THE ANNUAL CYCLE OF WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS NUTTALLI*) IN COASTAL CALIFORNIA

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The basic unit of temporal organization in long-lived animals is the annual cycle. In birds this includes most prominently the periods of winter maintenance, reproduction, molt, and migration or dispersal. To attain maximal, or at least adequate, fitness, all of these essential processes must occur and be timed in individuals and populations so that conflicting demands for time and energy are minimized and they must exploit as well as possible the cyclic variations of the environment. The structure of the annual cycle thus represents evolutionary tendencies toward optimization, including, for instance, the length of the reproductive period, the pattern and duration of molt, and the proclivity for migration.

Although much can be learned about the adaptive basis of the annual cycle by intensive investigation of individual taxa or geographic populations, much more can be learned by comparisons of taxonomic or geographic variants. Through nearly four decades of research, beginning with the pioneering investigations by Blanchard (summarized by DeWolfe 1968), the annual cycles of the crowned sparrows, *Zonotrichia* spp., have been analyzed especially thoroughly in this context. It is paradoxical that certain aspects of the annual cycle and general biology are least well known in the form of *Zonotrichia leucophrys* that is most readily accessible from urban and academic centers. *Z. l. nuttalli*, hereafter called Nuttall's Sparrow, is the only nonmigratory form of *Zonotrichia* in North America, and is thus of particular interest in a comparative context. Nuttall's Sparrow inhabits the narrow coastal fog zone of California between about 34° and 40° N latitude. We report below the results of a five-year investigation of the cycles of reproduction and molt in Nuttall's Sparrows on Point Reyes, near the middle of their latitudinal range.

STUDY AREA AND METHODS

The study area, hereafter referred to as Palomarin, overlooks the Pacific Ocean along seven km of the outer coast on Point Reyes National Seashore just N of Bolinas in central California. Our data were obtained in a capture-recapture program involving 366 trapping and netting sites occupying about 600 ha of coastal scrub, grassland, and forest edge between the tops of the coastal bluffs and the forest on Inverness Ridge. The area extends NW from the field station of Point Reyes Bird Observatory at the mouth of Arroyo Hondo, including Abalone Point, Bass Lake, Pelican Lake, Double Point, Ocean Lake, and Wildcat Lake.

Extending from the 60-m contour level at the tops of the coastal bluffs (an old marine terrace) to the 300-m level inland, the study area is dissected by V-shaped valleys with small intermittent or permanent spring-fed streams. In several places the highly unstable shale bedrock has slumped to form natural lakes and ponds. Marine terraces at 60 and 180 m elevation were previously cultivated, and the entire area was grazed by cattle prior to 1964. The northwestern 60% of the area remained pasture until 1970. Remnant grasslands, previously maintained by cattle grazing, are now undergoing successional revegetation by Northern Coastal Scrub (Munz and Keck 1959). This immediate coastal zone dominated by sclerophyllous trees and shrubs gives way on the ridge tops a few kilometers inland to a moist forest dominated by Douglas fir (*Pseudotsuga menziesii*).

The climate of Palomarin is of the warm, summer-dry Mediterranean type (Fig. 1) with moderate to strong onshore winds and frequent fog, especially in summer. Mean monthly air temperatures range from 4° to 15°C, and typical daily ranges are from 3° to 10°C in winter and 8° to 18°C in summer. Winter temperatures frequently drop to 0°C on slopes facing away from the ocean and may rise to 30°C in later summer with occasional airflow from the interior. Annual rainfall (Fig. 1), usually restricted to the months from October to April, varied from 60 to 125 cm at Palomarin in the five seasons of our study.

Nuttall's Sparrows were captured by both traps and mist nets in all months of the year from May 1966 through August 1970. Four-cell Glenhaven-Standby traps were baited with cracked corn and wheat. About 100 traps were rotated periodically through more than 300 trap sites along ridges, terrace edges, old ranch roadways, and grassland-scrub edges. On a typical workday, from 12 to 20 traps were inspected at 1- to 2-h intervals from dawn to midafternoon (dusk in winter). Mist nests were used extensively near the Observatory in the south part of the study area, and occasionally as supplements to traps elsewhere. U.S. Fish and Wildlife Serivce bands were used on all birds.

At each capture and recapture, we recorded age, sex (when discernible), body weight, wing length, amount of fat, molt, and reproductive condition. The birds were immediately released at or near the place of capture. Nuttall's Sparrows are called hatching-year birds (HY) through 31 December of their
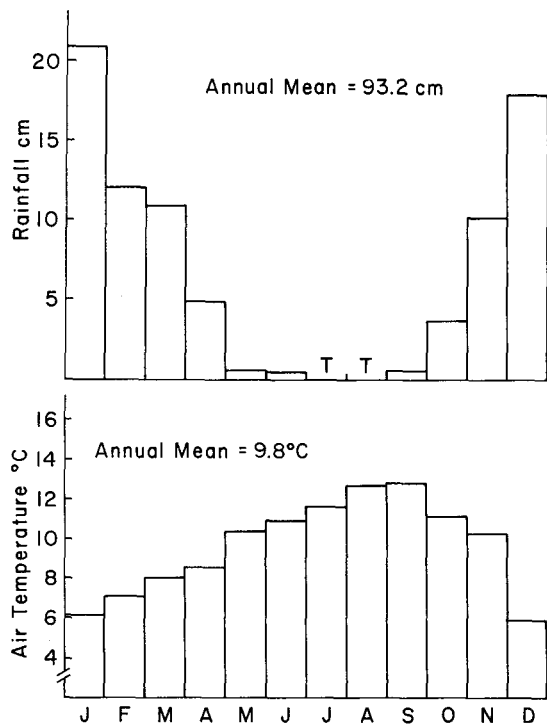
FIGURE 1. Mean monthly rainfall and air temperature through a nine-year period (1966–1974) at Palomarin (Point Reyes Bird Observatory).

