COMPARATIVE PATTERNS OF NESTLING GROWTH IN WHITE-CROWNED SPARROWS

JAMES R. KING

AND

JOEL D. HUBBARD

ABSTRACT.—To examine the hypothesis that the growth rates of emberizines are physiologically maximized and hence geographically invariant, we weighed the eggs and nestlings of White-crowned Sparrows (*Zonotrichia leucophrys*) from subarctic, subalpine, and low-altitude montane populations. We augmented these data with published information on another subalpine population and a Pacific maritime population. Clutch sizes ranged from a mode of three in the south to five in the north. Geographic variation in fresh egg weight was closely correlated with the size of the adult female. Other sources of variation, if any, were small. The mean incubation period was geographically invariant (about 12.2 d). The weight (water) loss of eggs during incubation averaged 18.4%, without statistically significant differences among four localities. There were no consistent differences in the synchrony of hatching in clutches of three, four or five eggs. Runt nestlings resulting from late hatching were atypical in the mainly five-egg clutches in the subarctic, but were more common in the unusual five-egg clutches of subalpine populations. The postnatal growth curves of nestlings in all six sample populations were virtually congruent, and thus independent of mean brood size and locality. We believe that it is unlikely that this would occur in such diverse populations unless growth rate were physiologically maximized. We would expect to find greater diversity if growth rates were submaximal and "optimized" in relation to the local environment.

Avian growth patterns are diverse and have evidently differentiated in response to a variety of social and environmental variables (Ricklefs 1968, O'Connor 1977, Case 1978), including most prominently the modes of parental care and the predictability and stability of food supply for the young. Within any given pattern, the intrinsic rate of postnatal growth appears to have been maximized through selection (Maher 1964, Ricklefs 1973) so that seasonal or geographic differences are absent or small except in obvious cases of malnutrition. The data supporting this conclusion are nevertheless sparse (Ricklefs 1968), and this and other aspects of interpopulational variability of growth patterns merit continued examination. As a by-product of other investigations, we measured the growth of nestling White-crowned Sparrows (*Zonotrichia leucophrys*) in diverse habitats. In an attempt to reveal the magnitude and forms of intraspecific adaptability of the growth patterns of this widespread emberizine, we combine in this report these new data with others previously published by Banks (1959) and Morton et al. (1972b).

MATERIALS AND METHODS

We weighed and measured eggs and nestlings of White-crowned Sparrows in three localities: (1) near Fairbanks, Alaska (*Z. l. gambelii*, 64°48′N, about 140 m above sea level, in 1973, with incidental observations also from 1962–1965); (2) at Hart Mountain National Antelope Refuge, Oregon (*Z. l. oriantha*, 42°42′N, about 1,890 m, a shrubsteppe habitat, in 1975–1976); and (3) on Niwot Ridge, Boulder Co., Colorado (*Z. l. oriantha*, 40°03′N) in two habitats including a burn dominated by spruce and second-growth brush at about 3,290 m (1974) and the forest-tundra ecotone at about 3,475 m (1972–1975). Except as noted later, we observed each nest only once each day to minimize disturbance and predation; hence, the order of egg-laying and hatching were usually unknown. Soon after dawn we measured the body weight of individually marked nestlings to the nearest 0.1 g and measured the length of the innermost primary remex (P1), when present, to the nearest 0.5 mm. To these new data we added those of Morton et al. (1972b) from near Tioga Pass, Mono Co., California (*Z. l. oriantha*, 37°55′N, about 2,900 m) and of Banks (1959) from Berkeley, California (*Z. l. nuttalli*, 37°48′N, about 60 m). The subspecies *gambelii* and *oriantha* are medium-distance intracontinental migrants, and *nuttalli* is a nonmigrant. *Oriantha* is montane or subalpine in its breeding distribution. *Gambelii* breeds in the taiga zone at its northern limit of distribution and in subalpine meadows at the southern limit. *Nuttalli* is a permanent resident of the Mediterranean chaparral of coastal California. The growth and development of the

TABLE 1.   Weights of eggs of White-crowned Sparrows on day 1 of incubation.

