

VARIATION OF BODY WEIGHT IN GAMBEL'S WHITE-CROWNED SPARROWS IN WINTER AND SPRING: LATITUDINAL AND PHOTOPERIODIC CORRELATES

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ABSTRACT.—*Zonotrichia leucophrys gambelii* overwinters from Washington State to central México, and wintering populations are therefore subjected to large differences in climate and photoperiod that may affect the dynamics of winter fattening and vernal premigratory fattening. We measured body weights periodically from October to the onset of vernal migration in 14 sample populations ranging from 32°N (southern Arizona) to 46°N (southern Washington) and combined the results as four latitudinal averages. Contrary to an earlier hypothesis, all populations exhibited congruent and nearly equal cycles of winter fattening (weight increase), regardless of different thermal stresses associated with latitude. The rate of premigratory fattening (weight increase) was alike in all populations. The date of the abrupt onset of premigratory fattening was a linear or near-linear direct function of latitude, averaging 3.3 days later for each degree of latitude northward. This is exactly proportional to daylength between the winter solstice and the vernal equinox and is explicable as a neuroendocrine integration of daylength and elapsed days after the winter solstice. Alternative photoperiodic hypotheses are not successful in predicting the linear latitudinal cline. This, together with sparse experimental data, indicates that the photoperiodic response mechanism in *Z. l. gambelii* is not geographically differentiated. Received 10 November 1980, accepted 24 March 1981.

GAMBEL'S White-crowned Sparrow (*Zonotrichia leucophrys gambelii*, hereafter called Gambel's Sparrow) overwinters in a broad latitudinal band of the intermountain West and Pacific states of North America from southern Washington to central México. Wintering populations are therefore subjected to substantial geographic variation in weather and daylengths that potentially affect adaptive responses in body-weight dynamics in winter and in vernal premigratory fat deposition. These subjects have been studied in detail, however, only near the northern limit of the winter range in Washington (King and Farner 1959, 1966) and at one locality in central California (Blanchard and Erickson 1949). In an attempt to generate a more sensitive analysis of geographical variation of body weight and its environmental correlates in Gambel's Sparrow, we examine in this report the data from autumn, winter, and early spring provided by the cooperators of the Western Bird-Banding Association White-crowned Sparrow Project (Mewaldt 1975, 1976).

METHODS

Most of the data used in this report were obtained between 1974 and 1979 by the cooperators in the project (see Acknowledgments). Birds were caught (nearly all in the forenoon) in mist nets or traps and were weighed (± 0.1 g, except ± 0.5 g at one site) within a few minutes after capture. We summarized the data for each station as monthly means from September through February (with an exception explained later) and as 10-day means from March to May. Forty weight records per period were the maximum used, and values were extracted at random from the upper quartile of weights (see beyond) when more than 40 records were available. Adult (AHY) birds were distinguishable from subadults by plumage pattern until roughly the midpoint of the prenuptial molt in March. The subadults are therefore designated as first-year (FY) birds in this report, rather than by the official title of HY until 31 December and AHY thereafter (U.S. Fish and Wildlife Service 1976). The sex of White-crowned Sparrows cannot

TABLE 1. Body weights of migrating Gambel's Sparrows captured near Pullman, Washington in September, 1955-1962 [mean \pm SE(*n*)].

Category	Males	Females	Males plus females
Adults (AD)	27.3 \pm 0.39 (50)	25.5 \pm 0.34 (50)	26.4 \pm 0.27 (100)
First-year (FY)	26.7 \pm 0.39 (50)	25.0 \pm 0.23 (50)	25.8 \pm 0.24 (100)
AD plus FY	27.0 \pm 0.28 (100)	25.2 \pm 0.21 (100)	26.1 \pm 0.18 (200)

be distinguished reliably in the nonbreeding season by means of external characteristics. This creates a serious statistical problem in the comparison of samples in which sex ratio may differ and in the analysis of temporal series that may be invariant in sex ratio but in which males and females may be out of phase with each other (as in the vernal premigratory weight increase). This can be a large source of bias, because the sex composition of wintering populations of Gambel's Sparrows varies from about 80% males at the northern limit of our sample sites toward about 25% males at the southern limit (King et al. 1965). To explore the statistical overlap between subclasses (males vs. females, AHY vs. FY) and to seek ways to minimize or eliminate biases resulting from unknown but potentially variable sample composition, we analyzed first a sample of September migrants of known sex (ascertained by laparotomy and gonadal inspection) captured at Pullman, Washington between 1955 and 1962. We reasoned that this sample of passage migrants was the most representative one available for birds that would be wintering farther south and that the 8-yr series would help to minimize year-to-year idiosyncrasies in the data. We found (Table 1) that AHY birds weigh more than FY birds but that the difference is statistically insignificant [2.23% of AHY weight in males ($P > 0.2$) and 2.19% in females ($P > 0.1$)]. We subsequently ignored this source of bias as too small to be factored out by the sample sizes available to us, even though our data consistently show that AHY birds weigh 2-3% more than FY birds until at least March.

