TEMPERATURE MODULATION OF PHOTOPERIODICALLY INDUCED VERNAL PHENOMENA IN WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS*)[1]

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At mid and high latitudes spring is a period of rapid amelioration and trophic enrichment of the environment. The annual cycles of most birds that breed at these latitudes are so controlled that the time of production of young occurs as food becomes abundant. Because the latter is temporally restricted and because the physiologic preparation that precedes reproduction requires many weeks, breeding at these latitudes has become possible, with rare exceptions, because of the evolution of relatively precise control mechanisms based on information that has a fixed, temporally antecedent relationship to the period in which the production of the young occurs. It is thus not surprising that the annual cycle in day length is the primary source of environmental information that controls the timing of vernal migration and reproductive function in many species (for recent reviews, see Farner and Lewis 1971; Lofts et al. 1970; Lofts and Murton 1968).

However, the onset of "spring," in the phenological sense, occurs at somewhat different times each year. Within limits, most species of birds show corresponding adjustments in the onset of breeding (for examples, see Immelmann 1971; Lack 1966). Such adjustments in the timing of breeding and other vernal functions imply that the basic control system is sensitive to at least one modifying factor.

Data from experiments agree with the above-stated observations and inferences. Even in species such as the White-crowned Sparrow (*Zonotrichia leucophrys*) in which the experimentally induced photoperiodic responses are very precise, it is evident that other environmental information is involved in the fine tuning of the vernal phase of the cycle under natural conditions (Farner and Lewis 1971; Lewis and Orcutt 1971). This appears to be especially true for females, in which information in addition to day length is essential to the induction of vitellogenesis and the culminative stages of ovarian maturation (Farner et al. 1966; Kern 1972; Lewis 1971).

Experimental evaluation of photoperiodic functions has yielded a rich body of quantitative information and a correspondingly sophisticated theoretical structure. But, largely because of the difficulties in experimental approach, our knowledge of the environmental factors that modify the timing of the vernal events of the cycle is sparse and largely inferred from field observations. Analyses of the difficulties of this approach have been presented by Koskimies (1950), Nisbet and Drury (1968), and Enright (1970).

Field investigations have frequently suggested that ambient temperature, either directly or indirectly, is a modifier of the rates of development of the vernal events associated with reproduction (Davis 1955; Immelmann 1963, 1971; Lack 1950, 1966; Lofts and Murton 1968; Newton 1964). There is a very limited body of experimental data that suggests that the rate of photoperiodically induced testicular growth is a small, but probably significant, function of ambient temperature in the Starling (*Sturnus vulgaris*) (Burger 1948), the White-crowned Sparrow (*Z. l. gambelii*) (Farner and Mewaldt 1952, 1953; Farner and Wilson 1957), and the Dark-eyed (= Slate-colored) Junco (*Junco hyemalis*) (Engels and Jenner 1956). Limited data from laboratory experiments also suggest that the onset of vernal *Zugunruhe* in caged birds is influenced by ambient temperature (see Eyster 1954; Kendeigh et al. 1960; Nisbet and Drury 1968).

In the races and populations of *Z. leucophrys* thus far studied, prominent photoperiodic elements have been identified in the timing of gonadal function, prenuptial molt, vernal migration, and migratory fat deposition. The photoperiodic responses of *Z. l. gambelii* and *Z. l. pugetensis* are quantitatively precise under

adequately controlled conditions. Gonadal development and related vernal phenomena do not occur under "winter" day lengths. Nevertheless, variations in the natural annual cycles of these finches do occur (Blanchard 1941; Blanchard and Erickson 1949; Cortopassi and Mewaldt 1965; Lewis 1971; Oakeson 1954), and very meager data suggest that the temperature in winter and early spring could be involved (Blanchard 1941; Farner and Mewaldt 1952, 1953, 1955; Lewis 1971). The investigation described herein was thus designed as a partial test of the hypothesis that gonadal growth rates, vernal premigratory fattening, and the development of vernal *Zugunruhe* in experimentally photostimulated White-crowned Sparrows are modified by ambient temperature.