Locality	Egg weight, g (mean ± SE)	No. of Eggs	No. of Clutches	Female wing[a] mm	Wing/egg ratio[b]
Fairbanks	2.82 ± 0.067	17	4	72.3	51.2
Hart Mountain, or	3.02 ± 0.044	24	6	74.2	51.3
Tioga Pass	3.04 ± 0.20[c]	42	—	74.2	51.2
Niwot Ridge					
3,290 m	3.14 ± 0.026	20	5	75.0	51.2
3,475 m	3.07 ± 0.025	27	7	75.7	51.4

[a] Chord of the wing in fresh plumage; data from Banks (1964) or from local records when available.
[b] Wing length (mm) divided by the cube root of mean egg weight (g).
[c] Mean of weights at various stages of incubation, and hence submaximal (Morton et al. 1972a).

other subspecies of *Z. leucophrys* (*leucophrys* and *pugetensis*) have not yet been investigated.

RESULTS AND DISCUSSION

EGG WEIGHT

Variation in the mean body weight of the adult female accounts for about 98% of the variation in mean egg weight in fringillids ($r = 0.99$, Rahn et al. 1975). Thus, it is to be expected that geographic variation of mean egg weight in White-crowned Sparrows depends almost entirely on geographic variation of adult body size and our data confirm this. Differences among localities essentially disappear when body size is factored out by dividing the mean wing length of adult females by the cube root of mean egg weight (Table 1). We used wing length rather than body weight as an index of body size because it is less variable in time than is body weight, particularly during ovogenesis. We conclude that mean egg weight in the samples available to us is not significantly variable in response to latitude or habitat per se.

The foregoing does not take into account intra- or interclutch variability of egg weight within localities. Such variability may reflect geographic differences of nutrients or reproductive tactics, and we were interested in identifying any patterns that revealed "runt" eggs reflecting nutrient deficits or selection for options in brood reduction. It is, however, apparent a priori that variation of egg weight not explicable by body size is small and of questionable ecological significance. The coefficients of variation for fresh egg weights derived from Table 1 reflect variability both within and among clutches, but range only from 3.7 to 9.8%. Inspection of the means shows a continuous gradation of egg weight within clutches in localities for which we have adequate samples (Table 2), with no evidence of "runt" eggs. These sparrows apparently elude trophic stresses reflected in egg

weight. "Runt" nestlings may, of course, result not only from subnormal eggs, but also from asynchronous or delayed hatching. We will recount later some cases in which the last hatchling in (unusual) broods of five near the upper altitudinal limit of distribution in this species grew more slowly than its sibs and was more likely to die before fledging.

INCUBATION PERIOD AND WEIGHT LOSS OF EGGS

Estimates of the incubation period (defined as the interval between the laying and the hatching of the last egg of a clutch) are inexact not only because of inexact definition but also because of error in ascertaining the times of egg-laying and hatching. Our own estimates are accurate to only about ±0.3 d, and we surmise that others are subject to a similar uncertainty. In view of this, expressions of statistical variance are nearly meaningless. The averages assembled in Table 3 nevertheless reveal clearly enough that (1) the mean incubation period does not vary geographically or by subspecies, apparently being minimized at about 12.2 d; and (2) slight deviations from this average

TABLE 2.   Variability of egg weight within clutches.

Clutch size and locality	Rank order by mean weight, g 1	2	3	4	5	% range[a]
Four eggs						
Hart Mountain						
(11)[b]	2.82	2.73	2.66	2.52	—	10.6
% reduction	3.1	2.6	5.3			
Fairbanks (4)	2.76	2.55	2.42	2.35		15.3
% reduction	7.6	5.1	2.9			
Five eggs						
Hart Mountain (5)	2.92	2.86	2.72	2.66	2.58	11.6
% reduction	2.1	4.9	2.2	3.0		
Fairbanks (11)	2.85	2.74	2.64	2.54	2.44	14.6
% reduction	3.9	3.6	3.8	3.9		

[a] Difference between largest and smallest as a percentage of the largest.
[b] Number of clutches.

TABLE 3.   Mean incubation period and age at fledging (days).

Locality	Incubation	Fledging age	Source
Fairbanks, AK	11.9 (14)[a] 1963–64	—	This study
	12.1 (10) 1973	8.0 (17, 4)[b]	This study
	—	8.4 (15, ?)	DeWolfe 1968
Mountain Village, AK	12 (2)	9.0 (23, ?)	DeWolfe 1968
Hart Mountain, OR	12.2 (16)	9.0 (33, 10)	This study
Tioga Pass, CA	10.9 (20) 1968	—	Morton et al. 1972a
	12.5 (19) 1969	9.5 (221, ?)	Morton et al. 1972a
	13.4 (16) 1970[c]	—	Morton et al. 1972a
Niwot Ridge, CO			
3,290 m	11.9 (5)	9.7 (26, 10)	This study
3,475 m	12.2 (3) 1972	9.5 (11, 4)	This study
	13.0 (3) 1973[c]	9.6 (7, 2)	This study
	12.3 (2) 1974	9.4 (10, 3)	This study
	12.4 (6) 1975[d]	9.4 (42, 14)[e]	This study
Friday Harbor, WA	—	9.6 (26, ?)	DeWolfe 1968
Berkeley, CA	12.3 (10)	10.1 (23, ?)	DeWolfe 1968

