REPRODUCTIVE BIOLOGY OF THE WHITE-CROWNED SPARROW. II. ENVIRONMENTAL CONTROL OF REPRODUCTIVE AND ASSOCIATED CYCLES

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This is the second of two papers concerning the temporal organization of reproduction and its control in *Zonotrichia leucophrys pugetensis*. In the first paper (Lewis 1975), the phenology of the breeding season and associated physiological and behavioral cycles were described and analyzed. Results of that study and that of Lewis and Farner (1973) suggested that information from the environments of the wintering grounds and/or migration route were of primary importance in controlling the onset of breeding and of vernal gonadal growth and development. For this reason and because photoperiodic mechanisms are known to play a strong role in regulating the annual cycles of *Zonotrichia* (Farner and Lewis 1971, 1973), the present investigation was designed to characterize quantitatively the photoperiodic responses of *pugetensis*. My experiments were designed to further our understanding of the environmental control of annual reproductive and associated cycles of this finch. When possible, other taxa of Crowned Sparrows were included in these experiments for comparative purposes. Inclusion of *Z. l. gambelii* is especially useful because of its well-established and well-characterized photoperiodic responses.

MATERIALS AND GENERAL METHODS

SOURCES AND PRELIMINARY TREATMENT OF EXPERIMENTAL BIRDS

The birds to be employed in the experiments were captured by use of Japanese mist nets. Sex was ascertained by laparotomy (surgical opening of the abdominal wall) well before experimental usage. Except in experiment four, all birds were retained in outdoor aviaries in Seattle, Washington, for 3–9 months following capture and were then placed in controlled environmental chambers on nonstimulatory photoperiods (6 hr of light per day; LD 6:18) for 1.5 to 4 months prior to experimentation. The birds of each experimental group were maintained under identical conditions of care, housing, and photoperiodic regime prior to experimentation.

Sources of experimental birds. (1) All *pugetensis* except those employed in experiment three (see below), were taken from Island County, Washington, in late summer or autumn. Approximately 90% of these were taken from the northwest quadrant of Whidbey Island and the remainder from the north-central portions of Camano Island. Nearly all of these birds can reasonably be considered to be from the breeding population of Island County, since only five individuals of those taken for experimental purposes had completed postnuptial or postjuvenal molt prior to capture (Lewis 1975).

(2) The *nuttalli* and *pugetensis* employed in experiment three were kindly provided by L. R. Mewaldt, San Jose State College, San Jose, California. The *nuttalli* were captured at San Jose on 26 January 1969, and the *pugetensis* were taken from a wintering population at the Point Reyes Observatory, California, on 15 January 1969. It is unlikely that these *pugetensis* were drawn from the same population that breeds in Island County, Washington.

(3) All *gambelii* were captured during autumn migration through the Kittitas Valley (Thorp Township, Kittitas County, Washington) or were taken from a previously described population that winters in Alfalfa Township, Yakima County, Washington (Lewis et al. 1968). At least some of the *gambelii* that migrate through Thorp Township spend the winter in Alfalfa Township (Lewis, Mattocks, and Farner, unpubl. banding returns). Furthermore, *gambelii* taken from these two areas do not show significant differences in photoperiodic gonadal growth rates (Lewis, Farner, and Morton, unpubl. data).

(4) The *Z. atricapilla* were captured in autumn on Whidbey Island. Some were also taken in association with *gambelii*, either during autumnal migration in Thorp Township or in winter in Alfalfa Township. The *atricapilla* from these different sites have similar photoperiodic responses (Lewis, Farner, and Morton, unpubl. data).

GENERAL METHODS

All experiments were conducted in controlled environment chambers at constant ambient temperatures (20 ± 0.5°C) and relative humidity (55 ± 5 per cent). Except where noted, birds were housed two per cage in small wire cages (41 × 26 × 22 cm). Incident illumination (400–440 lux at the floor of each cage) was provided by incandescent lamps. All males were fed throughout the experimental treatment on a mineral-enriched chick starter mash with a vitamin supplement. Females were fed a 3:1 mixture of a poultry layer mash and Purina trout chow. Food and water were freely available to all birds. Following sacrifice by decapitation, the gonads (and the oviducts of females) were removed and placed in a fixative composed of 10 parts glacial acetic acid, 10 parts formalin, 30 parts 95% ethanol, and 50 parts distilled water. After five days, these tissues were transferred to 70%
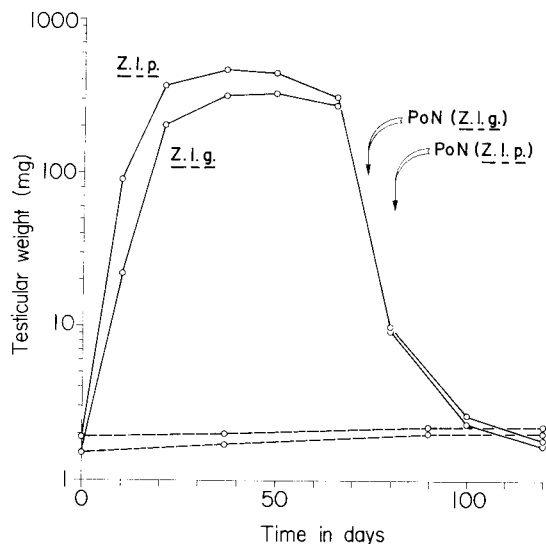
FIGURE 1. Photoperiodically induced testicular growth in Z. l. pugetensis and Z. l. gambelii in response to long (LD 16:8) daily photoperiods during experiment one (solid lines) compared with that of controls retained on short (LD 6:18) daily photoperiods (dashed lines). The time of onset of postnuptial molt (PoN) in the long-day groups is also indicated.

ethanol and after five additional days, they were carefully debrided of extraneous tissue (the mesovarium being retained intact), blotted, and weighed on a precision balance. Tissue specimens weighing 10.0 mg or less were weighed to the nearest 0.01 mg and larger specimens were weighed to the nearest 0.1 mg. The greatest diameters of the largest preovulatory follicles were measured to the nearest 0.1 mm under a dissecting microscope, using fine dividers. Body weight was measured to the nearest 0.1 g on a triple-beam balance. Except where noted, estimates of central tendency and statistical variance are given in terms of the sample mean and 95% confidence intervals ($X \pm t_{0.05} s_{\bar{x}}$) (Snedecor 1956).