The body-weight excess of males over females is larger than between the age classes and is significant in both AHY birds (6.66% of male weight, $P < 0.001$) and FY birds (6.62%, $P < 0.001$). It is therefore inaccurate to compare statistically two or more samples in which the sex ratios are not known to be alike. Our only recourse in solving this problem was to attempt to confine the primary analysis to one sex. We chose males for this because they tend to be more numerous than females in most of the populations that we examined (King et al. 1965). We found from the Kolmogorov-Smirnov test (Sokal and Rohlf 1969: 571) that the data sets for all males and for all categories combined in Table 1 did not differ significantly ($P < 0.01$ in both cases) from a random or normal curve of distribution. This enabled us to estimate the overlap of all bird weights with male weights from the standard deviations of these groups in relation to the corresponding areas beneath the normal curve (Rohlf and Sokal 1969: Table P). From this, we computed that the upper quartile of the sample in Table 1, and presumably of the analogous samples reported by our cooperators, includes only 10.1% females, and so we used this standard quartile to confine analysis essentially to males. We emphasize that the mean weights of the upper quartiles are *not the same* as the mean weight of all males, but rather the mean weights of a subsample that excludes some of the lighter-weight males as well as most females.

The effect of disregarding sexual heterogeneity in the samples is shown in Fig. 1, in which the rapid premigratory increase of weight may be detected in the combined samples as well as the upper quartile at some sites (Fig. 1B) but not at others (Fig. 1A, 1C). This justifies our use of only the upper quartile of weights.

A second potential source of bias among samples is the potential year-to-year variation (even among unisexual samples) in the phasing of fluctuations of weight. If samples are combined for years in which phasing (e.g. the onset of premigratory fattening) is substantially different, then biologically significant changes may be masked. We already knew that the year-to-year precision of weight cycles (at least the onset of premigratory fattening) is remarkably good near the northern limit of the winter range, showing a range of ± 5 days from the median criterion in 8 yr of observation (King and Farner 1965). From the data assembled in this report, we find a similar or better year-to-year precision in more southerly latitudes as well (examples in Fig. 2), and so we felt justified in combining samples for 2 or more years.

Finally, we have chosen to report here only the means for the upper quartile of weights. The values for the entire samples, because of the statistical biases that we have described, are misleading in a comparative context.

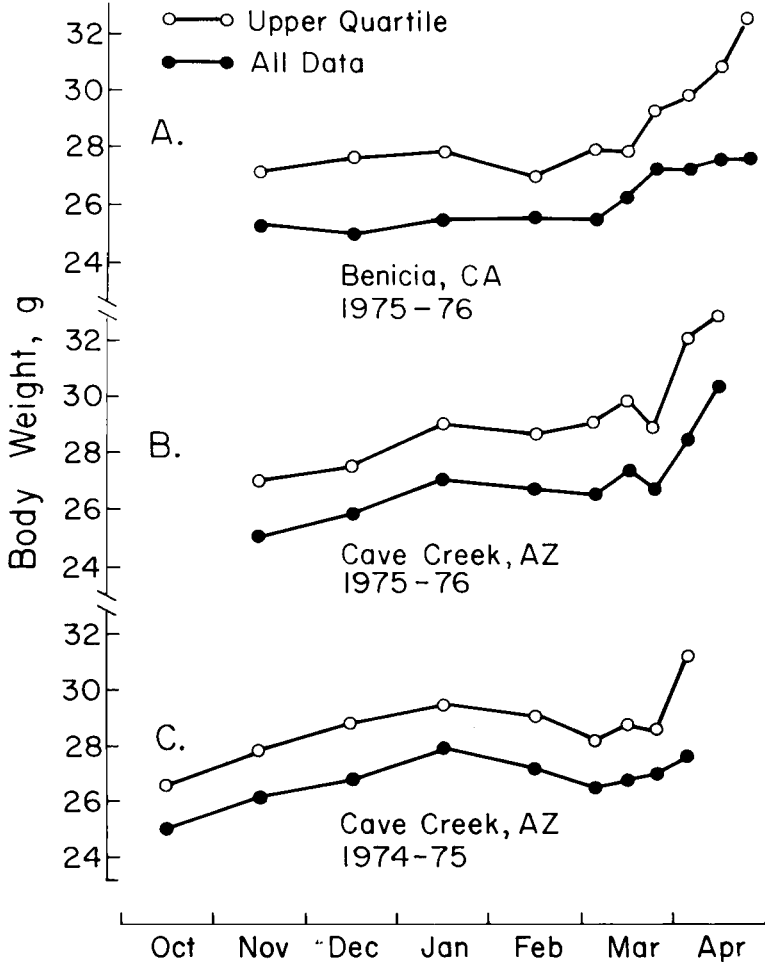


Fig. 1. Typical patterns of concordance and difference between weight variations based on means of all data (males and females) or the means of the upper quartile of samples (see text).