TABLE 1. Cloacal protuberance index of White-crowned Sparrows at Palomarin, 1966–70.

Interval	Mean	n	% frequency of index			
			0	1	2	3
1–10 Mar	0.4	39	66.7	30.8	2.5	—
11–20	0.8	64	34.4	59.4	6.3	—
21–31	1.4	162	8.0	52.5	32.7	6.8
1–10 Apr	2.1	119	5.0	18.5	37.0	39.5
11–20	2.6	182	0.5	7.1	26.9	65.4
21–30	2.6	126	2.3	5.6	25.4	66.7
1–10 May	2.7	122	—	2.5	21.3	76.2
11–20	2.6	109	1.0	3.6	30.3	65.1
21–31	2.5	164	—	8.5	29.9	61.6
1–10 June	2.5	136	1.0	11.8	24.3	63.2
11–20	2.6	108	—	9.3	25.0	65.7
21–30	2.4	120	—	16.7	31.7	51.6
1–10 July	1.7	224	—	50.9	29.0	20.1
11–20	1.4	136	0.8	67.6	21.3	10.3
21–31	1.3	168	1.8	73.8	17.9	6.5
1–10 Aug	1.0	22	9.1	86.4	4.5	—
11–20	1.1	35	—	94.3	5.7	—
21–31	1.0	16	—	100.0	—	—

Total n = 2,051.

first year of life, second-year birds (SY) from 1 January for as long as they were distinguishable from older birds (by retention of brown feathers in the crown until August), and adults (ASY or AHY) thereafter, as recommended in the North American Bird Banding Manual (1972). Body weights were measured to the nearest half gram by a Pesola spring balance that was frequently checked at the 20-g point with a standard weight. Wing length was measured to the nearest millimeter with a zero-stopped steel scale. The cloacal protuberance of males was rated from 0 (no enlargement) to 3 (maximum enlargement). A regressing cloacal protuberance could be rated as 2 or 1 on its way to the nonbreeding condition. The brood patch of females was rated from 0 (patch area feathered), 1 (area bare and including initial vascularization), 2 (moderate edema and thickening), 3 (maximum development), and 4 (regressing or regressed patch, or patch area bare prior to refeathering in postnuptial molt).

The field data for each bird captured or recaptured were transcribed on a 5 × 8 in marginal-punch Unisort Analysis Card overprinted for multiple entries. A single card was used for each of the approximately 5,000 Nuttall's Sparrows banded from May 1966 through August 1970. About 22% of these birds were not captured again. The average number of recaptures was about 4.5, ranging from 1 to 37 times. About 23,000 data entries accrued for the 5,000 birds during the five years of study, providing our principal source of information.

RESULTS AND DISCUSSION

We first present composite data for the five-year period, and subsequently examine year-to-year variants in timing of the annual cycle, mainly in relation to the progress of the postnuptial molt.

REPRODUCTIVE PERIOD

Males. In Nuttall's Sparrows, the first perceptible enlargement of the testes above the resting condition begins soon after the winter solstice at Berkeley, California, about 60 km SE of the present study area (Blanchard 1941). The birds there become reproductively active by early March, Blanchard noting earliest copulations during four seasons as 3, 7, 19 March, and 2 April (the latter a year of inclement winter and spring weather). Captive Nuttall's Sparrows from six coastal populations including Bolinas (near Palomarin) held in an aviary at San Jose began testicular growth in late February and early March (Mewaldt et al. 1968). Our data for Palomarin, assuming that a cloacal protuberance index of 2 (CP 2) indicates sexual competence, likewise show that a few males are sexually active by the first decade of March (Table 1). This fraction progressively increases, and CP 2 + CP 3 reaches a plateau near or above 90% of the population during the second decade of April, remains there through mid June, and rapidly decreases thereafter (Fig. 2). Inspection of a sample of individual males for which we have sufficient serial observations (Fig. 3) shows that most adults remain reproductively competent

TABLE 2. Brood patch index of White-crowned Sparrows at Palomarin, 1966–70.

Interval	Mean[a]	n	% frequency of index				
			0	1	2	3	4
1–10 Mar	0.0	12	100.0	—	—	—	—
11–20	1.3	20	33.3	66.7	—	—	—
21–31	1.3	24	—	75.0	25.0	—	—
1–10 Apr	1.5	26	3.8	50.0	38.5	7.7	—
11–20	2.2	78	1.3	21.8	32.0	44.9	—
21–30	2.4	83	6.0	7.2	30.1	56.6	—
1–10 May	2.6	87	—	5.7	29.9	64.4	—
11–20	2.1	85	—	29.4	24.7	43.5	2.4
21–31	1.9	130	—	33.8	28.5	31.5	6.2
1–10 June	2.2	100	—	24.0	30.0	44.0	2.0
11–20	1.8	103	—	35.9	33.0	26.2	4.9
21–30	1.3	74	1.4	36.5	17.6	20.2	24.3
1–10 July	1.1	179	—	35.4	19.6	11.7	33.3
11–20	0.7	126	—	31.7	12.7	4.8	50.8
21–31	0.5	143	0.8	21.2	12.6	2.1	63.5
1–10 Aug	0.4	32	—	14.4	9.4	3.1	73.1
11–20	0.1	44	—	4.1	4.5	—	91.4
21–31	0.0	18	—	—	—	—	100.0

[a] In computing the mean, index 4 was considered to be index 0.
Total n = 1,315.