[a] Number of nests.
[b] Number of nestlings and clutches, respectively.
[c] Unusually cold breeding seasons.
[d] Mean for all four years = 12.4 d.
[e] Mean for all four years = 9.5 d.

are correlated with cold temperatures or snow at least in the subalpine populations at Tioga Pass (Morton et al. 1972a) and Niwot Ridge, where mean incubation periods of 13.4 and 13.0 d coincided with unusually cold breeding seasons.

The weight loss of eggs is linear with time during incubation (Drent 1975) and results almost entirely from the loss of water. We weighed eggs on known days of incubation and computed linear regression equations expressing the rate of weight loss (Table 4). Statistical variability was substantial, and the equations did not differ significantly ($P > 0.05$) from each other in either elevation or slope, even though there were apparent trends of increasing weight of fresh eggs (Y-intercept) and rate of weight loss (slope) with increasing altitudes. The mean total weight loss during incubation (18.4%) was close to the average of 18% reported for birds in general (Rahn and Ar 1974) and within the limits reported for emberizines (Drent 1970).

HATCHING

We recorded the times at which we observed nestlings with the down still wet from hatching and assumed, as did Morton et al. (1972b), that hatching occurred 15–30 min earlier. More than two-thirds of eggs hatched before noon in alpine or subalpine populations of *oriantha* at Tioga Pass (73.5%) and Niwot Ridge (71.5%), with a lesser peak of hatching in the afternoon (Table 5). We agree with Morton et al. (1972b) that observations at these sites may be biased, and that more nestlings probably hatch at night or earlier in the morning than our observations could reveal. Skutch (1952) found that 27% of 93 eggs of 11 species hatched before dawn (or "at night") in Costa Rica.

Observations can be more exact in the essentially continuous summer daylight at Fairbanks, where we found that hatching was concentrated about equally in two peaks near dawn and dusk, but might occur less frequently at any time of the day or "night." We do not have sufficient data from Hart Mountain or other sites to reveal reliably the temporal distribution of hatching.

The concentration of hatching near dawn or in the early daylight hours can be regarded as adaptive, as Skutch (1952) has suggested, since it allows a full or at least par-

TABLE 4.   Linear regression equations for the weight loss of eggs during incubation.

Locality	Altitude m	Equation Y = g, X = days	$S_{y \cdot x}$	S_b	n[a]	% loss[b]
Fairbanks, AK	140	Y = 2.86 − 0.041X	0.1074	0.01671	64	17.2
Hart Mountain, OR	1,890	Y = 2.96 − 0.043X	0.2694	0.00827	98	17.4
Niwot Ridge, CO	3,290	Y = 3.04 − 0.050X	0.1897	0.00904	42	19.7
	3,475	Y = 3.19 − 0.052X	0.1536	0.00293	62	19.6

[a] Number of eggs.
[b] Weight loss during a 12-d incubation period as a percentage of initial weight.

TABLE 5. The temporal distribution of hatching times.

Clock time[a]	Fairbanks n	Fairbanks %	Tioga Pass[b] n	Tioga Pass[b] %	Niwot Ridge n	Niwot Ridge %
00–02	16	22.9	0	—	0	—
02–04	5	7.1	0	—	0	—
04–06	4	5.7	8	23.5	6	28.6
06–08	6	8.6	7	20.6	5	23.8
08–10	6	8.6	8	23.5	3	14.3
10–12	3	4.3	2	5.9	1	4.8
12–14	2	2.9	5	14.7	1	4.8
14–16	0	—	4	11.8	3	14.3
16–18	16	22.9	0	—	2	9.4
18–20	9	12.8	0	—	0	—
20–22	2	2.8	0	—	0	—
22–24	1	1.4	0	—	0	—
Number	70	100.0	34	100.0	21	100.0
Sunrise[c]	01:05		04:14		04:03	
Sunset[c]	23:05		19:54		20:05	

[a] Standard time. The data should be expressed in terms of local solar time, but those from Tioga Pass could not be corrected retrospectively to this value.
[b] From Morton et al. (1972b).
[c] At median point in the hatching seasons. At Fairbanks, this is expressed as civil sunrise and sunset (twilight is continuous); at Tioga Pass and Niwot Ridge, expressed as civil sunrise or sunset plus or minus civil twilight.