RESULTS AND DISCUSSION

Winter weight dynamics.—We examined the data in relation to two hypotheses: (1) birds overwintering in the north will be larger (heavier) than in the south because of the presumed advantages of larger size and larger fat reserves in thermoregulation and endurance when fasting (for review, see Ketterson and Nolan 1976, Ketterson and King 1977); and (2) the winter cycle of weight (fattening) is correlated with ambient temperature and hence decreases in amplitude from north to south (for review, see King and Farner 1966).

Our results do not support the first of these hypotheses and are equivocal in relation to the second. First, although we lack a sample from 33–35°N in October, the mean weights at the extreme latitudes do not differ significantly in these post-migratory birds (Table 2), suggesting that there is no latitudinal segregation by

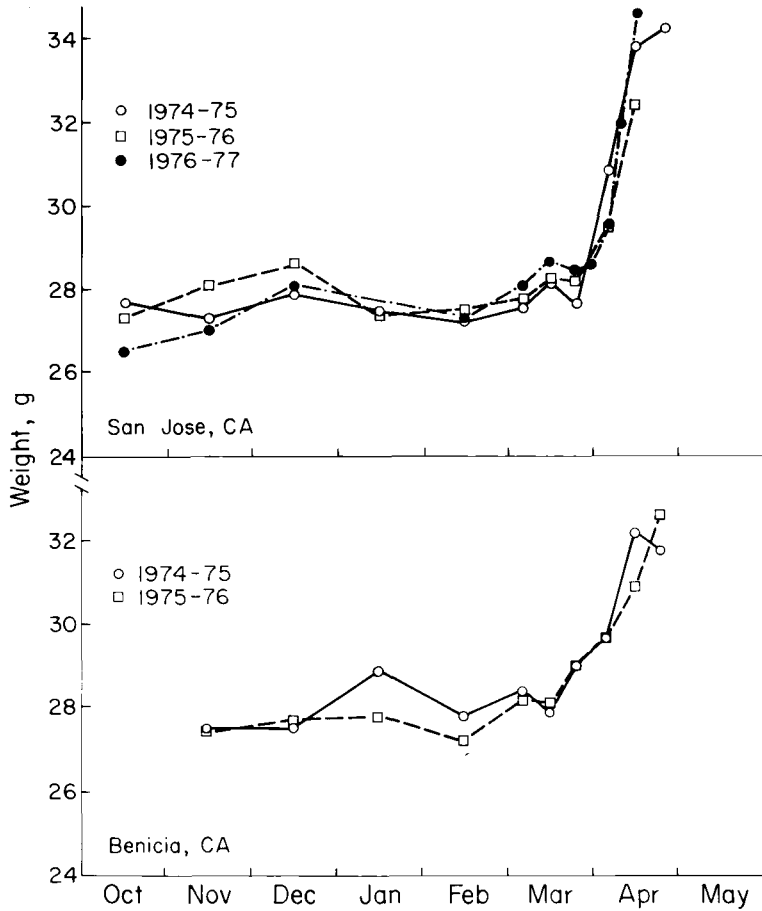


Fig. 2. Typical patterns of year-to-year concordance in the onset of vernal premigratory fattening.

weight in males. During the cycle of winter fattening (November–February) there is a general tendency for the heavier (fatter) males to occur in the south, not in the north as expected (Table 2). The extreme differences are statistically significant at $P < 0.05$ or better throughout the winter.

In regard to the second hypothesis, we find no clear latitudinal trend in the winter-weight cycles. In all but the southernmost sample (in which the irregular winter-weight cycle, if any, may be obscured by mergence with premigratory fattening), there is an obvious weight cycle peaking in January and of essentially uniform amplitude between 46–47°N and 31–33°N (Fig. 3).

Finally, we reiterate that the hypothesis that we proposed earlier to account for winter fattening implied a graded response to stresses correlated with latitude (temperature, snow cover, daylength for foraging, nocturnal duration of fasting) and would therefore predict winter weight (fat) cycles of decreasing amplitude as these supposed stresses ameliorate from north to south. Within the latitudinal band from 47°N to at least 33°N the winter weight cycles of Gambel's Sparrows, however, are nearly uniform. The original hypothesis must therefore be modified or abandoned. An alternative explanation that merits attention is that birds from all latitudes are

TABLE 2. Body weights (g) of free-living *Zonotrichia leucophrys gambelii*: means of the top quartile of weights.