THE EXPERIMENTS

THE PILOT EXPERIMENT (Experiment One)

Materials and methods. Photosensitive *pugetensis* (36 males and 17 females) and *gambelii* (36 males and 20 females) were employed. All were retained in outdoor aviaries on natural photoperiods from the time of capture in late summer or early autumn of 1967 until 1 January 1968. They were laparotomized at this time and gonadal weight (males) or stage (females) was estimated by comparison with a set of reference gonads. The average error of this method (males) is $\pm$ 20%. The birds were then placed in controlled environment chambers on a photocycle of 6 hr of light and 18 hr of dark per day (LD 6:18). Four males and four females of each taxon were retained on LD 6:18 throughout the ex-

periment. All but eight experimental birds of each race were laparotomized again on 9 April 1968, and the experimental light regime of LD 16:8 was initiated. These birds were laparotomized at approximately 2–3-week intervals during the succeeding 140 days and gonadal weight (males) or stage (females) was assessed (see below). The 16 males mentioned above were housed individually in a cage where locomotor activity was recorded. This was effected by means of a centrally located, spring-loaded perch mounted on a microswitch that was closed by the weight of the bird, thus activating one channel of an Esterline Angus Event Recorder. In this way locomotor activity (hops onto a perch) was recorded continuously and information on the development of nocturnal activity or *Zugunruhe* (Farner et al. 1954, Lewis and Farner 1973) was obtained.

Ovarian weights are not reliably estimated by laparotomy, hence the ovaries were staged as follows. *Stage 0*: Fully regressed (or immature); the ovary at this stage is a small, whitish, triangular structure. The surface is smooth or slightly vesicular in gross aspect and no follicles are seen. *Stage 1*: Whitish or gray follicles up to about 1 mm in diameter are seen. *Stage 2*: Large follicles up to 2.5 mm are seen, some of which may be yellowish. *Stage 3*: The ovary is fully developed with one or more large, yolky preovulatory follicles (ca. 3–10 mm diameter). These stages are roughly comparable to forms zero-three of Polikarpova (1940).

Results. The preliminary laparotomies (1 January) revealed fully regressed testes ($\leq$ 3.0 mg) and ovaries (stage 0; $\leq$ 6 mg). Laparotomies on the first day of the experiment (9 April), after 98 days on LD 6:18, revealed no significant change in the gonadal condition. The testes of the birds of both races, however, grew exponentially in response to LD 16:8 (fig. 1), reaching peak weights comparable to those of breeding males (King et al. 1966, Lewis 1975). Testicular growth during the logarithmic phase was much more rapid in *pugetensis* than in *gambelii*. After approximately eight weeks of photostimulation, the testes began to regress, reaching minimal levels by day 120. Ovarian development was substantially greater and more rapid in *pugetensis* than in *gambelii*. Maximum ovarian development was reached in both taxa by about day 50 after which the ovary underwent a rapid involution reaching stage 0 by about day 70 (fig. 2). The gonads of males and females of both races that were retained
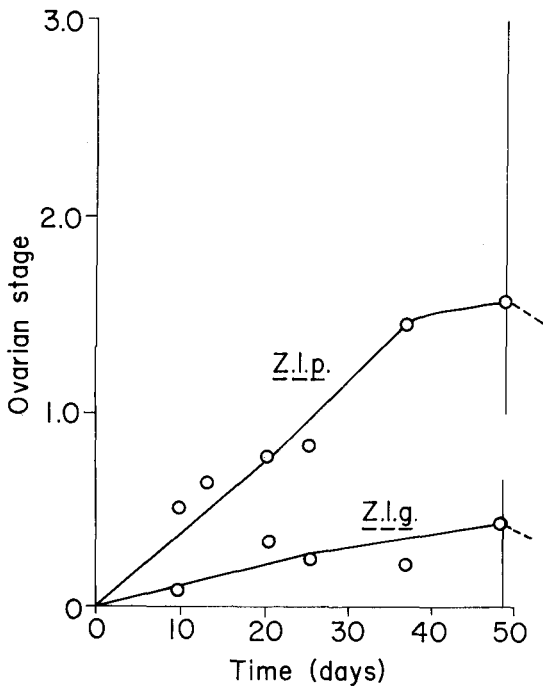
FIGURE 2. Photoperiodically induced ovarian development in Z. l. pugetensis (N = 13) and Z. l. gambelii (N = 16) in response to long (LD 16:8) daily photoperiods during experiment one. Females retained on short daily photoperiods (LD 6:18) remained at stage 0 (the vertical bar indicates the range observed on day 48). The photostimulated birds returned to stage 0 by about day 70. (See accompanying text for description of ovarian stages.)

FIGURE 3. Intensity of Zugunruhe in male Z. l. pugetensis and Z. l. gambelii subjected to LD 16:8 in experiment one. Activity is expressed as the number of 10-min intervals during the daily dark period during which a bird exhibited any activity; each curve represents the average activity of eight birds.

on LD 6:18 remained small (at essentially winter levels) for at least 197 days.

Most individuals of both races failed to undergo a prenuptial type of molt in response to the long photoperiods. However, a typical postnuptial type molt began when the regressing testes were below 50 mg (fig. 1) or as the regressing ovaries approached stage 0. The postnuptial molt of gambelii began, on the average, 10 days earlier than pugetensis. Females of both races showed temporal patterns of molt that were essentially similar to those
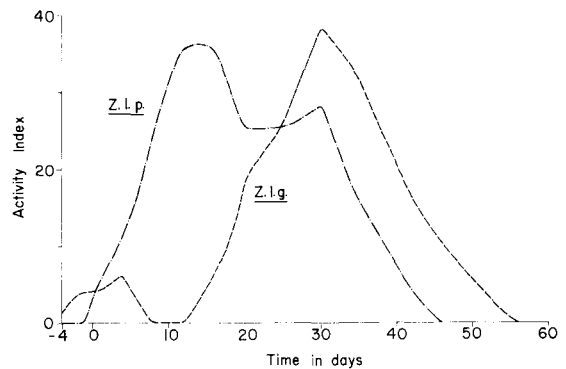
of males. Postnuptial molt was still in progress when this experiment was ended. Short-day controls failed to undergo a postnuptial type of molt.

Because photoperiodic induction of the development of the incubation patch had not been reported previously in Zonotrichia leucophrys, I was surprised to find that all of the pugetensis females and many of the gambelii females that experienced LD 18:6 underwent substantial development of the incubation patch. Loss of feathers was complete and vascularization and edema appeared to be maximal in some of the pugetensis. No development was observed prior to day 37, and maximum development was seen on about day 56. Thereafter, the patch regressed and the down of the ventral apterium was replaced during the postnuptial molt. The ventral apterium of the short-day controls and that of the males on LD 18:6 remained completely down-covered throughout the experiment.

There was a modest but consistent increase in body weight of all of the pugetensis subjected to LD 18:6, followed by a slow decline.