tial feeding day for the new-hatched young and also helps to reduce the competitive disadvantage of nestlings hatched a day or more later than their siblings (see beyond). This cannot, however, be regarded as an overriding selective pressure, since in all of our samples a secondary peak of hatching occurred near dusk, allowing but one or two hours of feeding time at Tioga Pass and Niwot Ridge before onset of the eight-hour night. At Fairbanks during the hatching season the "night" was merely a period of variable twilight, but there was a conspicuous lull in adult activity (singing nearly ceases, adults roost in dense foliage if not on the nest) from about 21:30 to about 23:30, or a functional "night" of about two hours. It may be significant that hatching was concentrated about equally near dawn and dusk at this latitude, leading to the inference that the relatively short fasting period for nestlings

imposes a lesser disadvantage than the longer nights at lower latitudes.

The synchrony of hatching in our sample was tight, 77–83% of eggs hatching on the same day, 16–21% within 24 h later, and very small numbers still later (to a maximum of 46 h after the hatching of the first egg in a clutch) (Table 6). We found no consistent differences in synchrony between three-, four-, or five-egg clutches when the data were analyzed either within or between localities (e.g., the birds at Fairbanks laid predominantly five-egg clutches, the others in Table 6 laid predominantly four-egg clutches, but synchrony was similar in all localities). The existence of such synchrony suggests that there should be very few "runt" nestlings as a result of the nutritional disadvantages of late hatching. Our analysis of the growth-rate data supports this assumption (see beyond).

GROWTH: BODY WEIGHT

Table 7 summarizes our data together with those of Morton et al. (1972b) for Tioga Pass and Banks (1959) for Berkeley. All of these data sets yield excellent linear relationships when fitted to the logistic equation by the method of Ricklefs (1967). This graphical method, however, does not yield estimates of variance, and, although it is suitable for large-scale interspecific comparisons, it is not discriminating enough for testing the reality or biological significance of the relatively small differences occurring in intraspecific comparisons (Ricklefs 1973). We therefore adopted a conservative course and relied only on examination of the primary data.

Since we found no consistent trends of significant differences in the growth of chicks in broods of three, four, or five at Fairbanks and Hart Mountain (as analyzed both in terms of body weights and growth rates as computed by $\ln W_{n+1} - \ln W_n$, where W_n and W_{n+1} are body weights on

TABLE 6. Synchrony of hatching.

Locality	Hatching on Day 0[a] No.	Hatching on Day 0[a] %	Hatching on Day 1 No.	Hatching on Day 1 %	Hatching on Day 2 No.	Hatching on Day 2 %	No. of Eggs	No. of Clutches
Fairbanks, AK	63	82.9	12	15.8	1	1.3	76	17
Hart Mtn., OR	46	80.7	10	17.5	1	1.8	57	17
Tioga Pass, CA	222	76.8	61	21.1	6	2.1	289	77
Niwot Ridge, CO								
3,290 m	23	79.3	6	20.7	0	—	29	9
3,475 m	99	81.1	22	18.0	1	0.8	122	35

[a] The day on which one or more eggs of a clutch hatched.

TABLE 7. Body weights of nestlings (g, mean ± SE, n).