Latitude (°N)	October	November	December	January	February	March			April			May
						1-10	11-20	21-31	1-10	11-20	21-30	1-10
46-47 ^a												
Mean	27.1	27.2	27.9	28.4	27.8	27.5	27.9	27.3	27.6	27.6	29.9	31.3
SD	2.10	1.66	1.90	1.85	1.72	1.26	1.53	1.04	1.68	2.07	2.54	2.91
n	40	40	40	40	40	16	18	20	18	22	18	24
36-38 ^b												
Mean	27.1	27.4	28.1	28.4	27.9	28.2	28.3	28.6	29.8	32.7	33.1	—
SD	1.15	1.02	1.00	1.07	0.95	1.02	1.00	1.39	1.54	2.07	1.42	—
n	53	63	66	64	78	76	66	76	82	81	24	—
33-35 ^c												
Mean	—	27.7	28.4	29.3	28.8	28.1	29.5	29.6	31.9	34.4	35.4	—
SD	—	0.78	0.98	1.06	0.84	0.86	1.32	1.30	1.64	1.94	1.44	—
n	—	15	17	25	38	28	23	19	35	14	7	—
31-33 ^d												
Mean	27.3	28.1	27.9	28.8	28.2 ^e	29.4	30.2	30.2	31.8	32.5	—	—
SD	1.56	1.67	1.40	1.12	1.63	2.22	2.51	2.03	2.04	2.34	—	—
n	24	32	32	46	78	36	36	29	33	15	—	—

^a Near Pullman, Washington.

^b San Jose, Fresno, Menlo Park, Benicia, and Grizzly Island, California.

^c Woodland Hills, San Luis Obispo, California; Cave Creek, Arizona.

^d Tucson, Portal, Yuma, Arizona; Fallbrook, San Diego, California.

^e Subdivided in Fig. 3 because of evident onset of premigratory fattening in February: 1-10 February, 28.3 g; 11-20 February, 28.6 g; 21-29 February, 27.8 g.

storing fat reserves at a maximal level in midwinter as an evolutionary response to episodic but unpredictable stresses or "stringencies" (Wilson 1975), rather than to long-term average conditions. These reserves may be needed only in winters entailing unusual stresses but will then be vitally important. Why the midwinter maximum of fat reserves should be less than the migratory maximum is a question that we have raised previously (King 1972) but for which we still do not have an answer. The foregoing makes it clear that the physiological ecology of winter fattening in Gambel's Sparrow requires continuing study.

Vernal premigratory fattening.—By analogy with the scheduling of prenuptial molt in Gambel's Sparrows, we hypothesized that the onset of the premigratory weight increase in spring would be progressively delayed from south to north by 3-4 days per degree of latitude (Mewaldt and King 1978). Because premigratory increases of weight are closely correlated with fat deposition (King and Farner 1959), we use the terms "weight increase" and "fat deposition" interchangeably beyond this point.

We estimated the date on which premigratory fattening began as the median date of the last data point before a continuous increase of weight in spring (open circles in Fig. 3). The mean latitudes of the sample stations and the estimated dates for the onset of premigratory fattening are summarized in Fig. 4. The northward delay of the weight increase is a linear or near-linear function of latitude within the range of our data and averages (by linear regression) 3.3 days per degree (Fig. 4). This is essentially identical with the latitudinal delay in the onset of prenuptial molt (3.4 days per degree: Mewaldt and King 1978). The difference is trivial, amounting to a total of 1.4 days between the latitudinal extremes (14°) of our samples. If the temporal cline depicted in Fig. 4 remains linear to the southern limit of the winter range of Gambel's Sparrow (about 22°N), then the regression predicts that premi-

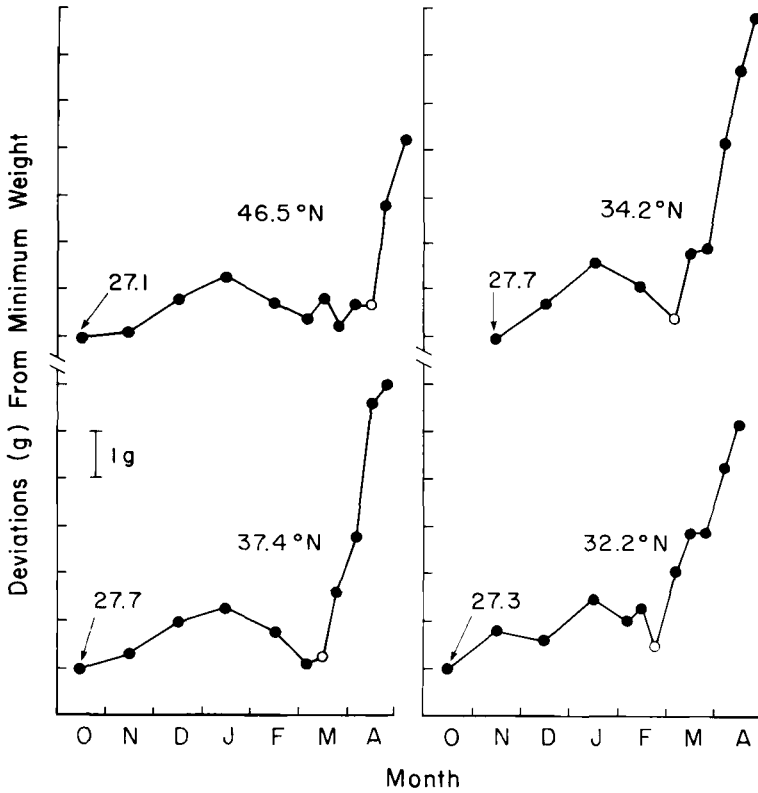


Fig. 3. Patterns of variation in the means of the upper quartile of body weights at the mean latitudes of four sample groups. The data are expressed as deviations from the minimum mean weight (September or October) shown at the left end of each set. The vertical axis is marked at 1-g intervals. See Table 2 for the original data. The open circle in each set indicates the median date on which premigratory fattening began.