throughout the breeding season, although perhaps varying between CP 2 and CP 3 (e.g., birds 047, 272, and 995), but that a few (perhaps 10%) do not become active at all (e.g., 009) or are active for only part of the season (e.g., 809). We find no substantial evidence that first-year males differ from older adults in the development and maintenance of the cloacal protuberance. While the frequency distributions in Table 1 suggest that 5–10%
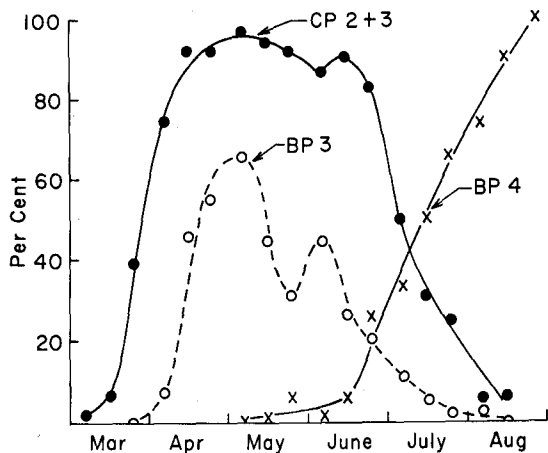

FIGURE 2. Percentages of Nuttall's Sparrows having a functional cloacal protuberance (CP 2 + 3), functional brood patch (BP 3), or regressing or regressed brood patch (BP 4): A composite sample for 1966–70 (see Tables 1 and 2).
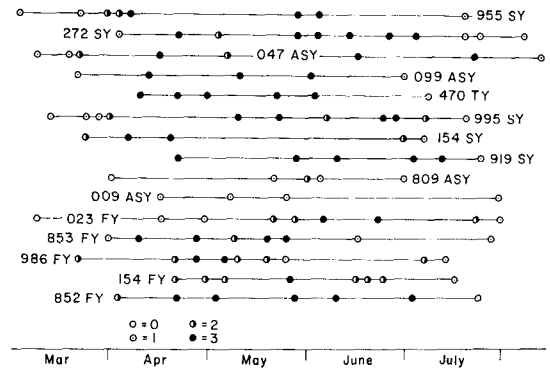

FIGURE 3. Within-season variation of the cloacal protuberance index in representative Nuttall's Sparrows. FY = first breeding season; SY or ASY = second or subsequent breeding season.

of males do not surpass CP 1 during the peak of the breeding season (late April–early June), an indeterminate fraction of these may result from asynchrony among individuals having only a relatively short breeding period (e.g., 809) or a temporary relapse to CP 1 (e.g., 986).

Females. Brood-patch development first becomes evident in mid March (Table 2; Fig. 2) but the earliest fully functional brood patches (BP 3) are observed in early April, after which an erratic plateau is maintained until the steady decline to the inactive condition beginning in mid June. During the course of the season, brood-patch condition varies rapidly in individuals (Fig. 4) between BP 1 (initial development or inter-nesting interval) and BP 3 (incubating). Our records for individuals (Fig. 4) show that BP 4 marks the end of reproductive effort for the year.
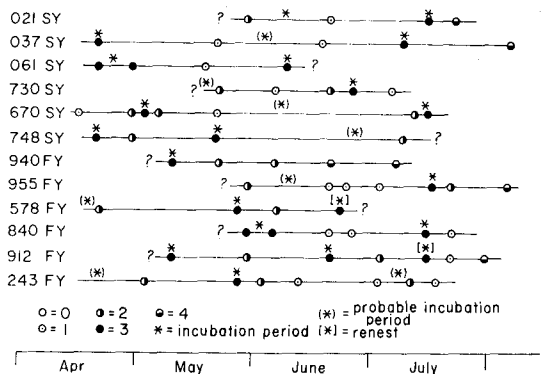

FIGURE 4. Within-season variation of the brood patch index in representative Nuttall's Sparrows. FY = first breeding season; SY = second breeding season.

TABLE 3. Temporal components of the nesting cycle in *Zonotrichia leucophrys nuttalli*[a].

Nest-building, range = 7–9 days	8 days
Average interval between completion of nest and laying of first egg = 3.6 days	4 days
Laying period[b]	3 days
Incubation period	12 days
Nestling period	10 days
Independence of nestlings: 15 days after leaving nest; female begins building of second nest after 10 days	10 days
Sum	47 days

[a] Data from Blanchard (1941).
[b] Clutch size = 3.27.

From this, it appears that a small fraction of females (2–6%) incubate only one or two broods early in the season (e.g., 940), but that others either spread their broods further apart in time or incubate three clutches (excluding renests). The interval between the earliest and latest BP 3 is about 125 days. Summing the time requirements of component phases indicates that a single nesting cycle requires about 47 days, or that about 34 days elapse between the end of an incubation period and the earliest possible beginning of a subsequent one (Table 3). An individual female can easily rear two broods, perhaps three in some years. A sample of serial records for individuals in a given season shows that two incubation periods are common, and in some cases three are likely (Fig. 4). In instances of nest mortality, more than this are possible, but none of our records shows more than three episodes of BP 3 per season. In sum, a very small fraction of females incubate only one clutch per season, most incubate two clutches, and a few incubate three. During the peak of the nesting season, from 30% to 65% of females are incubating concurrently. The brood-patch data and, to a much lesser extent, the cloacal protuberance data (Fig. 2) suggest a bimodal distribution of reproductive activity, having a main peak in early May and a lesser peak in early June. We cannot exclude, however, the possibility that this is a statistical artifact resulting from the collation of data having slight phase differences among the five seasons. The samples for the individual years are too small for conclusive statistical analysis. Furthermore, the temporal distribution of estimated fledging times (see beyond) appears to be unimodal.
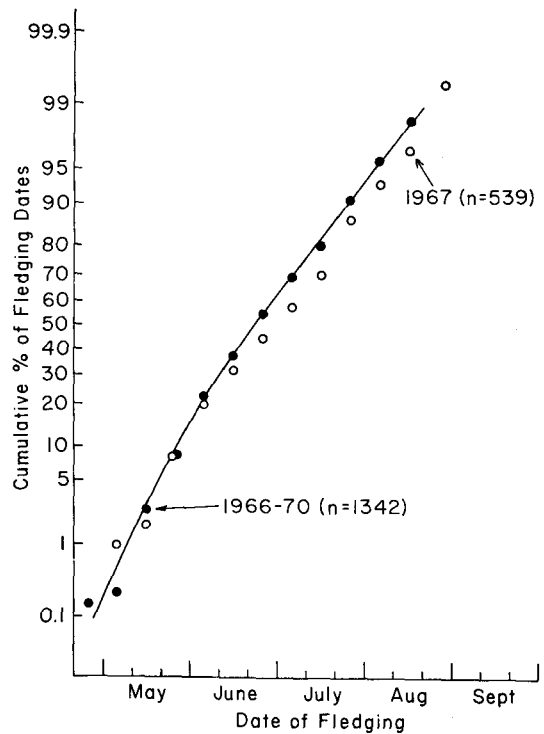