Day	Fairbanks	Hart Mtn.	Tioga Pass	Niwot Ridge 3,290 m	Niwot Ridge 3,475 m	Berkeley
0	2.66 ± 0.06 (65)	2.71 ± 0.06 (54)	2.70 ± 0.06 (56)	2.61 ± 0.08 (27)	2.72 ± 0.06 (65)	2.4 ± 0.04 (19)
1	4.10 ± 0.07 (76)	4.19 ± 0.11 (51)	4.28 ± 0.09 (95)	4.12 ± 0.20 (29)	4.22 ± 0.08 (69)	3.5 ± 0.09 (26)
2	6.47 ± 0.11 (76)	5.96 ± 0.19 (50)	6.56 ± 0.09 (96)	6.11 ± 0.20 (27)	6.27 ± 0.12 (67)	5.4 ± 0.17 (22)
3	9.22 ± 0.13 (74)	9.34 ± 0.33 (34)	9.24 ± 0.13 (93)	8.81 ± 0.30 (25)	9.10 ± 0.18 (66)	7.6 ± 0.27 (19)
4	12.16 ± 0.18 (66)	11.96 ± 0.48 (28)	12.19 ± 0.17 (96)	11.56 ± 0.42 (23)	12.14 ± 0.24 (57)	10.3 ± 0.32 (19)
5	14.35 ± 0.20 (66)	13.65 ± 0.65 (17)	16.12 ± 0.19 (95)	14.62 ± 0.40 (27)	14.97 ± 0.25 (54)	12.8 ± 0.40 (19)
6	16.36 ± 0.25 (65)	15.94 ± 0.88 (11)	17.62 ± 0.38 (65)	16.98 ± 0.38 (24)	17.55 ± 0.30 (48)	15.5 ± 0.47 (16)
7	18.22 ± 0.22 (51)	18.77 ± 0.69 (10)	19.44 ± 0.20 (56)	19.00 ± 0.37 (22)	19.35 ± 0.29 (44)	16.9 ± 0.49 (16)
8	18.86 ± 0.33 (14)	19.53 ± 0.26 (6)	20.14 ± 0.24 (45)	19.86 ± 0.44 (20)	20.12 ± 0.24 (40)	18.1 ± 0.55 (16)
9	—	—	20.36 ± 0.33 (17)	20.93 ± 0.39 (11)	20.72 ± 0.56 (18)	19.0 ± 0.62 (14)
10	—	—	20.78 ± 0.56 (6)	—	20.80 ± 0.82 (4)	—

successive pairs of days) we pooled the data regardless of brood size. There were likewise no statistically significant differences in weights or growth rates between broods of three or four on Niwot Ridge, although broods of five did differ significantly from these and thus merit brief discussion below. Banks (1959) also found no differences in growth rates in broods of three or four at Berkeley, and Morton et al. (1972a, b) pooled their data regardless of brood size, implying that they detected no effect. The scant comparative data available (for review, see Ricklefs 1968) on this subject show that the average growth of nestlings is commonly independent of brood size, but not always so.

To determine if nestling growth rates differed significantly as a function of brood size we compared regression coefficients of growth curves for broods of three, four, and five at Niwot Ridge. Growth rates in broods of three and four were statistically indistinguishable, but each was significantly different ($P < 0.05$) from broods of five. Since most of this difference was presumed to result from the presence in broods of five of one or two late-hatching individuals whose growth was considerably slower than that of their siblings, we also compared growth rates within this group. Probably as a result of small sample size (four broods), paired comparison among siblings revealed no significant differences in growth rates. However, we found a significant difference when we compared the smallest (youngest) individual with pooled values for its four siblings, suggesting that late-hatching "runt" individuals were at a competitive disadvantage with nest-mates. In fact, they were never found to attain equivalent weights while in the nest.

Such "runt" individuals may represent a tendency toward increasing brood size while minimizing the competitive liability to the rest of the brood when food resources are unpredictable (Lack 1968). Evidently this pattern is not generally advantageous on Niwot Ridge, since broods of five constituted only a small proportion (8.2%) of nests found. In contrast, near the northern limit of distribution of Z. leucophrys at Fairbanks, five-egg clutches comprised 67% of the total, and postnatal growth in broods of five did not differ from that in broods of four. The longer daylength and perhaps the greater productivity of foods at the higher latitudes apparently enables the adults to

TABLE 8. Some comparisons of nestling and adult body size.

	Fairbanks	Hart Mountain	Tioga Pass	Niwot Ridge[a]	Berkeley
Basic data					
Adult wt., g[b]	24.8	29.1	28.9	29.2	26.6
Adult wing, mm[c]	73.9	76.4	76.6	77.3	70.6
Day 4 nestling wt., g	12.7	12.0	12.9	12.0	10.0
Day 8 nestling wt., g	18.9	19.5	20.1	20.1	18.1
Derived indexes					
Day 4 wt./ad. wt.	0.49	0.41	0.45	0.41	0.39
Day 8 wt./ad. wt.	0.76	0.67	0.70	0.68	0.68

[a] Sublocalities averaged.
[b] Mean male + female weight at the median date of the fledging period.
[c] Chord, unworn feathers.

TABLE 9. The length of the innermost primary feather (mm, mean ± SE, n) in relation to days after hatching.