TABLE 1. Student's t-test of the difference between paired samples (Experiment 1).[a]

	$\overline{W}_i$	$\overline{W}_p$	$\overline{d}$	N	$s_d{}^2$	t	p
Z. l. pugetensis							
FY males	27.41	28.66	1.25	18	3.05	3.041	.01 > P > .001
FY females	24.74	25.87	1.13	10	1.07	3.456	.01 > P > .001
Ad males	27.51	28.29	0.80	7	2.28	1.411	.2 > P > .3
Ad females	23.47	23.77	0.30	4	0.786	0.677	.4 > P > .5
Z. l. gambelii							
FY males	27.38	32.95	5.57	22	12.683	7.348	P ≪ .001
FY females	23.94	29.78	5.86	14	2.702	13.348	P ≪ .001

[a] Measurements are of body weights in grams of photosensitive individuals weighed at the beginning of photostimulation ($\overline{W}_i$) and of peak observed weights ($\overline{W}_p$) in Experiment 1. $\overline{d}$ = the mean difference between the paired measurements; $t = \overline{d}/\sqrt{s_d{}^2/N}$; P is the probability of observing a value of t greater than the sample t for N − 1 degrees of freedom.

TABLE 2.   Testicular growth rates as expressed by k as days^{-1} $\pm$ 95% confidence intervals (Experiment 2).

Photoperiod	Age	Z. l. pugetensis	Z. l. gambelii
LD 12:12	Ad	$k = 0.057$ (± 0.003); N = 15	$k = 0.024$ (± 0.007); N = 16
LD 16:8	FY	$k = 0.0713$ (± 0.0031); N = 16	$k = 0.0654$ (± 0.0037); N = 16
LD 20:4	Ad	$k = 0.120$ (± 0.002); N = 15	$k = 0.104$ (± 0.007); N = 16

When the initial and maximum weights were analyzed by the method of paired comparisons (Simpson et al. 1960; table 1), the increases in body weight of both male and female first-year *pugetensis* were found to be significant under stringent conditions ($0.01 < P < 0.001$). Increases in body weight of adults, however, were not statistically significant, possibly because of the small sample size. The increases in weight of both male and female *gambelii* are very highly significant. Males averaged significantly heavier than females of the same race.

Males of both races when subjected to LD 16:8 developed an intense *Zugunruhe*. Females are known to respond in similar fashion (Lewis and Farner 1973). Maximum nocturnal activity occurred much earlier in *pugetensis* (fig. 3).

GONADAL GROWTH OF Z. L. PUGETENSIS AND Z. L. GAMBELII (Experiment Two)

Materials and methods. Three groups of photosensitive male and female *pugetensis* and *gambelii*, after maintenance on nonstimulatory (LD 6:18) photoperiods for more than four months, were placed in controlled environment chambers on constant long days (LD 12:12, 16:8, or 20:4). Samples were sacrificed on the first day of treatment and again when a testicular weight of 100–200 mg or an ovarian weight of ca. 30–50 mg was reached.

Results. The testicular growth of *gambelii* (to a combined weight of about 200 mg) and the ovarian growth (to a weight of about 50 mg) can be described by the equation:

$$\mathrm{Log}_{10}W_t = \mathrm{Log}_{10}W_0 + k_p t$$

where W_0 is the initial weight of the gonad in mg, W_t is the weight of the gonad after t days of photostimulation and k is the logarithmic growth constant in days^{-1} for a given constant photoperiod of duration p (hours of light per day) (Farner and Wilson 1957). This equation also describes the photoperiodically induced gonadal growth rates of several other species of birds. The results of experiment one indicate that the testicular growth of *pugetensis* (to a weight of about 200 mg) can also be reasonably expressed by this equation. Similarly, the data of experiment three confirm the

applicability of this equation to photoperiodically induced ovarian growth in *pugetensis* (table 4, fig. 5). The results of experiment two are thus summarized in tables 2 and 3 in terms of gonadal growth constants (k) together with 95% confidence limits as determined by least squares analysis of the logarithms of the gonadal weights.

As in the pilot experiment (experiment one), moderate to considerable brood patch development was noted in *pugetensis* females and light to moderate development among most of the *gambelii* females. The ventral apterium remained completely down-covered in all males.

Considerably greater follicular development was seen in the *pugetensis* than in the *gambelii*. The largest preovulatory follicles grew from a diameter of less than 0.4 mm in the adult females of both races to a mean diameter at day 45 of 3.1 mm (range 2.04–5.11) in *pugetensis* and of 1.8 mm in *gambelii*. By day 54, the mean diameter of the largest follicle had reached 1.9 mm in the latter. The average rate of increase in diameter of the largest follicle (0.050 mm/day) of adult *pugetensis* was approximately twice that of adult *gambelii* (0.029 mm/day). Furthermore, in most cases there was some deposition of yolk in the larger follicles of the *pugetensis* females (i.e., some vitellogenesis), but not in those of the *gambelii*, which failed to develop beyond the fluid-filled vesicular stage. At least one *pugetensis* ovulated, and when autopsied after 45 days of photostimulation, had a fully formed unshelled egg in the distal third of the mag-

TABLE 3.   Ovarian growth rates as expressed by k as days^{-1} $\pm$ 95 % confidence intervals.

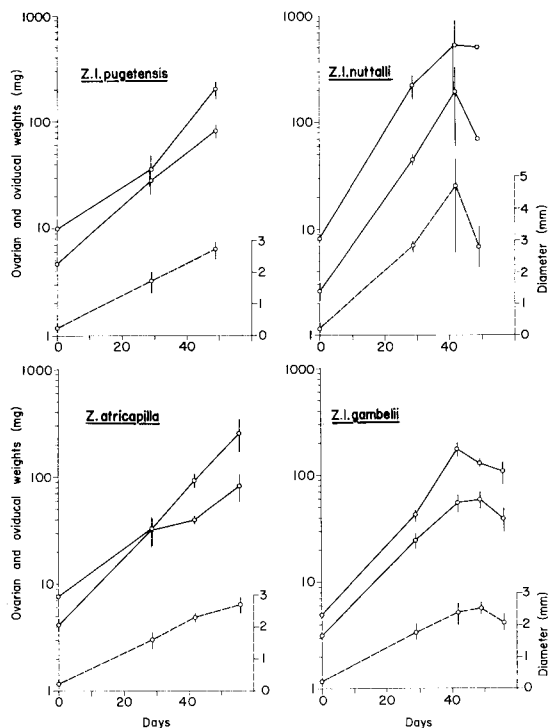| Age	Taxon	N	k_{ovary}
(Experiment 2; LD 16:8)			
Ad	Z. l. pugetensis	13	0.029 ± 0.005
Ad	Z. l. gambelii	19	0.021 ± 0.002
FY	Z. l. pugetensis	8	0.025 ± 0.005
FY	Z. l. gambelii	12	0.015 ± 0.003
(Experiment 3; LD 18:6)			
Ad	Z. l. nuttalli	14	0.040 ± 0.013
Ad	Z. l. pugetensis	12	0.031 ± 0.012
Ad	Z. l. gambelii	19	0.028 ± 0.005
Ad	Z. atricapilla	19	0.023 ± 0.005