gratory fattening will begin there on about 17 January and that (by analogy with more northerly populations) migration will begin soon thereafter. There is no information available for Mexican populations of Gambel's Sparrow with which to verify or refute this prediction, but we regard it as unlikely. If so, then the relation shown in Fig. 4 must become nonlinear south of the range of our data or is actually a shallow curvilinear function throughout the range, but not shown clearly by our samples.

Photoperiodic correlates of premigratory fattening.—What causes the latitudinal cline in the timing of premigratory fattening in Gambel's Sparrows? This report is not the appropriate place to engage in a review of all of the ramifications of this complex subject. Suffice it to say that annual physiological cycles may be either self-sustaining "circannual" rhythms (Gwinner 1975) that are kept in proper phase with the seasons by environmental cues (phase control only) or may be sequences that require environmental cues to stimulate their occurrence as well as control their phase. The role of these alternative hypotheses in Gambel's Sparrows is still not clear (King and Farner 1974, Sansum and King 1976), but the difference is not

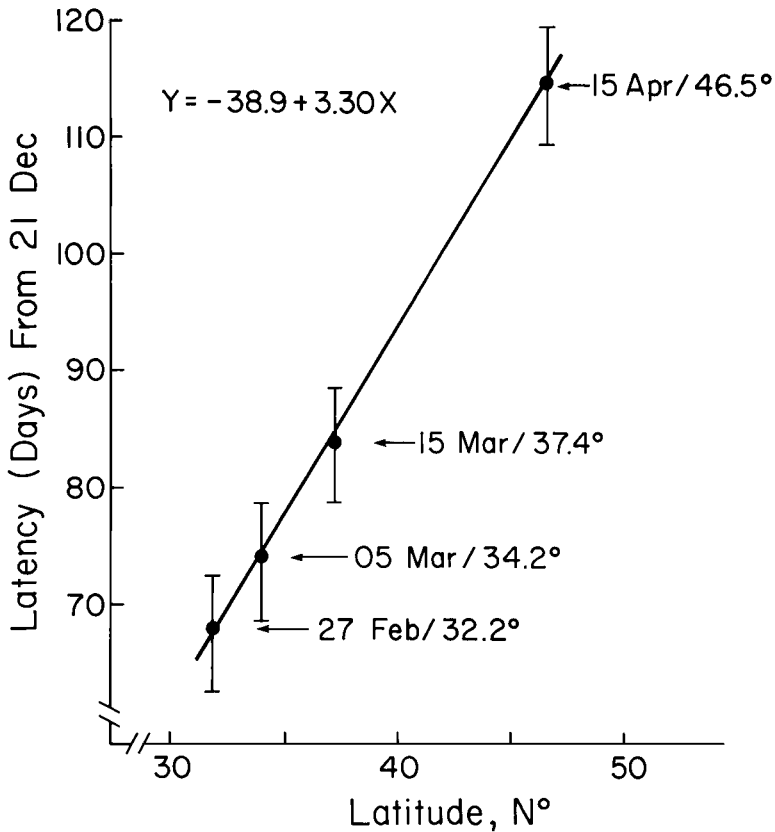


Fig. 4. The relative timing of the onset of vernal premigratory fattening (reckoned as "latency" from 21 December) in relation to the mean latitude of the sample groups. The original data (date of onset/mean latitude) are shown at the right of the regression line. Vertical bars at each point indicate the maximum range of uncertainty in the date of onset, reckoned as the median date of the sample period ± 5 days.

crucial for the following analysis, which explores only correlations between organismal and environmental phasing.