FIGURE 5. Temporal course (cumulative percentages) of fledging dates of Nuttall's Sparrows plotted on a probability scale for a composite sample (1966–70) and for one season (1967). See text for explanation.

TEMPORAL DISTRIBUTION OF FLEDGING DATES

We estimated the date of fledging with an accuracy of about ±5 days by extrapolation from the status of postjuvenal molt in individuals. By mischance, the seasonal distribution of sampling prevents us from presenting an analysis of the full breeding season except in 1967 (Fig. 5). In this and other years we can delimit the season, however, by the earliest (data valid for four years) and latest (two years) captures of volant young having the juvenal plumage still growing and rectrices still soft. The earliest dates of observation (which are fully consistent with extrapolations from birds caught later in the season) are 11 May 1967, 9 May 1968, 14 May 1969, and 12 May 1970. As expected, the observations as a group fall about 40 days later than the earliest BP 3 indexes in the composite data (Fig. 2, Table 2). The peaks of the curves of reproductive status in adults (Fig. 2) and the occurrence of fledglings (50% point in Fig. 5) are also separated by about 40 days, reinforcing our belief that these independent portrayals of the course of the nesting season are accurate.

The latest observations of newly fledged young were on 28 August 1966 and 31 August 1967. The low variance of the early (9–14 May) and late (28–31 August) dates suggests that the nesting seasons themselves recur with remarkable temporal precision from year to year at Palomarin. This is not consistent with the direct observations of Nuttall's Sparrows at Berkeley (Blanchard 1941), in which the dates of first eggs in small samples (5–7 females per year) ranged from 3 March to 3 April through five consecutive years. It is impossible to tell from the data available if this difference is attributable to locality or to statistical error. Blanchard's 5-year investigation encompassed greater extremes of weather than did ours. Nevertheless, on the basis of the assumption derived from our own data that variability in the limits of the nesting season is slight at Palomarin, we have considered the data for all five years as a composite sample, as in the case of the brood-patch and cloacal protuberance data, and have analyzed them as a cumulative frequency distribution. Plotted on a probability scale (Fig. 5), the data show that the temporal distribution of fledging dates forms a quasi-normal curve, skewed very slightly toward the second half of the season and showing no evidence of bimodality. The span of time between the 1% and 99% points is 103 days. The equivalent span for 1967 (the only year for which we have complete data) is 97 days. Accordingly, from these data we suggest that 100 days is our best estimate of the duration of the nesting season in an average year. Another estimator of the duration of the nesting season in the population is the span between the 1% points in the curve of BP 3 (Fig. 2), which is about 120 days. Subtracting a few days from each end of this span to account for the periods of transition of the brood patch to and from a functional status reduces this estimate toward 100 days, which is satisfactory agreement with the fledging span, considering the disparate sources of data.

Although the composite data for fledging date, as well as the results for 1967 alone, indicate a quasi-normal time course (although vaguely bimodal in 1967), we believe it unlikely that this is so in all individual years. Our partial data for 1969, for instance, suggest a fledging curve that is skewed strongly toward the first half of the season, and for 1968 skewed toward the second half. We believe, but cannot demonstrate clearly, that it is these year-to-year variants in the tem-
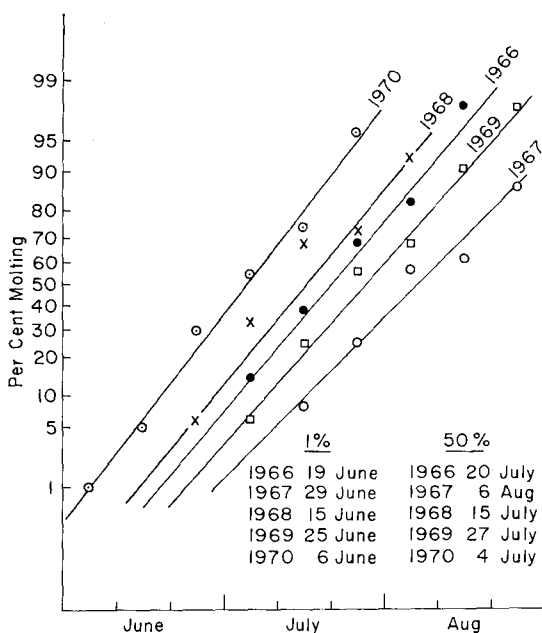

FIGURE 6. Temporal course (cumulative percentages) of the onset of postnuptial molt in Nuttall's Sparrows, plotted on a probability scale by years. The lines were fitted to the points by a least-squares regression of the rectified data.

poral distribution in fledging that account for the year-to-year variability of molt schedules mentioned later.