Day	Fairbanks	Hart Mtn.	Niwot Ridge
2	nil (15)	nil (27)	nil (11)
3	1.0 ± 0.12 (15)	1.2 ± 0.28 (29)[a]	1.4 ± 0.33 (11)
4	3.1 ± 0.17 (20)[a]	4.0 ± 0.43 (34)[a]	3.7 ± 0.40 (14)[a]
5	6.1 ± 0.16 (20)[a]	7.8 ± 0.59 (22)[a]	7.1 ± 0.54 (16)[a]
6	12.4 ± 0.28 (20)[a]	12.8 ± 0.81 (18)[a]	12.1 ± 0.76 (13)[a]
7	17.5 ± 0.33 (14)[a]	17.8 ± 0.75 (15)[a]	15.7 ± 0.66 (13)[b]
8	21.3 ± 0.43 (8)[a]	22.0 ± 0.79 (10)[b]	21.3 ± 0.75 (16)[a]
9	—	24.0 (2)	23.7 ± 1.32 (7)[c]
10	—	—	26.3 ± 0.76 (8)[c]

[a] Length differs from that of preceding day at $P < 0.001$.
[b] $P < 0.01$.
[c] $P < 0.1$.

nourish more young adequately, as Lack (1954) suggested.

A step-by-step horizontal comparison of mean weights on the same day of nestling life (Table 7) by the SNK test (Sokal and Rohlf 1969) revealed no statistically significant differences ($P > 0.05$) or consistent trends in the montane and subarctic populations through day 4, and only erratic differences thereafter. For example, mean weights at all montane and subarctic localities as well as at Berkeley were significantly less ($P < 0.05$) than those at Tioga Pass on day 5, but this difference disappeared on day 6, when only the means at Hart Mountain and Berkeley were significantly less than the others. This trend continued through day 7 and disappeared on day 8. In short, the weight curves for *gambelii* and all the populations of *oriantha* were virtually identical when superimposed (Fig. 1).

Nestlings in the Berkeley population (*nuttalli*) weighed significantly less than the others through day 4 but did not differ ($P > 0.05$) or differed only marginally ($P \cong 0.1$) from the Fairbanks and Hart Mountain populations on days 5–8. By day 8 (the last day on which we had data for all six populations) and beyond, the nestlings at Berkeley weighed less than those in all other populations, but the difference was significant ($P < 0.05$) only in comparison with the subalpine forms of *oriantha* (Tioga Pass and Niwot Ridge).

The slight differences in body weight of nestlings among localities or subspecies are undoubtedly related at least in part to differences of adult body size. The ranges of variation are too small, however, to enable us to factor out this effect clearly and to identify residual ecological effects, if any, on nestling growth. Adult *gambelii* at Fairbanks and *nuttalli* at Berkeley weigh less
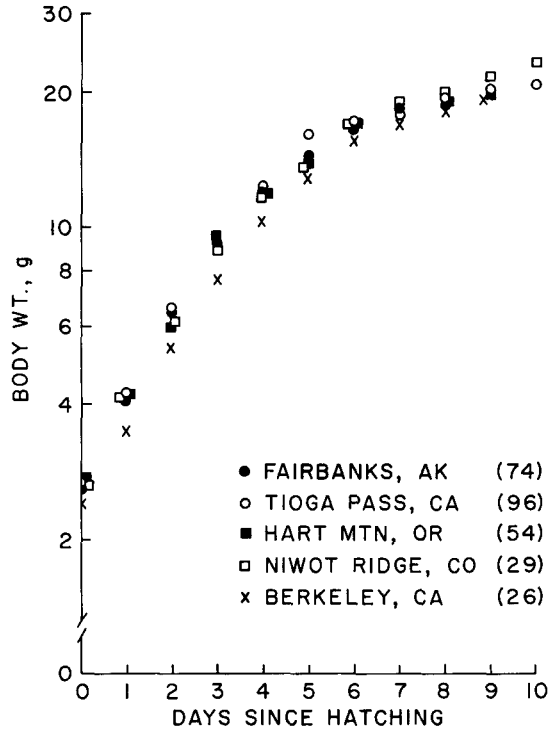

FIGURE 1. Semilogarithmic plot of mean body weight of nestling *Z. leucophrys* at five localities in relation to age. To avoid clutter, only the data from 3,290 m on Niwot Ridge are included. Numerals in parentheses show maximum sample sizes. See Table 7 for statistical details.

and have shorter wings than *oriantha*. On both day 4 (log-linear phase of growth) and day 8 (upper flexure) of nestling life the weights of nestlings per unit adult weight appear to be nearly alike in *nuttalli* and *oriantha* but on both days greater in *gambelii* (Table 8). This suggests that the growth of nestling *gambelii* at Fairbanks relative to adult weight is comparatively faster or greater than in other subspecies or localities, but the differences are very small and of questionable ecological significance.