There is ample experimental evidence that some aspect of the annual change of daylength is the main stimulus or temporal cue for the onset and progress of pre-migratory fattening and related events (gonadal growth, prenuptial molt, migratory activity) in Gambel's Sparrows (for review see Farner and Wilson 1957, Farner et al. 1966, King 1961). Photoperiodic theory includes the experimentally verified concepts of photorefractoriness (a period of insensitivity to long days), photoperiodic threshold (minimum daylength for response), and a rate response that is proportional to daylength in the case of gonadal growth (Farner and Wilson 1957, Farner et al. 1966). The success of Farner and Wilson (1957) in predicting accurately the course of natural testicular growth in spring on the basis of experimental data indicates that a theory invoking a photoperiodic threshold and a rate dependence on daylength is fundamentally sound for this process in Gambel's Sparrows. Premigratory fattening, however, is an "on/off" phenomenon in which the rate of fat deposition is

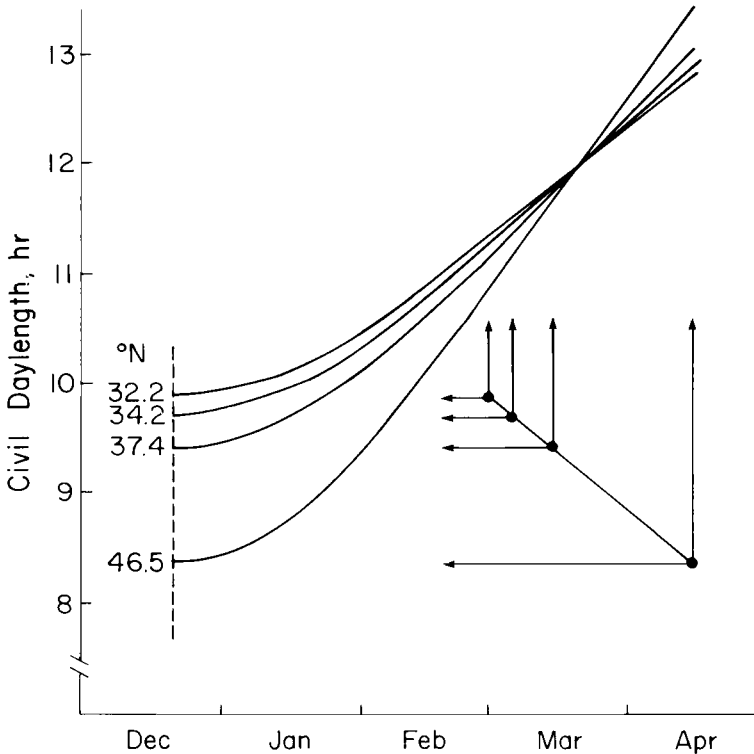


Fig. 5. Civil daylength at the mean latitudes of the sample groups, computed by the equations of Sellers (1969) using solar declinations for the years and dates involved obtained from appropriate volumes of the "American Ephemeris and Nautical Almanac" (U.S. Govt. Printing Office). The relationship of daylength to date is symmetrical before and after the winter solstice (vertical broken line) and only the post-solstitial period is shown. In the coordinates at the lower right, the horizontal arrows point to solstitial daylengths and the vertical arrows point to the estimated dates on which premigratory fattening began. The line slanting downward to the right joins the X-Y coordinates and illustrates that the date on which fattening begins is a linear function of solstitial daylength (or of any other relative daylength between the autumnal and vernal equinoxes: see Fig. 6).

evidently maximized and independent of daylength in both natural (Fig. 3) and experimental settings (cf. Dolnik 1975, for *Fringilla coelebs*). In the case of vernal premigratory fattening, the dependent variable is thus not the rate of response, but either the date of response or the span of time (latency) between the occurrence of a stimulus or cue and the date of response. Various investigations have shown that latency is inversely proportional to experimental daylengths in *Junco hyemalis* (non-linear proportionality: Winn 1950, data summarized by Wolfson 1966) and *Fringilla coelebs* (linear proportionality: Dolnik 1975). We use the term "latency" here only to describe a lapse of time, and do not imply in this that we are invoking mechanisms akin to those of neural or neuroendocrine latency.

The latitudinal cline shown in Fig. 4 provides us with an unusual opportunity to examine the correlations of various features of the annual photocycle with the relative onset or relative latency of premigratory fattening in the sample populations. It is merely a platitude that uniform correlations are not definitive proof of cause and effect, nor are noncorrelations necessarily proof of no cause-and-effect relation-

TABLE 3. Civil daylength and rate of change of daylength on the day on which premigratory fattening begins at various latitudes.

Mean latitude (°N)	Daylength (h)	Rate of daylength change (min/day)
46.5	13.39	3.15
37.4	11.78	2.40
34.2	11.45	2.10
32.2	11.32	1.95

ship in a complex setting. Nevertheless, this mode of analysis helps to separate the plausible from the implausible and to focus on profitable lines of future inquiry.