MOLT

Adult Nuttall's Sparrows undergo a complete postnuptial molt. The partial prenuptial molt is very restricted, involving some body feathers, crown feathers, and wing coverts, but not the two central rectrices ("decks") or secondaries 7, 8, or 9. Mewaldt et al. (1968) found that the extent of this body molt increases slightly from south to north. Birds of the population at Palomarin typically replace only a few contour feathers; many second-year birds retain extensive brown and buff in their crowns through the first breeding season (see also Ralph and Pearson 1971). This very sparse prenuptial molt begins in late January and tapers off through early April (Mewaldt et al. 1968).

Postnuptial molt. The calendar of molt at Palomarin can be expressed most efficiently in terms of the cumulative percentage of adults engaged in molt at the beginning (Fig. 6), or beginning and end (Fig. 7) of the molt period. Most of the data can be fitted reasonably well by straight lines when plotted on a probability scale (only 1968 is a poor fit, but is nevertheless obviously between 1966
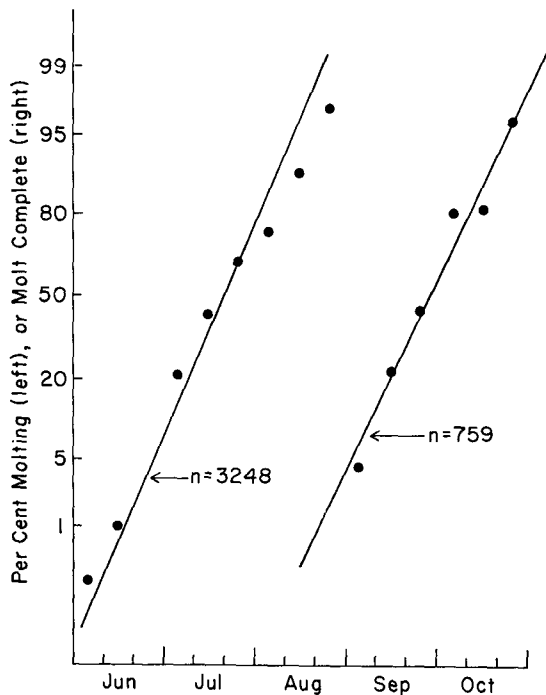
FIGURE 7. The temporal course (cumulative percentages) of the onset (left) and completion (right) of postnuptial molt in Nuttall's Sparrows: A composite sample for 1966–70 (lines fitted as described in Fig. 6).

and 1970 in timing), and show that molt begins (the 1% point) in the second half of June, or exceptionally in early June (1970). This coincides on the average (Fig. 7) with the waning of the cloacal protuberance and the rapid increase of BP 4 (Fig. 2). The duration of postnuptial molt in the population averages about 127 days (1% onset to 99% end) for the 5-year sample in Figure 7. This graph also demonstrates that the onset and end of molt in the population are distributed in time as normal curves (cumulative percentages are approximately straight lines on a probability scale). Assuming that the earliest birds to begin the postnuptial molt are the first to complete it, and so on sequentially through the season, it is possible to estimate the duration of molt in an average individual as the number of days between the lines. The least-squares regressions of the transformed data for the two lines are almost parallel (the slopes do not differ significantly; $P > 0.5$), and the distance between them averages 68 days (range, 65–71 days). We cannot make similar estimates for the individual years, because the data sets for either the onset or end of molt in a given year are too erratic, owing to small sample sizes, to yield clear linear plots. Nevertheless, none of the several hundred individuals for which we have serial observations is inconsistent with this estimate, which is statistically our best.

Suspended molt in adults. Under conditions not fully understood, crowned sparrows of either sex may begin to molt remiges and then suspend further feather loss, apparently during a late-season attempt at nesting or renesting. Such a pause in the annual molt following at least one nesting cycle (and thus truly postnuptial molt) has been called "suspended" molt (King 1972a) or "interrupted" molt (Payne 1972). This contrasts with a permanent "arrest" of molt midway through the remigial sequence, as is known in some neotropical forms of Zonotrichia, as well as other species (King 1972a).

We observed suspended molt in Nuttall's Sparrows at Palomarin in four of the five seasons (2 cases in 1967, 2 in 1968, 1 in 1969, and 13 in 1970). Of these 18 cases, one involved primaries 1 to 3, seven involved primaries 1 and 2, and ten involved only primary 1. In all cases these primaries were fully grown bilaterally, or nearly so, before the shedding of the next primary in the sequence. Five of the 18 birds were recaptured when remigial molt was complete or continuing beyond the point of suspension. Sixteen of the cases of suspended molt were detected early in the molting season (7–18 July), and two other cases were found on 5 and 18 August. We suspect, as did King (1972a), that suspended molt is correlated with the terminal nesting cycle, or a late renesting cycle. Payne (1972) reviewed the scant evidence suggesting that sex steroids suppress molt.