MATERIALS AND METHODS

SERIES I. (TEMPERATURE AS VARIABLE)

Adult male and female *Z. l. gambelii* and adult female *Z. l. pugetensis* were employed. The *gambelii* females were captured from a previously described population in Yakima County, Washington (Lewis et al. 1968) during the winter of 1970–71. The males were captured in Kittitas County, Washington, in April 1971. The *pugetensis* females were provided by Dr. Eberhard Gwinner who captured them during the winter of 1970–71, near Stanford, California. The latter were retained in outdoor aviaries at Stanford on natural photoperiods until shipped by air to Seattle on 8 March 1971.

In the region in which the *pugetensis* used in our experiments were obtained, minimum daily temperatures seldom fall below 5°C during the vernal phase of the annual cycle (January through March). The climate of the wintering grounds of the *gambelii* used in this experiment is more severe; mean daily temperatures below 0°C are reported for January in most years. Mean daily maxima are somewhat less than 20°C during this period in the *pugetensis* environment and about 9°C in the case of the *gambelii*. Mean daily minima are about 9–10°C for the *pugetensis* and about –2°C for the *gambelii*. The mean amplitudes of the daily temperature cycles are approximately 9 and 11°C, respectively. These generalizations are based on a review of the Climatological Data summaries published by the U.S. Department of Commerce for the appropriate stations in Washington and California and on unpublished data (Lewis and Farner) from the Yakima County wintering grounds. The microhabitat of the *gambelii* at least (Lewis and Farner, unpubl. observ.) is probably less variable than indicated by weather-station data.

All experimental birds of both races were placed in large outdoor aviaries immediately following arrival in Seattle. Sex was ascertained by laparotomy within 2 weeks of arrival at the laboratory. More than 3 months prior to the experiment, all birds were transferred to controlled environment chambers where they were retained on a nonstimulatory photoperiodic regime of 7 hr of light and 17 hr of darkness per day (7L 17D). Light was provided by tungsten lamps arranged to provide a minimum light intensity of 420 ± 20 lux at the floor of each cage. Ambient temperature was 20 (±0.5)°C; the dew point was 10.7 (±0.5)°C.

TABLE 1. Ambient conditions obtaining throughout Series I (temperature as variable).[a]

Group	Ambient temperature ($\bar{x} \pm$ max. error)	Vapor pressure ($\bar{x} \pm$ max. error)	Rate of air flow ($\bar{x} \pm$ SD)
	°C	mm Hg	km/hr
I	5.2(±0.5)	5.44(±0.14)	0.59(±0.02)
II	15.1(±0.5)	5.54(±0.23)	0.61(±0.04)
III	25.8(±0.5)	5.31(±0.24)	0.65(±0.05)
IV	34.1(±0.5)	5.54(±0.25)	0.82(±0.05)

[a] Values in the table represent those recorded from the center of several sample cages within each controlled environment chamber. Vapor pressure values were computed from temperatures measured within cages; however, the dew point on which these values were based was recorded from the return air of the chamber where the rate of air flow was much higher.

Two weeks prior to institution of the experimental light regime, the birds were assigned randomly to four chambers maintained on 7L 17D. The ambient temperature for group I was decreased at a rate of 2.0°C daily to 5.2°C; for group II, temperature was decreased 1.0°C daily to 15.1°C; for group III, temperature was increased by 1.0°C daily to 25.8°C; and for group IV, temperature was increased at the rate of 2.0°C per day to 34.1°C. In all groups, the dew point was reduced at the rate of 1°C daily until 3.0°C was reached. At the termination of this 14-day pretreatment period, initial controls were sacrificed and the photoperiod of all experimental groups was increased to 18L 6D. Air flow in the chambers was vertically downward; its velocity was measured with a hot wire anemometer. The ambient conditions are summarized in table 1.

In the controlled environment chambers, the experimental birds (except those in activity cages, see below) were housed two per cage (41 × 26 × 22 cm) with sexes and races housed separately. Water and mineral-enriched chick starter mash (Purina Chick Startena) with vitamin supplement were freely available.

At 3–5 day intervals, the birds were weighed to the nearest 0.1 g and body molt was assessed subjectively as heavy, moderate, light, or none. Locomotor activity was continuously recorded for five birds from each sex and race in each of the four experimental groups. Each of these 60 birds was housed individually in a cage with a centrally positioned, spring-loaded perch mounted on a microswitch that is activated by the weight of the bird.