FIGURE 4. Ovarian and oviducal growth (solid lines) and growth of the largest preovulatory follicle (dashed line) in four taxa of Crowned Sparrows, *Zonotrichia*, in response to long daily photoperiods (LD 18:6) during experiment three. The oviducts are initially heavier than the ovaries.
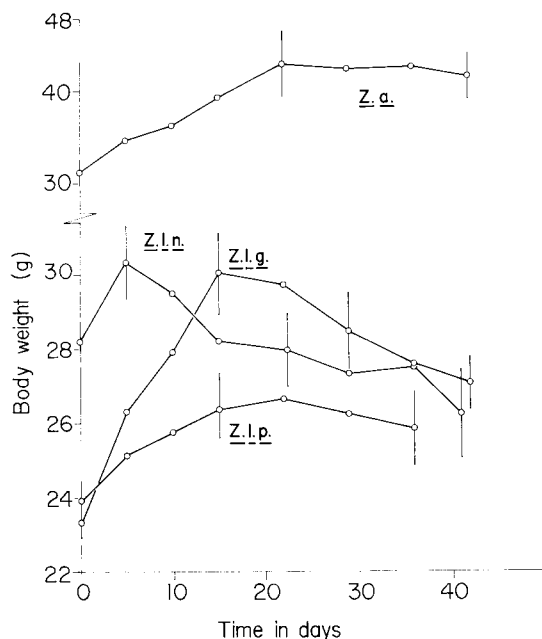

FIGURE 5. Changes in body weight of female Crowned Sparrows, *Z. l. nuttalli*, *Z. l. pugetensis*, *Z. l. gambelii*, and *Z. atricapilla*, subjected to LD 18:6 in experiment three. All four taxa, including the non-migratory *Z. l. nuttalli*, exhibited a significant weight gain. A pronounced increase in weight was, however, exhibited only in the relatively long-distance migrants, *Z. l. gambelii* and *Z. atricapilla*.

num. Furthermore, the largest preovulatory follicle (5.1 mm in diameter) contained much yolk; the fixed ovary weighed 238.3 mg and the oviduct weighed 1260 mg.

COMPARATIVE PHOTOPERIODIC RESPONSES OF FEMALE *ZONOTRICHIA* (Experiment Three)

Materials and methods. Adult females of four taxa of *Zonotrichia* were employed (*Z. l. nuttalli*, *Z. l. pugetensis*, *Z. l. gambelii*, and *Z. atricapilla*). All were retained on identical photoperiods and under the same conditions of housing and of ambient temperature for more than nine months prior to initiation of the experiment. Pretreatment consisted of nine weeks of nonstimulatory light regimes (six to eight hours of light per day). On 3 January 1970, initial controls were sacrificed and the remaining subjects placed on LD 18:6. Birds of the same taxon were housed two per cage. All birds were weighed and examined for incubation patch development and molt at approximately six-day intervals. In addition to initial controls, samples from each taxon were sacrificed at approximately regular intervals from day 28 through day 57 of photo-stimulation, and the ovaries and oviducts were treated and weighed according to the stan-

dard method described earlier. The diameter of the largest ovarian follicle of each bird was measured.

Development of the incubation patch of each subject was assayed by use of a subjective scale modified from that of Hinde (1962):

(1) Loss of feathers:
    0 = no loss of feathers
    1 = slight loss of feathers (= less than ⅓ defeathered)
    2 = moderate loss of feathers (= less than ⅔ defeathered)
    3 = nearly complete loss of feathers (= more than ⅔ defeathered)

(2) Vascularity:
    0 = no blood vessels visible in gross aspect
    1 = one or a few small blood vessels clearly visible
    2 = a network of blood vessels clearly visible
    3 = an extensive network of blood vessels evident, the larger vessels standing out above the apterial surface

(3) Edema:
    0 = no evident edema
    1 = slight edema, the apterial epidermis is "somewhat loose" (slight turgor pressure may be sensed by light touch)
    2 = moderate edema, the apterial epidermis is very loose and folded
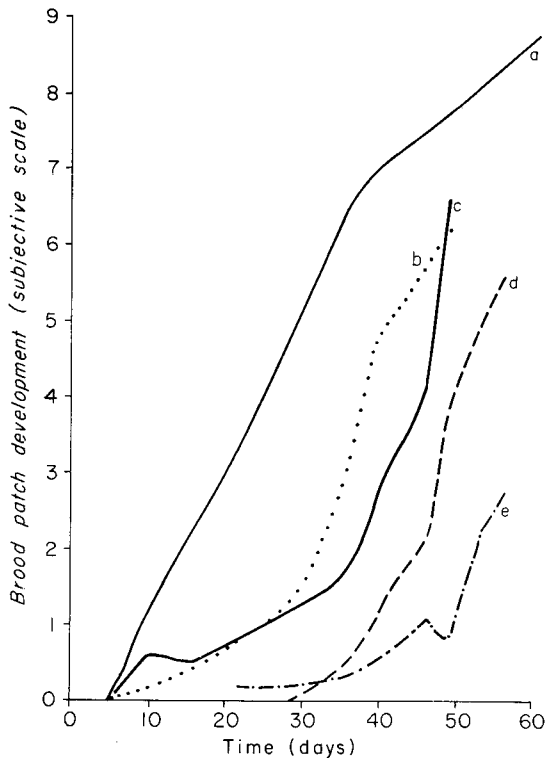   3 = pronounced edema, the skin is thick and greatly folded

FIGURE 6. The rate of development of the incubation patch of female *Zonotrichia* subjected to LD 18:6 in experiment three (*b* = *Z. l. nuttalli*; *c* = *Z. l. pugetensis*; *d* = *Z. l. gambelii*; *e* = *Z. atricapilla*); these are contrasted with the rate of development in feral Camano Island *Z. l. pugetensis*, *a*. (Lewis 1975). See accompanying text for description of the scale employed.

On this scale, the fully developed incubation patch of a feral female *pugetensis* would receive a summed score of 8–9 (Lewis 1975). Similarly, a score of 6–7 represents moderate development. Males sometimes receive scores of 1–2.

Results. Gonadal and oviducal responses are summarized in table 3 and figure 4. The

regression equations relating to ovarian and oviducal growth appear in table 4. Changes in body weight are summarized in figure 5.

Incubation patch development was evident in some *nuttalli* and *pugetensis* by day 10 of photostimulation. Comparable development was not observed in *gambelii* and *Z. atricapilla* until day 36. By day 49, complete or nearly complete development was observed in some individuals of *nuttalli* and *pugetensis*. The progress of development of the incubation patch of the four taxa are presented and compared with the natural rate of development recorded from samples of the Camano Island population of *pugetensis* (Lewis 1975) (fig. 6). Loss of feathers begins in nearly all individuals before evident vascularity or edema and is complete by the time that moderate vascularity is observed.