Postjuvenal molt. The growth of the juvenal plumage is completed in the immediate postfledging period and is followed about 20 days later by the onset of the postjuvenal molt, in which the cryptic juvenal plumage is replaced by a first-winter plumage resembling that of second-year birds except that brown and buff substitute for the black and white of the adult crown pattern. Analysis of a sample of 20 juveniles for which we have serial observations spanning the season shows that the postjuvenal molt occupies 55–65 days in individuals, averaging about 60 days. The breast plumage becomes clear gray, free of juvenal speckles, about 35 days after the onset of molt. Because of the apparently obligatory 20-day period between the end of growth in the juvenal plumage and the onset of the postjuvenal molt, young birds can be found in molt as early as the end of May and as late as mid October. Thus, molt is not synchronous in the juvenile population, and
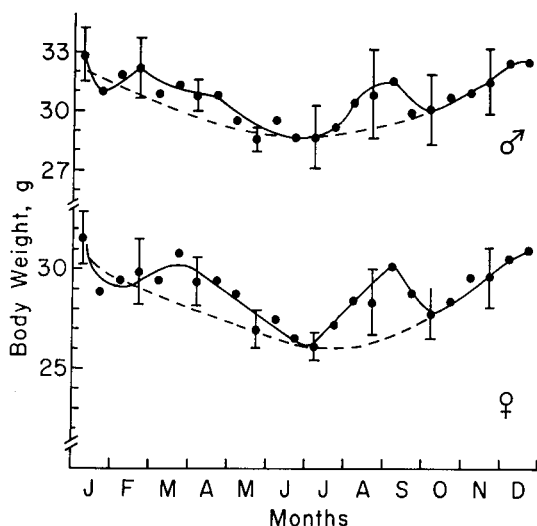
FIGURE 8. The annual cycle of body weight in adult male and female Nuttall's Sparrows (points, and unbroken line): A composite sample for 1966–70. Weight samples were confined to 1000–1400 h. Each data point = 10 birds (total n for each sex = 480 birds); Vertical bars = 95% confidence range for each fourth sample; the broken line suggests the basic (air-temperature dependent?) cycle upon which other perturbations are imposed.
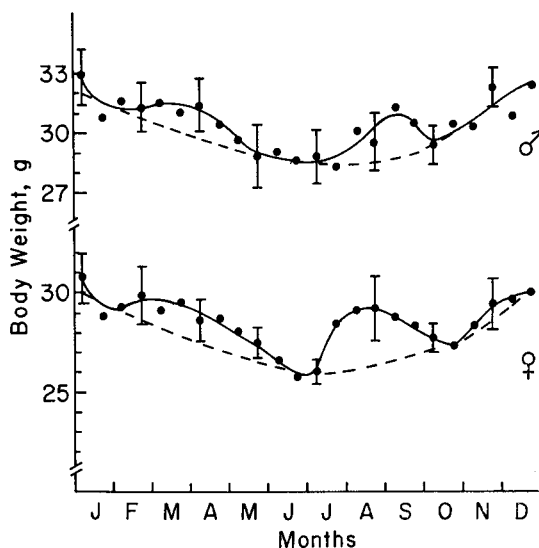
FIGURE 9. The annual cycle of body weight in immature male and female Nuttall's Sparrows (HY from 1 June through 31 December, SY from 1 January through 31 May). See Fig. 8 for further explanation.

the dates of postjuvenal molt follow the dates of fledging by about 20 days.

The relatively brief interval between fledging and the onset of postjuvenal molt resembles that of *Zonotrichia capensis* in Panama (Kalma 1970) and Colombia (Miller 1961), but not in northern Argentina (King 1972a), where the juveniles molt almost synchronously near the end of the six-month-long nesting season. This again raises the question noted by King (1973) about the adaptive significance of replacing immediately an aerodynamically serviceable and cryptically colored juvenal plumage. We know from the case of *Z. capensis* in northern Argentina that the juvenal plumage is aerodynamically adequate for at least four months after fledging; hence the selection pressures fostering quick replacement must pertain to other functions of the plumage.

BODY WEIGHT

Composite samples for the five-year period of investigation reveal in both sexes and age classes an annual cycle of body weight having a maximum in early winter and a minimum in midsummer (Fig. 8, Fig. 9). The mean weights in December are significantly greater than June weights in all sex-age classes ($P < 0.001$) by 11–13% (adults) and 9–10%

(immatures) of the mean June weights. This conforms with the annual cycle observed in captive Nuttall's Sparrows by Mewaldt et al. (1968), but the free-living birds consistently weighed more (by 2–6 g in the semimonthly means) than the captives. This difference has previously been reported in crowned sparrows (King et al. 1966) and results, at least in part, from atrophy of the skeletal musculature accompanying prolonged captivity. An annual cycle in body weight with a peak in midwinter is common among free-living temperate-zone birds (for review, see King and Farner 1966, King 1972b) and is thought to result from increased fat reserves in winter. Our data for Nuttall's Sparrows do not reveal a cycle of visible subcutaneous fat (fat classes fluctuated slightly and erratically from 0 to 1 on a scale of 3), but this does not preclude a substantial variation of fat reserves in visceral depots, where fat may be accumulated preferentially at low levels of storage.

Superimposed on the basic annual cycle of weight changes are conspicuous increases coinciding in both males and females with the period of the postnuptial molt (Fig. 8) or postjuvenal molt (Fig. 9). Less clear weight gains coincide with the prenuptial molt, perhaps being prolonged into the spring in females by the enlargement of the reproductive organs and some deposition of fat. These molt-related changes either do not occur in captive Nuttall's Sparrows or are masked by other

sources of variation (Mewaldt et al. 1968). Nevertheless, such changes are commonly observed in free-living populations of other species of finches, the major increment of weight being body water (for review, see Chilgren 1977).

At almost any time of the annual cycle, adults of both sexes are significantly ($P <$ 0.05) heavier than immatures by 3–6% of adult weight except for males in June (1.3%, $P > 0.2$). After May in the second year of life (SY or AHY birds) this difference disappears. Males are always heavier than females. When tested at the extremes of the cycle in June and December, the mean weights of males exceed those of females by 5.6–7.4% (adults) and 9.0–9.3% (immatures) of male weight (in all classes, $P < 0.001$). In summary, Nuttall's Sparrows become slightly heavier between the first and subsequent years of life, and the sexual dimorphism of weight slightly decreases.