Samples of the experimental birds were sacrificed during the course of the experiment and the testes, ovaries, and oviducts were removed, fixed, and weighed using established procedures (Farner and Wilson 1957; Farner et al. 1966). The thyroid glands also were removed, debrided of all extraneous tissue, fixed in Bouin's fluid, transferred to 70% ethanol after 1 day and, after 5 additional days, weighed on a torsion balance to the nearest 0.01 mg.

SERIES II. (THERMOPERIOD AS VARIABLE)

First-year male *gambelii* were captured in Kittitas County, Washington, on 20–23 September 1968, transported to Seattle on the day of capture, and placed in large outdoor aviaries. They were then transferred to a controlled environment chamber on 28 September. The initial photoperiod (13L 11D) was reduced decrementally through 10 days to 6L 18D. All were retained on this light regime at an ambient temperature of 20.0° (±0.5°C) and a relative humidity of

55 ($\pm$5)%. In this series, relative humidity, rather than the dew point, was maintained constant. Illumination and all other conditions of housing and environment were as described for Series I. Nine initial controls were taken on day 0; gonads were fixed and weighed as in Series I. Experimental birds were weighed on day 0 (2 December), randomly divided among three groups, and placed on a photoperiodic regime of 18L 6D.

Group I. "Positive" thermoperiod. For this group a daily increase in ambient temperature began 15 min before the onset of the daily photoperiod; the excursion was from 14 ($\pm$0.5)°C to 26 ($\pm$0.5)°C at a mean rate of 0.5°C per min; the temperature similarly returned to base line beginning 15 min before the end of the light period. Relative humidity, except during the actual temperature transitions, was maintained constant at 55 ($\pm$5)%.

Group II. "Negative" thermoperiod. The temperature increase began 15 min before the end of the light period and the decrease, 15 min before the beginning of the photoperiod. Rates of change in temperature were as in Group I. Maximum temperature during the dark period was 26.0°C; minimum during the light period was 14.0°C. Relative humidity was maintained as in Group I.

Group III. Constant ambient temperature (20 $\pm$ 0.5°C) and relative humidity (55 $\pm$ 5%) were maintained.

RESULTS

GONADAL GROWTH

In both *gambelii* and *pugetensis*, testicular growth to a combined weight of about 200 mg and ovarian growth to a weight of about 50 mg, as induced by constant daily stimulatory photoperiods, are approximately logarithmic (Farner and Wilson 1957; Farner et al. 1966; Kern 1972; Lewis 1971).

Gonadal responses in the present investigation were evaluated in terms of a logarithmic growth rate constant (k, in days^{-1}) as determined by least-squares analysis of the logarithms of gonadal weights. In both races, ovarian growth rates and variances in the responses were unaffected by temperature, whereas the testicular growth rates of *gambelii*
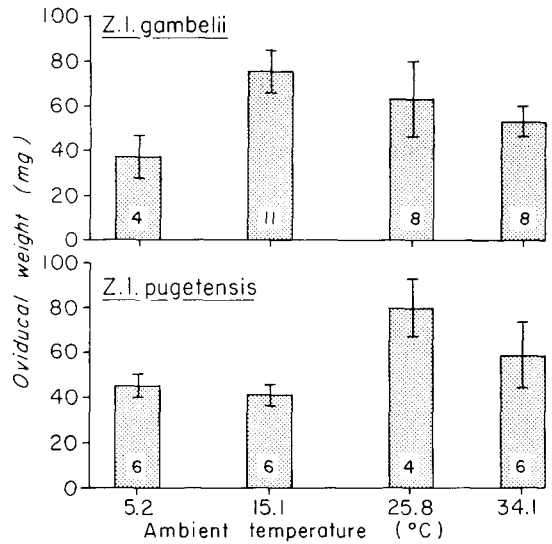

FIGURE 1. Weight of oviducts as a function of temperature following 33 (*Z. l. pugetensis*) and 35 (*Z. l. gambelii*) days of photostimulation. Vertical lines represent the 95% confidence intervals ($\bar{x} \pm t_{.05}$ $s_{\bar{x}}$; Snedecor 1956); numbers within bars are sample sizes. Initial weights of *Z. l. gambelii* oviducts averaged 6.51 ($\pm$0.83) mg ($N = 8$) and those of *Z. l. pugetensis* averaged 6.87 ($\pm$0.52) mg ($N = 5$).