We begin with the assumptions that (1) some feature of the annual photocycle is the prepotent stimulus or cue governing the timing of premigratory fattening, and (2) there is essentially no geographic variation among wintering populations of Gambel's Sparrows in their responses to photoperiodic stimuli. The evidence for the latter is that (a) with a few local exceptions, breeding populations of Gambel's Sparrows are nearly alike morphometrically (Banks 1964), suggesting genic exchange approaching panmixis; (b) there is only a very small statistical variability in the response to photoperiodic experiments in samples of migrating Gambel's Sparrows caught at 46–47°N latitude (Farner and Wilson 1957), which are undoubtedly from a variety of breeding localities and heading for a variety of wintering sites; and (c) Gambel's Sparrows captured from wintering populations at Rancho Mirage, California (33.9°N), San Jose, California (37.2°N), and Pullman, Washington (46.5°N) all began vernal fattening and migratory activity at essentially the same time when exposed to natural photoperiods at Pullman, indicating a uniform rather than differentiated photosensitivity (King and Farner 1963). This is illustrated also by the logarithmic growth-rate constant (k , day⁻¹) for testicular development induced by long days. We have data from Gambel's Sparrows captured at Rancho Mirage (D. S. Farner, unpubl.) and at Pullman (Farner and Wilson 1957, Laws 1961). Comparisons must be made carefully, because the value of k differs between adult and first-year males (Farner and Wilson 1957) and also as a function of time after the end of the photorefractory period (Laws 1961). The best comparison available to us is between a group of first-year birds from Rancho Mirage, first exposed to the experimental photoperiod (LD 20:4) on 15 February, and a group of first-year birds from Pullman, first exposed on 31 January (Laws 1961, Group 4).

TABLE 4. Latency of premigratory fattening in relation to cumulative hours of civil daylength and mean daylength in relation to latitude.

Mean latitude (°N)	Latency of premigratory fattening					
	From 7 November			From 21 December		
	Days	Cumulative hours	Mean daylength	Days	Cumulative hours	Mean daylength
46.5	160	1,578	9.86	115	1,200	10.43
37.4	129	1,294	10.02	84	866	10.31
34.2	119	1,205	10.13	74	766	10.35
32.2	113	1,175	10.39	68	707	10.39

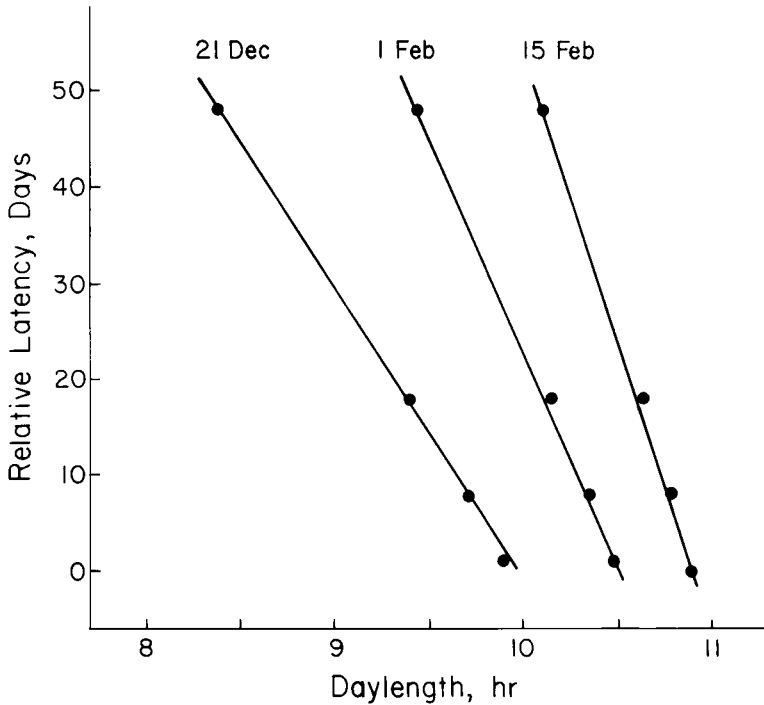


Fig. 6. The relative temporal ordination (latency, with the date at 32.2°N = day 1) of the onset of vernal premigratory fattening in relation to civil daylength. The slopes of the lines are progressively steeper to the right and equal zero on the vernal equinox (21 March). This shows that the relative date of the onset of fattening is proportional to daylength on any date between the autumnal and vernal equinoxes.

The mean ($\pm 95\%$ confidence limits) values of k for these were 0.103 ± 0.017 and 0.106 ± 0.005 , respectively. The difference is not significant ($P > 0.05$) and supports our assumption that geographic variation of photosensitivity is slight in Gambel's Sparrows. Cognate data from other species (which may, in any case, be irrelevant because of the possibility of interspecific differences) are scant. Russian populations of *Fringilla coelebs* apparently exhibit some geographical differentiation of testicular response to daylength (Dolnik 1963), but Finnish and German populations of *F. coelebs* and *Sturnus vulgaris* do not (Berthold 1969).

The daylength regimes to which our samples were exposed are shown in Fig. 5. We examined the following hypotheses (which are variously plausible in relation to the experimental evidence and the sensory capacities of the birds), that the onset of vernal fat deposition is timed by:

1. an immediate stimulus or cue at the time of fattening, i.e.:
 - a. the increase of daylength above a threshold value on the day of response
 - b. the rate of change of daylength on the day of response
2. a previous stimulus or cue that starts a timing mechanism initiating fattening at the end of a fixed span of time (latent period), i.e.:
 - a. a timing mechanism that counts days since the occurrence of the stimulus or cue

- b. a timing mechanism that sums daylengths since the stimulus or cue.
- c. a timing mechanism that integrates daylengths and days since the cue.