YEAR-TO-YEAR VARIABILITY OF THE ANNUAL CYCLE

Our most exact estimator of the phase of the annual cycle is the progress of postnuptial molt (Fig. 6), which shows a variability of about ±15 days from the 5-year median. Our quantification of the reproductive period is less exact, but an accounting is attempted in Table 4, showing the frequency distribution of cloacal protuberance indexes in the phases of recrudescence (March–April) and regression (June–July). The calendar ordination of regression is much more definite than that of recrudescence, and is closely correlated with the ordination of postnuptial molt (Fig. 10). This is to be expected, because repro-
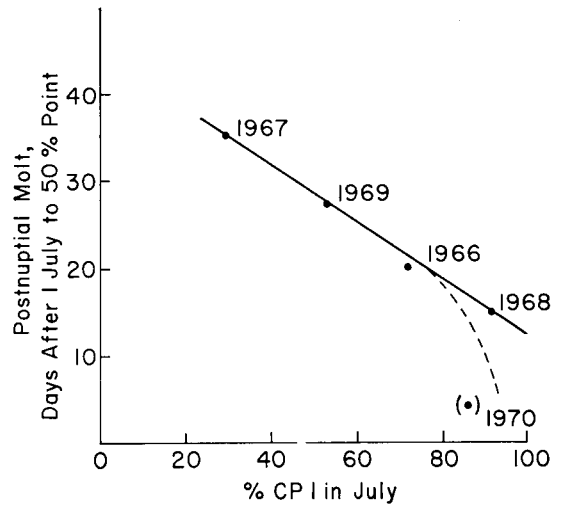

FIGURE 10. The temporal relationship between the end of the reproductive period (regression to CP 1) and the progress of postnuptial molt (see Fig. 6) in Nuttall's Sparrows at Palomarin, 1966–70.

duction and molt tend to be mutually incompatible in crowned sparrows (Morton et al. 1969, King 1974) as well as in a variety of other passerines (Payne 1972). The timing of postnuptial molt thus depends on the ending of previous reproductive events. The data point for 1970 in Fig. 10 does not conform with the trend of the other points. This may be a result either of a relationship that is actually curvilinear, as suggested by the broken line, or of peculiarities of the 1970 season. For reasons to be considered shortly, reproductive recrudescence was unusually early in males in 1970 (Table 4), and nesting waned rapidly in late June owing to low spring and summer rainfall and an unusually warm and windy spring.

TABLE 4. Year-to-year variability of cloacal protuberance indexes in selected seasons.

Season	1966	1967	1968	1969	1970
Recrudescence (% CP 2 + 3)[a]					
March	—	10.7	33.3	31.0	41.8
	(0)	(101)	(39)	(46)	(79)
April	—	84.0	93.5	81.3	95.1
	(0)	(125)	(77)	(107)	(118)
Temporal order[b]	?	4	2	3	1
Regression (% CP 1)[a]					
June	0.0	2.9	44.4	2.9	16.7
	(7)	(70)	(63)	(147)	(72)
July	73.0	31.6	91.4	55.4	86.5
	(89)	(114)	(58)	(191)	(74)
Temporal order[b]	3	5	1	4	2

[a] Sample size in parentheses.
[b] 1 = earliest, 4 (or 5) = latest. Data are not available from the spring of 1966.

TABLE 5. Deviations of air temperature and rainfall from the 11-year norm (median) at Palomarin during various phases of the annual cycle.

Phase	1966 °C	1966 cm	1967 °C	1967 cm	1968 °C	1968 cm	1969 °C	1969 cm	1970 °C	1970 cm
Prereproductive (Jan–Mar)	−0.6	+1.5	−0.1	+15.7	+1.5	−3.2	+0.1	+13.1	+3.5	+15.2
Earliest nests (Apr)	+1.3	−1.8	−2.7	+ 7.9	+1.5	−4.3	+0.9	+2.1	−0.1	−4.8
Main nesting span (May–June)	+0.9	−0.3	−0.1	+ 6.1	+1.4	+1.6	+1.2	+0.8	−0.5	+2.0
Beginning of molt (July)	nil	nil	nil	nil	+0.8	nil	+0.8	nil	+0.5	nil

Blanchard (1941) showed that testicular growth in Nuttall's Sparrows is weakly directly related to air temperature during the prenesting period, and perhaps related to rainfall. We have examined various relationships between weather variables and the schedule of the annual cycle in Nuttall's Sparrows at Palomarin in an effort to identify elements of weather that affect the timing of the cycle. A summary of the deviations of air temperature and rainfall from the 11-year median at Palomarin is shown in Table 5 for key segments of the annual cycle. As others have already demonstrated, such a search for correlations can easily become a sterile exercise in the absence of information on elements of community phenology (e.g., seed fall, insect abundance, percent ground cover) that supplies the functional link between weather and avian responses. Lacking adequate phenological information, we confine our attention to what we can identify as plausible functional correlations or as useful predictive relationships whose functional bases are nevertheless obscure. We present one case in each of these categories.

The resurgence of androgenic activity in late winter, as indicated by the condition of the cloacal protuberance in the population of *nuttalli* at Palomarin, is a direct function of air temperature during the reproductive period (Fig. 11). This is consistent with the observation of a direct correlation between air temperature and testicular histology in free-living *nuttalli* at Berkeley (Blanchard 1941) and with the experimental evidence that photoperiodically induced testicular growth is potentiated by warm air temperature in *Z. l. gambelii* (Lewis and Farner 1973). In this relationship, air temperature must be exerting a direct physiological effect (at least in the captives, and probably in the free-living birds).

