity were due to decreased predation on White-crowned Sparrow nests during all years of the study, which in turn probably was related to differences in nest site selection between the species.

Higher productivity and lower density are seemingly contradictory characteristics of sympatric populations of closely related species; all other things being equal, higher productivity should lead to higher densities. This contradiction could be explained by a number of factors, including differences in overwinter survivorship of adults or young (Fretwell 1969, Ricklefs 1973b), interspecific competition, differences in habitat requirements, or historical events that cannot be documented.

The few data on return rates that I have show no consistent differences in overwinter survivorship between the species. No banded nestlings of either species returned to breed in their natal area, and average return rates for banded adults in 1990 and 1991 were similar for White-crowned Sparrows (33%) and Harris' Sparrows (39%) (Norment, unpubl. data). However, annual return rates appeared to be much more variable for White-crowned Sparrows. Very low return rates during some years could lead to lower population levels, as suggested for a declining population of *Z. l. oriantha* in Oregon (King and Mewaldt 1987). Experimental manipulations are necessary to demonstrate the presence or absence of competition (Connell 1983). However, there is little indirect evidence for interspecific competition between Harris' Sparrows and White-crowned Sparrows at WG. Lack of interspecific agonistic behavior, and the tendency of the two species to select different nesting and foraging habitats (Norment 1992), suggest that neither interference nor exploitation competition affected White-crowned Sparrow populations in the study area, at least not recently. The most likely explanation is that restricted availability of nesting habitat, perhaps combined with lower adult return rates in some years, affected White-crowned Sparrow densities in the study area. White-crowned Sparrows at WG always nest in thick, shrubby vegetation within 25 m of the forest edge, while Harris' Sparrows select a wider variety of nesting habitats at distances up to 127 m from the forest edge. The greater abundance of Harris' Sparrows in all parts of the forest-

tundra ecotone in northern Canada where breeding bird surveys have been conducted (Manning 1948, Harper 1953, Mowat and Lawrie 1955, McLaren and McLaren 1981, Norment 1985) also suggests that more nesting habitat is available for Harris' Sparrows than for White-crowned Sparrows.

The ultimate factor determining timing of the nesting season in birds is probably food supply for the young (Lack 1968). However, a complex series of proximate factors may influence the nesting cycle in arctic passerines, with its duration and timing limited by the short growing season and need for young to complete necessary development prior to migration (Hussell 1972, Custer and Pitelka 1977). At WG timing of snow melt, which directly influences availability of nest sites, appears to influence when Harris' Sparrows and White-crowned Sparrows begin nesting. Both species begin clutch initiation when about 60% of the ground is snow-free, which in turn means that the peak in fledging will occur just prior to maximum abundance of arthropod prey, and that young can remain on the breeding grounds for almost two months before migrating southwards.

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