THE NATURAL TERMINATION OF PHOTOREFRACTORINESS (Experiment Four)

Materials and methods. The time of "natural" termination of the photorefractory state (see General Discussion) was assayed in *pugetensis* that were captured on Whidbey Island, Washington, during August and September 1970. All were retained in outdoor aviaries on natural photoperiods until the beginning of experimental treatment. Adult and first-year birds of both sexes were randomly assigned to one of three experimental groups. Each group was transferred to a controlled environment chamber on the dates indicated in table 5, where they were exposed to long daily photoperiods (LD 20:4). On the first and last day of each test, the birds were laparotomized and gonadal weights estimated as described in experiment one.

Results. Because of the small number of test groups and the small sample sizes, these results (table 5) provide only preliminary

TABLE 4. Regression equations relating ovarian and oviducal weights of *Zonotrichia* subjected to LD 18:6 (Experiment 3).[a]

Taxon	Regression equations		$b + (0.95)$	r
Z. l. nuttalli	(1) Log W_{ovary} = 0.926 Log W_{ovid} − 0.416		0.143	0.968
	(2) Log W_{ovid} = 1.012 Log W_{ovary} + 0.551		0.157	
Z. l. pugetensis	(1) Log W_{ovary} = 0.893 Log W_{ovid} − 0.173		0.531	0.966
	(2) Log W_{ovid} = 1.045 Log W_{ovary} + 0.291		0.621	
Z. l. gambelii	(1) Log W_{ovary} = 0.808 Log W_{ovid} + 0.028		0.114	0.881
	(2) Log W_{ovid} = 0.961 Log W_{ovary} − 0.431		0.254	
Z. atricapilla	(1) Log W_{ovary} = 0.774 Log W_{ovid} + 0.103		0.213	0.880
	(2) Log W_{ovid} = 1.001 Log W_{ovary} + 0.282		0.276	

[a] The coefficient of rectilinear correlation, r, is also shown; in all cases, r is significant at the 99.9% level.
The general equations are:
(1) Log W_{ovary} = b Log $W_{oviduct}$ + a
(2) Log $W_{oviduct}$ = b' Log W_{ovary} + a'

TABLE 5.   Termination of gonadal refractoriness.

Group	Period of treatment	Age	Sex	N	Gonadal weight response positive	–	negative	Range of weights (mg)
A	12 October	FY	M	3	0		3	0.6 – 4.5
	30 October	Ad	M	3	1		2	1.0 – 75
		FY	F	3	0		3	4.0 – 6.0
		Ad	F	3	0		3	4.0 – 6.0
B	23 October	FY	M	8	4		4	1.1 – 80
	10 November	Ad	M	3	3		0	6 – 100
		FY	F	2	1		1	5 – 16
		Ad	F	3	1		2	6 – 26
C	3 November	FY	M	3	3		0	38 – 70
	20 November	Ad	M	3	3		0	95 – 140
		FY	F	5	3		2	4 – 20
		Ad	F	2	1		1	5 – 25

quantitative information on the dissipation of photorefractoriness in this race. Nevertheless, it is clear that the natural termination of photorefractoriness under the conditions of this experiment begins in the autumn by about mid-October. Furthermore, the process is gradual, some individuals remaining photorefractory to LD 20:4 until November.

GENERAL DISCUSSION

PHOTOPERIODIC CONTROL: PREDICTION

My results indicate that the annual cycle of the daily photoperiod, particularly the increasingly long days of spring, forms an indispensable component of the environmental information that controls the timing of the annual reproductive cycle of Z. l. pugetensis. Several phenomena that recur annually in the natural population (Lewis 1975, Farner and Lewis 1973) are stimulated experimentally by long daily photoperiods (i.e., testicular growth, ovarian and oviducal growth that is essentially similar to the vernal growth of wild females, partial or complete brood patch development, Zugunruhe). These phenomena fail to occur in photosensitive birds maintained under short-day conditions for at least six (males) or nine (females) months. Furthermore, experimentally induced gonadal growth is followed by rapid regression that is accompanied by a typical postnuptial type of molt and induction of photorefractoriness.

Photoperiodically induced testicular growth and the development of Zugunruhe are qualitatively similar in pugetensis and gambelii (experiments 1, 2). Both phenomena resemble those which would be expected if photoperiodic information is of primary importance in timing the vernal phases of reproductive development and the development of migratory behavior. Furthermore, the photoperiodi-

cally induced testicular response of pugetensis under controlled conditions is precise (table 2; experiment 2), $t_{0.95} s_{\bar{x}} = 1.7$ to 5.3% of k. Both the earlier time of vernal migration of pugetensis relative to gambelii and the earlier and more rapid testicular growth of wild pugetensis (Blanchard 1941, 1942, Blanchard and Erickson 1949, King et al. 1966, Lewis 1975) are explained most simply by the greater photosensitivity of this race over a wide range of photoperiods (fig. 7). In both races photoperiodically induced gonadal growth is only slightly modified by temperature (Lewis and Farner 1973).

The main differences in breeding schedules among populations of the Pacific coast White-crowned Sparrows are the earlier onset and
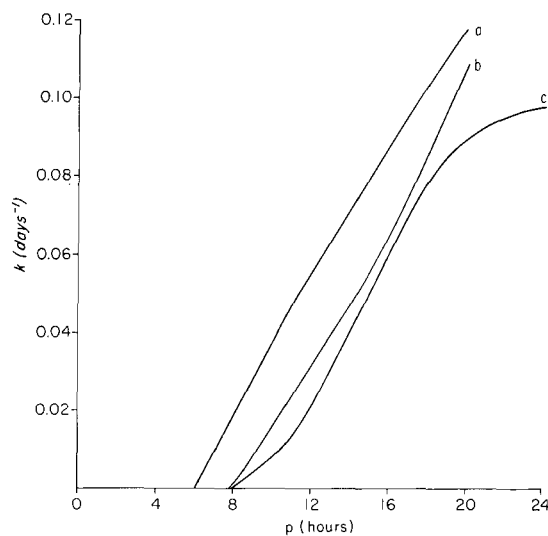

FIGURE 7.   The rate of testicular growth (k) as a function of the duration (p) of the daily photoperiod in (a) Zonotrichia leucophrys pugetensis (experiments 1 and 2); (b) Zonotrichia atricapilla (Lewis, Farner and Morton, unpubl. data); (c) Zonotrichia leucophrys gambelii (Farner and Wilson 1957).
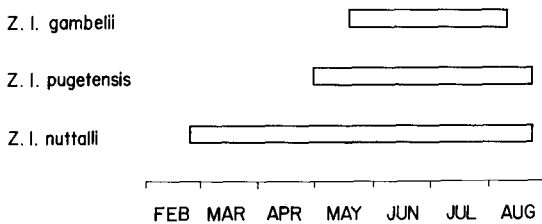
FIGURE 8. The breeding seasons of the lowland Pacific Coastal races of Z. *leucophrys*. The lengths of the bars represent the duration of the breeding season from the beginning of nest-building to the end of the period of partial dependence of the young upon parental care. Data in support of this figure were taken from DeWolfe (1968a,b,c), Kern (1972), King et al. (1965), King et al. (1966), Lewis (1975), Mewaldt et al. (1968), and Miller (1960).