GROWTH: REMIGES

The growth of the plumage tends to be more regular than the increase of body weight in nestlings, and is a more reliable index of age. To establish simple criteria of age for use in subsequent investigations, we measured the flattened length of the innermost primary feather (P1) with an accuracy of ±0.5 mm at daily intervals. We found no consistent differences among the three populations for which we had data (Table 9) regardless of slight differences of adult wing length (Table 1). The pinfeather of P1 emerged from the skin between days 2 and and 3 of nestling life, and the variance of

growth rate thereafter was sufficiently small so that the age of nestlings can be estimated with an accuracy of at least 90%, and usually 99%, on the basis of the length of this feather (Table 9).

Although our results show only minor geographic or interracial variation in the growth of nestling White-crowned Sparrows, they do not preclude the existence of adaptive differences in postfledging growth and development. Berthold et al. (1970, 1974) showed that a variety of postfledging developmental processes (e.g., attainment of adult body weight, pace of postjuvenal molt) are shorter, faster, or better synchronized in northern than in southern populations of sylviid warblers. Although these differences amount to only 10–12 d at a maximum, it is plausible that the reduction is significant in the time budgets of migratory populations occupying highly seasonal northern latitudes.

DEPARTURE FROM THE NEST

The age at which the young leave the nest is a more clear-cut geographic or subspecific variable than body weight in the development of Z. leucophrys, and Morton et al. (1972b) and Oakeson (1954; see DeWolfe 1968 for additional data) noted that it diminishes northward. Our additional data are consistent with this, but introduce an altitudinal complication in oriantha, in which the age at fledging may decrease slightly with altitude. The mean age at fledging ranges from 10.1 d in nuttalli at Berkeley to 8.0 d in gambelii at Fairbanks (Table 3).

When we first detected the short nestling period at Fairbanks during investigations in the 1960's (only incidentally concerning nest biology, and thus lacking systematic observations) we regarded it as a result of human disturbance. In 1973 we tested this by observing "control" nests with as little disturbance as possible at about eight-h intervals. Nestlings that disappeared from the nest (predation was negligible at Fairbanks during all years of our work there) in the intervals between visits were assumed to have fledged on the median hour of that interval. Hence, the time of fledging was estimated with a maximum error of about 0.3 d and a probable error of about ±0.15 d. The mean age of fledging measured in this way was 8.0 d for 17 nestlings in 4 "control" nests, and 7.6 d for 43 nestlings in 10 other nests that were also observed thrice daily but weighed on one of these occasions. DeWolfe (1968) reported that the age of fledging was 8.4 d in 15 young at this same

locality—a discrepancy that may reflect year-to-year differences, but more likely reflects differences in data-handling or modes of observation, and cautions us against attaching much significance to small differences in this inexact variable.

Nevertheless, it is clear that the period of nestling life becomes shorter northward and that young crowned sparrows voluntarily depart the nest as early as seven days of age in the subarctic. This is the earliest age at which the torso is fully feathered and the birds are homeothermic (Morton and Carey 1971) and capable of perching on twigs. The difference between the latitudinal extremes is only about two days (Table 3) and of questionable significance to breeding-season time budgets even in the very time-limited subarctic populations. Why, then, does the age at fledging decrease northward? Maher (1964) assembled evidence that fledging is a behavioral trait independent of the stage of somatic development in emberizines. He suggested that selection for the length of the nestling period has operated independently of selection for developmental rates. Maher hypothesized that the progressively abbreviated nestling period northward is correlated with longer daylengths during the breeding season and hence with longer periods per day of pressure from avian predators (and presumably from other visual predators). A corollary of this hypothesis is that dispersal from the nest reduces the risk of predation because it multiplies the foci to which adults are delivering food. Maher's hypothesis seems reasonable and may well be correct on a global scale or in selected settings, but it does not persuasively explain the differences in age at fledging between nuttalli at Berkeley and gambelii at Fairbanks. Nest-predators are nearly nonexistent at Fairbanks. During the several years of our observations there we knew of only one nest in about 120 that was destroyed by a predator, which was a domestic dog. Elsewhere in Alaska (at least in maritime localities) nest predation may be more intensive than at Fairbanks, as documented by Oakeson (1954) and Williamson et al. (1966), but is still small compared with predation at lower latitudes. Predation on nestlings of nuttalli in central California is comparatively very intensive (Blanchard 1941), particularly by snakes (Petrinovich and Patterson 1978), which are visual predators. Maher's hypothesis applied to the Fairbanks-California samples would predict earlier fledging in the south. We suggest as an alternative hypothesis that the earlier