Hypotheses 1a and 1b and any derivatives thereof are incorrect, because neither daylength nor the rate of change of daylength are the same for all latitudes on the day on which fat deposition begins (Table 3), and it seems unlikely in any case that Gambel's Sparrows can measure a rate of change amounting to about 3 min or less per day.

Hypotheses 2a–2c require a reference date for the beginning of the latent period. Initially, we selected the winter solstice (21 December) not only as a convenient solar nexus, but also because the metabolic photorefractory period (the autumnal period during which premigratory-like fat deposition cannot be induced by experimental photostimulation) ends between about 3 December and 1 January (King et al. 1960). We also noted, however, that the regression in Fig. 4 extrapolates to zero latency on about 12 November, which coincides approximately with the end of the gonadal photorefractory period in Gambel's Sparrows (Miller 1954, Farner and Mewaldt 1955). We therefore examined correlations between both of these dates (12 November, 21 December) and the onset of premigratory fattening. Results in Table 4 show that hypotheses 2a and 2b are incorrect, but that hypothesis 2c (an integration of daylength and elapsed time) is consistent with the latent period beyond 21 December and yields essentially the same mean daylength on the first day of premigratory fattening at all latitudes. A hypothetical latency beginning on about 12 November deviates substantially from this and cannot explain the relationship shown in Fig. 4. The relationship beginning from 21 December is qualitatively in accord with experimental results showing that *Fringilla coelebs* times premigratory-like fattening by an integration of daylength and elapsed days from the first day of photostimulation (Dolnik 1975).

Until now, we have disregarded the concept of photoperiodic threshold. This value is quantitatively well-defined in the gonadal responses to photostimulation in several passerine species, lying between 9 and 11 h of light per day (Farner and Lewis 1971: 354), and by analogy has often been assumed to apply to other physiological cycles controlled by daylength. We have, however, already noted that premigratory fat deposition is an "on/off" phenomenon, unlike gonadal growth, and therefore potentially relies on a timing mechanism unlike that governing the dynamics of gonadal development. Our analysis of the field data from Gambel's Sparrows leads us to the tentative conclusion that the concept of a photoperiodic threshold is irrelevant to the explanation of the results, for these reasons: (1) it is implicit in hypothesis 2c and the data consistent with it that photostimulation is continuous, regardless of daylength at or after the beginning of the latent period; and (2) we noted that the relative ordination of the dates on which fat deposition begins is a linear or near-linear function of relative daylength at any latitude between the autumnal and vernal equinoxes. This is obvious visually in Fig. 5, especially at the solstice, and is shown explicitly in Fig. 6. This relationship is impossible to reconcile with a threshold daylength within the same span of time. Nevertheless, lest some subtle relationship be overlooked, we computed latency versus latitude for cumulative daylengths and mean daylengths beyond threshold dates corresponding with possible but hypothetical threshold daylengths (9.5–11.5 h, by 0.2-h intervals) between the winter solstice and the vernal equinox. We found that combinations yield strongly nonlinear relationships that are not concordant with the function depicted in Fig. 4.

Finally, we should mention that we disregarded civil twilights in computing daylengths, even though it might be argued that effective daylength includes some or all of the period of the civil twilights. Civil twilight varies slightly with season and with latitude, and inclusion of the dawn and dusk twilights would add roughly 1 h to the daylengths shown in Fig. 5, but their inclusion would not alter significantly any of our conclusions.

CONCLUSIONS

Contrary to expectation on theoretical grounds, male Gambel's Sparrows in winter between 47° and 32°N latitude do not manifest a latitudinal cline of body weight or of the amplitude of the winter-weight cycle (heavier or greater in the north than the south). We hypothesize that winter fat reserves are maintained at maximal quantities regardless of latitude as an adaptation to episodic but unpredictable environmental stresses, rather than to long-term average conditions correlated with latitude.

The date on which vernal premigratory fattening begins is a linear or near-linear function of latitude, with a northward delay averaging 3.3 days per degree. Various correlations between this date and selected features of the annual photcycle suggest that the latitudinal cline is best explained by the existence in the birds of a timing mechanism that integrates daylength and the lapse of time between about 21 December (or the end of the metabolic photorefractory period) and the seasonally appropriate date for the onset of premigratory fattening. There is no evidence of a photoperiodic threshold in this system.

We concede that it is easy to overlook explanations other than those that we have proposed (for instance, the speculation that the summation of daylengths is strongly nonlinear), but we have attempted to stay close to empirically verified concepts and to the simplest, testable hypotheses consonant with the data. It is a long step between the correlations that we have identified and their mechanistic explanations, but we emphasize that any future theories of the photocontrol of premigratory fattening in Gambel's Sparrows that are inconsistent with Fig. 4 are inviable.

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