FIGURE 9. Natural light regimes of three hypothetical populations of White-crowned Sparrows wintering at N. Latitude 33° and breeding at 33°N (Z. *l. nuttalli*, lower curve), at 47°N (Z. *l. pugetensis*, middle curve), and 65°N (Z. *l. gambelii*, upper curve). The data from which the figure was constructed were taken from Blanchard (1941, 1942), Blanchard and Erickson (1949), DeWolfe et al. (1973), Duncombe and Haupt (1965), King et al. (1966), King et al. (1965), Oakeson (1954), Morton (pers. comm.), and Lewis (1975).

longer duration of breeding with decreasing latitude (fig. 8). The breeding calendar (Lewis 1975) of Camano Island *pugetensis* and the studies of DeWolfe (Blanchard 1941, 1942, DeWolfe 1967, 1968a, b, c, Oakeson 1954) show that the latitudinal correlates of breeding duration are partly a function of alterations in the chronology of events. In particular there is a shortening of certain phases of the nesting cycle at higher latitudes and the development of multiple broodedness in the populations that breed at lower latitudes. Compression of the breeding cycle of *pugetensis* relative to that of *nuttalli* is achieved largely by shortening the interval between the fledging of one brood and laying the first egg of the second clutch. Because courtship, egg-laying, incubation, and rearing of the young occur in rather rapid succession in all three of the races under consideration, large temporal adjustments in breeding are not readily achieved by modification of these functions, and flexibility in the timing of the breeding seasons has been achieved largely by shifts in the annual onset of breeding (fig. 8). A number of observations collectively suggest that these adjustments are effected through rapidly evolved differences in rate of response to predictive information such as the natural photoperiodic cycle. Such information is implicated because of the relatively long period of gonadal development that precedes breeding and, in *pugetensis* and *gambelii*, a northward migration that results in arrival times that are relatively regular from year to year (Blanchard 1941, Blanchard and Erickson 1949, King et al. 1966, Lewis 1975, Oakeson 1954). Since all three races experience similar winter and early vernal photoperiodic environments (fig. 9), it is unlikely that basic differences in environmental information account
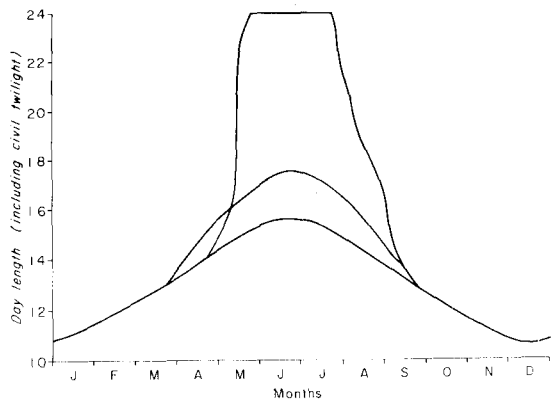
for most of the considerable differences in vernal migration and breeding times among the various populations of these finches. For example, *pugetensis* and *nuttalli* winter together in mixed flocks at Berkeley, California; *nuttalli* separate from these flocks and establish territories locally, while *pugetensis* remain in flocks and undergo a prenuptial molt prior to northward migration (Blanchard 1941). These differences in schedule imply different processing of identical information by the two populations.

The greater photosensitivity of male *pugetensis* from Island County, Washington, relative to that of *gambelii* (table 2, fig. 7), suggests that increasing responsivity with decreasing latitude of breeding is the primary mechanism that allows earlier (and thus longer) breeding at lower latitudes. Furthermore, these data, coupled with those of Blanchard (1941, discussed above) and those of Mewaldt et al. (1968), strongly suggest that the observed differences in breeding pattern are genetically fixed. The latter investigators studied captive *pugetensis* and *nuttalli* taken from 12 Pacific coastal populations that breed at latitudes ranging from ca. 30–57°N. They found, with minor exception, that the rate of vernal testicular development of the captives held in outdoor aviaries on the natural environment of San Jose, California, was inversely related to the breeding latitude; that is, "Populations tended to sort out in spite of

essentially identical environmental conditions." Several birds held over a second year showed only small differences in the timing of *Zugunruhe* and of prenuptial molt between years. Some adjustment of the annual cycle may be effected by local factors (e.g., temperature) that may act to modify a photoperiodic function (Lewis and Farner 1973). The degree to which photoperiodic species adjust breeding schedules by shifting their photoperiodic response as opposed to modification by local environmental factors may be variable. Dolnik (1963) reported a difference in photosensitivity between two populations of Chaffinch (*Fringilla coelebs*) separated by five degrees of latitude. Similarly, genetically fixed adjustments in the photosensitivity of three species of Rosy Finch (*Leucosticte*) wintering near Salt Lake City, Utah, and breeding in geographically (and partially latitudinally) distinct regions were reported by King and Wales (1965). On the other hand, in an investigation of the natural gonadal cycles of four photoperiodic species (*Sturnus vulgaris, Fringilla coelebs, Erithacus rubecula,* and *Phylloscopus collybita*) that have separate breeding populations in S.W. Germany and S. Finland, Berthold (1969) found pronounced differences in the timing of gonadal development and breeding schedule in different populations of these species. However, when *S. vulgaris* and *F. coelebs* were maintained under identical ambient conditions, either in outdoor aviaries or in controlled temperature chambers with a light schedule of LD 12:12 or 14:10, differences in the rate of gonadal development among populations of each of these species were not observed. Clearly, in this instance, the natural gonadal cycles are primarily adjusted by local environmental factors. Berthold also reported concerning one population of *F. coelebs* whose arrival at the breeding area was delayed by weather, that the gonadal cycle was also retarded.