fledging northward may reflect no more than slightly earlier neural development permitted by the longer daylength, the longer period of activity each day, and consequently more "practice" movements that hasten the maturation of the sensorium and of neuromuscular coordination. Our strong impression (which we are unfortunately unable to quantify except as a sort of "vexation index") was that nestlings at Fairbanks after about day 5 were more alert, fractious, and difficult to handle during weighing than nestlings at the same age in other populations. We doubt that this would confer any selective advantage in relation to predators at Fairbanks, although it may do so elsewhere. The adaptive significance of shorter fledging ages northward remains enigmatic except perhaps as a minor component of the complex of abbreviated behavioral events that characterize crowned sparrows at increasing latitudes or altitudes (Morton 1976).

ACKNOWLEDGMENTS

LITERATURE CITED

BANKS, R. C. 1959. Development of nestling White-crowned Sparrows in central coastal California. Condor 61:96–109.

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow Zonotrichia leucophrys. Univ. Calif. Publ. Zool. 70:1–123.

BERTHOLD, P., E. GWINNER, AND H. KLEIN. 1970. Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels, Sylvia borin, und eines weniger ausgeprägten Zugvogels, S. atricapilla. Vogelwarte 25:297–331.

BERTHOLD, P., E. GWINNER, AND U. QUERNER. 1974. Vergleichende Untersuchung der Jugendentwicklung südfinnischer und südwestdeutscher Gartengrasmücken Sylvia borin. Ornis Fenn. 51:146–154.

BLANCHARD, B. D. 1941. The White-crowned Sparrows (Zonotrichia leucophrys) of the Pacific Seaboard: environment and annual cycle. Univ. Calif. Publ. Zool. 46:1–178.

CASE, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q. Rev. Biol. 53:243–282.

DEWOLFE, B. B. 1968. Zonotrichia leucophrys nuttalli Ridgway: Nuttall's White-crowned Sparrow

p. 1292–1324, and Zonotrichia leucophrys gambelii (Nuttall), p. 1324–1338. In O. L. Austin, Jr. [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U. S. Natl. Mus. Bull. 237, Part 3.

DRENT, R. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Suppl. 17:1–132.

DRENT, R. 1975. Incubation, p. 333–420. In D. S. Farner and J. R. King [eds.], Avian biology, Vol. 5. Academic Press, New York.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

MAHER, W. J. 1964. Growth rate and development of endothermy in the Snow Bunting (Plectrophenax nivalis) and Lapland Longspur (Calcarius lapponicus) at Barrow, Alaska. Ecology 45:520–528.

MORTON, M. L. 1976. Adaptive strategies of Zonotrichia breeding in high latitude or high altitude. Proc. XVI Int. Ornithol. Congr. (1974):322–336.

MORTON, M. L., AND C. CAREY. 1971. Growth and development of endothermy in the Mountain White-crowned Sparrow (Zonotrichia leucophrys oriantha). Physiol. Zool. 44:177–189.

MORTON, M. L., J. L. HORSTMAN, AND J. M. OSBORN. 1972a. Reproductive cycle and nesting success of the Mountain White-crowned Sparrow (Zonotrichia leucophrys oriantha) in the central Sierra Nevada. Condor 74:153–163.

MORTON, M. L., J. R. OREJUELA, AND S. M. BUDD. 1972b. The biology of immature Mountain White-crowned Sparrows (Zonotrichia leucophrys oriantha) on the breeding ground. Condor 74:423–430.

OAKESON, B. B. 1954. The Gambel's Sparrow at Mountain Village, Alaska. Auk 71:351–365.

O'CONNOR, R. J. 1977. Growth strategies in nestling passerines. Living Bird 16:209–238.

PETRINOVICH, L., AND T. PATTERSON. 1978. Cowbird parasitism on the White-crowned Sparrow. Auk 95:415–417.

RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. Condor 76:147–152.

RAHN, H., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. Auk 92:750–765.

RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–983.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177–201.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman, San Francisco.

SKUTCH, A. F. 1952. On the hour of laying and hatching of birds' eggs. Ibis 94:49–61.

WILLIAMSON, F. S. L., M. C. THOMPSON, AND J. Q. HINES. 1966. Avifaunal investigations, p. 437–480. In N. J. Wilimovsky and J. N. Wolfe [eds.], Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Commission, Washington, DC.

Department of Zoology, Washington State University, Pullman, Washington 99164. Address of second author: Department of E.P.O. Biology, University of Colorado, Boulder, Colorado 80309. Accepted for publication 31 January 1981.