A strong but functionally obscure positive relationship exists between the temporal ordination of postnuptial molt and the rainfall in April (Fig. 12). Again, as in Figure 10, the data for 1970 do not conform with the linearity of the other years (molt occurring earlier than expected on the basis of the other data). We believe, but cannot clearly demonstrate, that this was caused by an early termination of nesting in 1970 associated with unseasonal drying of the vegetation. The reason for the very close correlation between April rainfall and the schedule of the postnuptial molt in the other years is uncertain, but is probably a secondary result of the effects of rainfall on the nesting season that our data are too insensitive to reveal. A factor-by-factor analysis of meteorological and organismal variables failed to illuminate any consistent relationships, and we prefer to shun speculation.
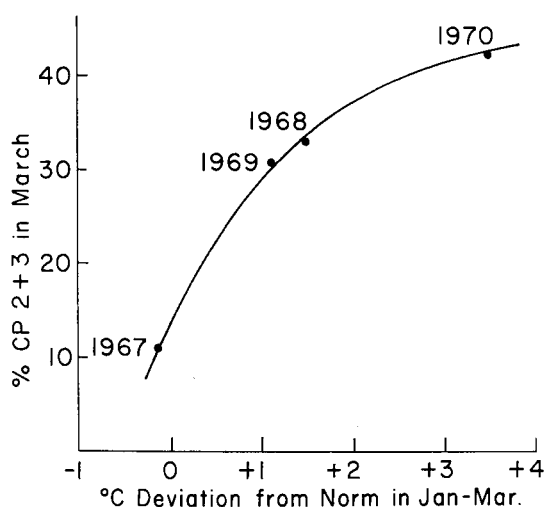

FIGURE 11. The relationship between air temperature during the prereproductive period (Jan–Mar) and reproductive recrudescence in Nuttall's Sparrows at Palomarin, 1969–70.
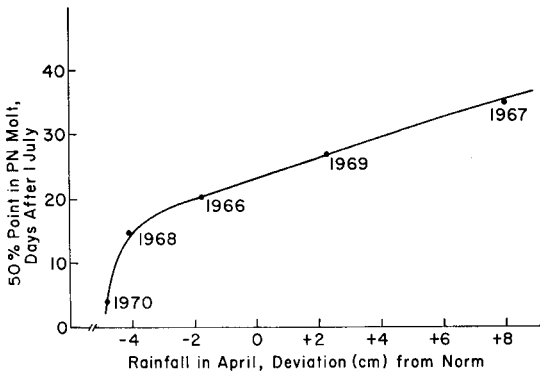
FIGURE 12. The relationship between rainfall in April and the progress of postnuptial molt (see Fig. 6) in Nuttall's Sparrows at Palomarin, 1966–70.

THE ANNUAL TIME BUDGET

The annual time budget of a species or population results from the coevolution of an intricate set of life-history variables in response to environmental seasonality and community attributes (King 1974). For an individual and its species to survive, time must be allocated effectively to essential processes (e.g., reproduction, winter maintenance, molt, and migration, if any) through behavioral and physiological adjustments. Time may be limited in some settings, for instance on high-latitude breeding grounds where behavioral and physiological sequences are greatly compressed; but in other settings the temporal constraints on vital processes may be more relaxed or essentially nil. Time and seasonality are thus actual or potential selection pressures that can help us to understand the interactions or coevolution of life-history variables such as clutch size, multiple-broodedness, mortality rates, molt patterns, migratory habits, and so on. This is a basic rationale for detailed analyses of annual cycles, such as the one reported herein.

By summing the time requirements for prominent events in the annual cycle of a hypothetical Nuttall's Sparrow, we find that it invests 32% of the year in nesting and functionally associated events, 35% in molt, and 33% in winter maintenance (maximum error of estimate is about ±3%). Molt and reproduction together occupy about 245 days. The frost-free season at Palomarin and several nearby places, as a crude comparative index of seasonality, averages 300 days per year. This reinforces our impression, based on the leisurely pace of the annual cycle, that these sparrows do not live in a stringently time-limited environment with respect to the annual cycle as a whole. In contrast, our preliminary

accounting of the time budget of Gambel's Sparrow (*Z. l. gambelii*) in central Alaska shows that reproduction and molt together require 83 days in a locale where the frost-free season lasts only 89 days. The foregoing are preliminary comparisons that illustrate the insights available from comparative analysis of annual cycles, but which cannot appropriately be extended in the present account.

SUMMARY

Nuttall's Sparrow is a nonmigratory form of White-crowned Sparrow that inhabits the Mediterranean plant community of the coastal fog zone of California. The major events of its annual cycle were investigated through five consecutive seasons near the middle of its latitudinal range in Marin County. The nesting season, following a sparse prenuptial molt lasting about 60 days, begins in late March and continues for about 125 days. Indirect evidence (brood-patch condition) indicates that most females incubate two broods per nesting season and some incubate three. A small minority apparently incubates only one brood. Postnuptial molt requires 68 days on the average, and is temporarily suspended in a small fraction of individuals late in the season. Postjuvenal molt begins about 20 days after the juvenal plumage has finished growing, and requires about 60 days on the average. Body weight in both adults and young undergoes an annual cycle having a maximum in midwinter and a minimum in midsummer. Much weight is added during the postnuptial molt, and a lesser amount during the prenuptial molt. During the investigation, the phase of the annual cycle with respect to calendar date varied about ±15 days from the median, delay being correlated with cold and (or) rainy weather during the prenesting period (but not correlated with weather during other phases of the annual cycle). Nuttall's Sparrow invests about one third of the year in reproduction, one third in molt, and one third in winter maintenance.

ACKNOWLEDGMENTS

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