The photoperiodically induced reproductive changes that occur in female *Zonotrichia* (experiments 1, 2, 3) are similar in rate and amplitude to the vernal changes observed in feral females (Blanchard 1941, Farner et al. 1966, Kern 1972, King et al. 1966, Lewis 1975). This is probably characteristic of primary photoperiodic species in general (Farner and Lewis 1971, Lofts et al. 1970, Lofts and Murton 1968). Usually, however, vitellogenesis and the culminative stages of ovarian development are not induced by photoperiodic stimulation alone. In addition, *Zugunruhe* that is indistinguishable from that of males
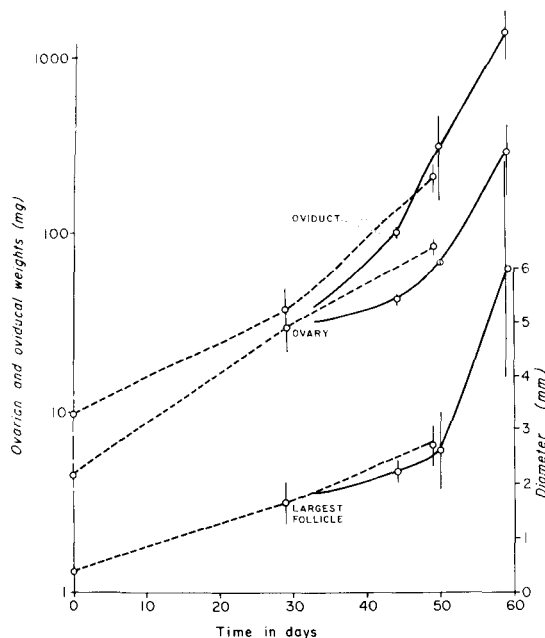

FIGURE 10. Ovarian and oviducal growth in adult *Zonotrichia leucophrys pugetensis* in response to photostimulation (experiment 3, LD 18:6) (dashed lines), and in wild adults from the time of arrival (22 April 1969) on the breeding grounds, Camano Island, Washington, to the peak of the first ovulatory cycle (solid lines) (Lewis 1975).

also develops in response to photostimulation in these two races (Lewis, unpubl. data, Lewis and Farner 1973), as does "premigratory" fattening (experiments 1, 3; King and Farner 1959, 1963, 1965, King et al. 1966, Lewis and Farner 1973).

Whereas I have no evidence of photoperiodically induced vitellogenesis in either *Z. atricapilla* or *Z. l. gambelii*, about 15–25% of photostimulated female *nuttalli* and Island County *pugetensis* do ovulate in response to experimental photostimulation (experiments 2, 3). Nevertheless, the terminal phases of female reproductive development and ovulation in natural populations of *pugetensis* are normally under a high degree of local environmental control (see Lewis 1975 and below).

The photoperiodic control of female reproductive development is well illustrated by *pugetensis*. While the growth of the ovary is a continuous process, two phases are evident (Bissonnette and Zujko 1936, Clavert 1948, Cuthbert 1945, Rowan 1929): 1) an initial slow growth of ovules from stage one to stage two of Van Durme (Cuthbert 1945, Van Durme 1914), and 2) a rapid growth phase during which most of the yolk is deposited and the follicles that comprise the prospective clutch (usually 3–5 in *pugetensis*) mature

(fig. 10). Only first stage ovules (see Cuthbert 1945) measuring 0.4 mm or less in diameter are seen in free-living *pugetensis* in December (Lewis, unpubl. field data collected near Bandon, Oregon). During the vernal stages of ovarian development, many of these develop into second-stage ovules, the largest of which are 2–3 mm in diameter. By the time *pugetensis* females arrive on the breeding grounds (Camano Island; fig. 10), the largest follicles are about 1.8 mm in diameter. Slow growth continues until nest-building is initiated; vitellogenesis and the rapid growth of the reproductive organs then begin. This greatly accelerated growth normally culminates in ovulation near the time of nest completion. By contrast, experimental photostimulation (LD 18:5) of Island County *pugetensis* affects ovarian growth that is comparable in rate and magnitude to that seen in the naturally occurring slow phase of ovarian growth (fig. 10). Such an ovary is an active endocrine organ as indicated by the considerable growth and hyperplasia of the oviduct (fig. 10) and substantial development of the incubation patch (fig. 6) (Eisner 1960, Kern 1972, Lehrman 1959, Steel and Hinde 1963). Thus, in terms of the temporal regulation of reproduction, photostimulation accounts for the entire winter and prenesting range of development. Similar conclusions can be drawn with respect to the photoperiodic responses of female *gambelii*, *nuttalli*, and *Z. atricapilla* (experiment 3). On the basis of field and laboratory investigations of the photoperiodic Tricolored and Red-winged Blackbirds (*Agelaius tricolor* and *A. phoeniceus*), Payne (1969) concluded that in these species, "the complete range of follicular development in early spring up to the time of nesting can be accounted for by the photoperiodic response. Apparently the later stages of ovarian development during nesting are a result of other conditions including presence of a singing male and availability of nest sites." The rate and extent of photoperiodically induced follicular growth in the Brown-headed Cowbird (*Molothrus ater obscurus*) resemble that observed in free-living females in the spring (Payne 1967).

TERMINATION OF REPRODUCTION

There has been much speculation, but little agreement, concerning factors that regulate postbreeding gonadal regression *per se* of birds (Davis and Davis 1954, Marshall 1959, Miller 1954, Wolfson 1958). Among primary photoperiodic species such as *Z. leucophrys*, gonadal regression and the termination of breeding are often regarded as functions of long daily photoperiods (Farner and Follett 1966, Farner and Lewis 1971, Hamner 1968, Schwab 1970). Terminating mechanisms, however, and the information that cues termination in a multiple-brooded bird such as *pugetensis* are more complex than can be explained by any single-component model. Farner (1970) speculated that several types of termination mechanisms may exist among photoperiodic species of birds. Of those that he proposed, only termination by the development of photorefractoriness would seem to be importantly involved in *pugetensis*.

Termination by photorefractoriness. Z. l. *pugetensis*, like other North American representatives of *Zonotrichia* (Farner and Lewis 1971, 1973, Lofts and Murton 1968), terminates reproduction in a photorefractory state that is not dissipated until autumn. This is demonstrated by the fact that photoperiodically induced ovarian and testicular growth in experiment 1 was followed by a period of regression resulting in "resting" gonadal weights that persisted for at least several months in the face of continued long days. When these subjects were placed on short days (LD 6:18) for several weeks, their refractoriness was dispelled and rapid gonadal growth followed reinstitution of long-day treatment (experiment 2). Adults of both sexes who were maintained on the natural photoperiods of autumn (experiment 4) failed to respond to light regimes of LD 20:4 until mid-October or early November.

The data of experiments 1 and 4, together with those of Lewis (1975) on the natural gonadal cycles indicate that the induction and course of termination of photorefractoriness in *pugetensis* are very similar to those of *gambelii* (Farner and Mewaldt 1955, King et al. 1966). However, photorefractoriness probably develops somewhat later in *pugetensis*, following the more protracted breeding season. The relatively long period (60–80 days) of high gonadal weights of breeding males (Lewis 1975) and the failure of experimental photostimulation to sustain peak gonadal weights for such periods, lead me to infer that photostimulation and photorefractoriness may involve separate mechanisms (see also Threadgold 1960, Laws 1961, Hamner 1968, Lofts et al. 1970). Certainly, any model for controlling the annual duration of reproductive competence and the number of broods reared must include extra-photoperiodic information (Lack 1950, Lehrman 1961, Lewis 1975, Lewis and Orcutt 1971, Marshall 1970).

Termination directed by local information. In an obligately single-brooded species or population such as *Z. l. gambelii*, reproduction may terminate naturally by means of a single-component mechanism that may or may not depend upon environmental information that is effective at or near the time of termination. In annually periodic, multiple-brooded species or populations such as Camano Island *pugetensis*—in which the number of broods reared per season (and hence the actual time of termination) may vary—locally variable information as well as annually periodic information is implicated in the etiology of breeding termination (Lewis 1975). Furthermore, in birds that rear a variable number of broods, terminating mechanisms probably have been selected that make use of predictive information and possibly of multiple or redundant controls. Even if a single type of signal is employed, it must be effective well before the failure of those conditions that support the prospective brood and perhaps energetically costly postseasonal functions such as molt and migration. There is considerable evidence that many species of temperate-zone birds cease breeding while substantial food is yet available. Even if termination is timed to coincide with the decline of the food supply, as is the case in the European Starling (*Sturnus vulgaris*) studied at Craibstone, Scotland, by Dunnet (1955), short-term predictive information may be involved. While it is appealing to suggest that egg-laying by multiple-brooded birds may continue as long as the local environment is "permissive," this would seem likely to lead often to low success in rearing terminal broods, and, particularly among migrants, might impair postseasonal survival of both adults and young.

As in most other primary photoperiodic species, the question of the regulation of the termination of breeding cannot be separated from that of the induction of photorefractoriness. Whereas *pugetensis* is clearly refractory in late summer, the etiology of photorefractoriness in this species and others remains unclear (Farner 1970, Hamner 1968, Farner and Lewis 1971, Lofts et al. 1970). As discussed earlier, one cannot discount the possibility that gonadal regression and photorefractoriness are induced independently in free-living birds.

TERMINATION OF PHOTOREFRACTORINESS

Adult and first-year male and female *pugetensis* that were maintained on the natural photoperiods of autumn failed to respond to normally stimulatory light regimes of LD 20:4 until about mid-October or early November. A period of postnuptial photorefractoriness has also been established for *gambelii* (Farner and Mewaldt 1955, King et al. 1966, Laws 1961) and several other North American *Zonotrichia*. Among the Crowned Sparrows, only *Z. capensis* fails to exhibit a photorefractory phase (Epple et al. 1972, Lewis et al. 1974, Miller 1955).

While the data of experiments 1 and 4 must be considered preliminary, they indicate that the termination of gonadal refractoriness is similar in *pugetensis* and most other primary photoperiodic birds that have been studied in this regard (Burger 1949, Farner and Lewis 1971, Hamner 1968): (1) short photoperiods dissipate refractoriness; (2) long daily photoperiods maintain the refractory state for at least several months; (3) termination of photorefractoriness appears to be a gradual process; (4) first-year birds exhibit a photorefractoriness that terminates at about the same time as that of adults; and (5) males and females terminate photorefractoriness naturally at about the same time.

In view of the limited data of experiment 4, it is unwise to speculate about the mechanism of termination of photorefractoriness in this finch. It is clear, however (especially from 1, 2, 4, and 5 above), that photorefractoriness is not an entirely endogenous function as has often been maintained (see Lofts et al. 1967 for review). Furthermore, the time of onset of photorefractoriness is modified by the timing of the last nesting cycle (Lewis 1975).

MEASUREMENT OF THE DURATION OF THE PHOTOPERIOD

The daily photoperiod is thought to time the annual cycle of many birds by the entrainment of an endogenous circadian cycle in photosensitivity (Pittendrigh and Minis 1964). There is good evidence that such a mechanism underlies the photoperiodic testicular response of *gambelii* (Farner 1964, 1965). A long-period (ca. circennial) endogenous rhythm may also be involved in molt cycles and fat deposition in *gambelii* (King 1968, 1970). On the other hand, we (Lewis, Farner, and Donham, unpubl. experiments) have failed to detect any evidence of endogenous long-period testicular cycles in *gambelii*. Assuming that there are no fundamental or qualitative differences in the timing mechanisms of the closely related *gambelii* and *pugetensis* and that the photoperiodic gonadal response of *gambelii* involves a circadian oscillator, the greater

photosensitivity of *pugetensis* at all stimulatory photoperiods tested can be explained most simply by a shift of the sensitive phase to an earlier time of day. This hypothesis could be tested partially by a "scotophase-scan" experiment, in which the scotophase of the daily light-dark cycle is interrupted at different times in different sets of birds by a relatively short light period (Farner and Lewis 1971). The results of such experiments on Japanese Quail (*Coturnix coturnix*) (Follett and Sharp 1969) and on *gambelii* suggest that the photoinductive phase of the quail may occur earlier in the day and thus partially account for its much higher rate of testicular development (Lofts et al. 1970) in response to long daily photoperiods.

SUMMARY

This paper concerns control of the annual cycle in the Puget Sound race of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). The photoperiodic responses of this finch were compared experimentally with those of three related taxa that have similar winter ranges, but that breed at different latitudes along the Pacific coast of North America (*Z. l. nuttalli, Z. l. gambelii,* and *Z. atricapilla*). The results indicate that the annual cycle of the daily photoperiod, particularly the increasingly long days of spring, forms an indispensable component of the battery of environmental information that controls the timing of the annual reproductive cycle of *pugetensis*. Several phenomena that recur annually in wild birds can be stimulated experimentally by long daily photoperiods (i.e., testicular growth, ovarian and oviducal growth that is essentially similar to the vernal growth of wild females, partial or complete brood patch development in females, *Zugunruhe*). These fail to occur under short-day conditions. Experimentally induced gonadal growth is followed by rapid involution that is accompanied by a typical postnuptial type of molt and by photorefractoriness.

The photoperiodically induced testicular growth and the development of *Zugunruhe* in *pugetensis* are qualitatively the same as those induced in *gambelii*. Both phenomena are also similar to those which would be expected if photoperiodic information is of primary importance in timing the vernal phases of reproductive development and migration. Furthermore, the photoperiodically induced testicular response of *pugetensis* under controlled conditions is quantitatively as precise as that of *gambelii*. Both the earlier time of vernal migration of *pugetensis* relative to *gambelii* and the earlier and more rapid testicular growth of wild *pugetensis* are explained most simply by the greater photosensitivity of this race over a wide range of photoperiods.

The photoperiodically induced reproductive changes that occur in female *Zonotrichia* are similar in rate and amplitude to the vernal changes observed in feral females. Analysis of the data indicates that photoperiodic information accounts for the entire winter and prenesting range of reproductive development in female *pugetensis* and probably also in the other taxa studied.

ACKNOWLEDGMENTS

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