appeared to be a small positive function of temperature (table 2). The rectilinear regression of k as a function of T_E is

$$k = 0.00040 \ (\pm 0.00016) \ T_E + 0.0738 \ (\pm 0.0018) \qquad (1)$$

where T_E is ambient temperature in °C, and the values in parentheses define the 95% confidence intervals. The coefficient of rectilinear correlation is 0.75, which is highly significant ($P \ll 0.001$ for a 2-sided test). The standard error of the estimate is 0.0039.

No differences in testicular response were observed among groups of the thermoperiodic series. In all groups $k = 0.08$ ($\pm$0.006).

GROWTH OF THE OVIDUCT

In both races, oviducal growth was favored at intermediate temperatures (fig. 1). It appears that oviducal growth of *pugetensis* may be inhibited over a wider range of "low" temperatures than is that of *gambelii*.

BODY WEIGHT

The relative increase in weight at all temperatures was greatest in *gambelii* females. With the exception of those held at 34.1°C, maximal weight was reached earlier in female *pugetensis* than in female *gambelii*. Neither relative increase in weight nor rate of weight gain in the female *pugetensis* appeared to be appreciably affected by temperature. The sample was small, however. In all groups the
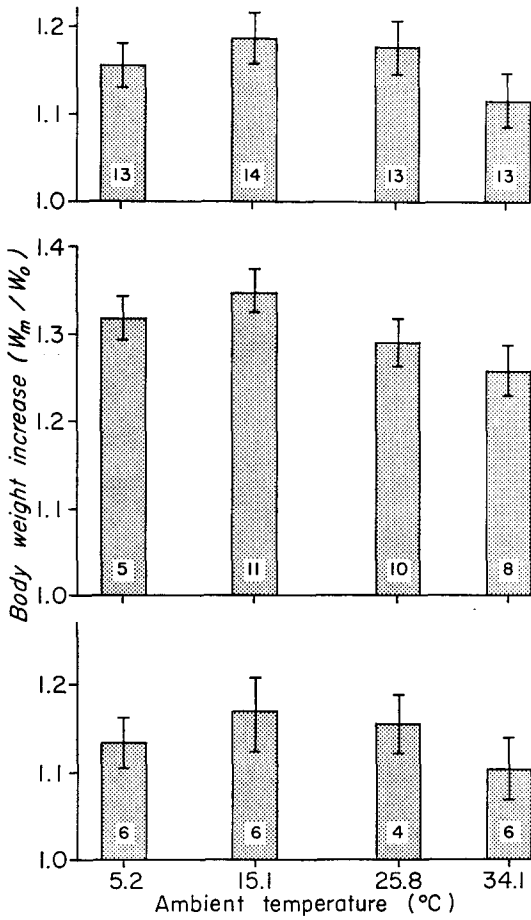
TABLE 2. Gonadal growth-rate constants (k) as a function of ambient temperature (T_E).

Race	Sex	T_E	k($\pm$95% conf. limits) days^{-1}	N
Z. l. gambelii	♂	5.2°C	0.0758($\pm$0.0058)	15
		15.1	0.0806($\pm$0.0046)	15
		25.8	0.0844($\pm$0.0059)	13
		34.1	0.0875($\pm$0.0046)	14
Z. l. gambelii	♀	5.2	0.0244($\pm$0.0056)	14
		15.1	0.0275($\pm$0.0037)	19
		25.8	0.0247($\pm$0.0046)	17
		34.1	0.0246($\pm$0.0043)	16
Z. l. pugetensis	♀	5.2	0.0255($\pm$0.0061)	11
		15.1	0.0256($\pm$0.0056)	11
		25.8	0.0282($\pm$0.0054)	9
		34.1	0.0231($\pm$0.0058)	11

FIGURE 2. Photoperiodically induced increase in body weight (W_m/W_o) as a function of ambient temperature. W_o = initial weight; W_m = maximal weight. Conventions are as in fig. 1. Upper set = male *Z. l. gambelii*; middle set = female *Z. l. gambelii*; lower set = *Z. l. pugetensis*.
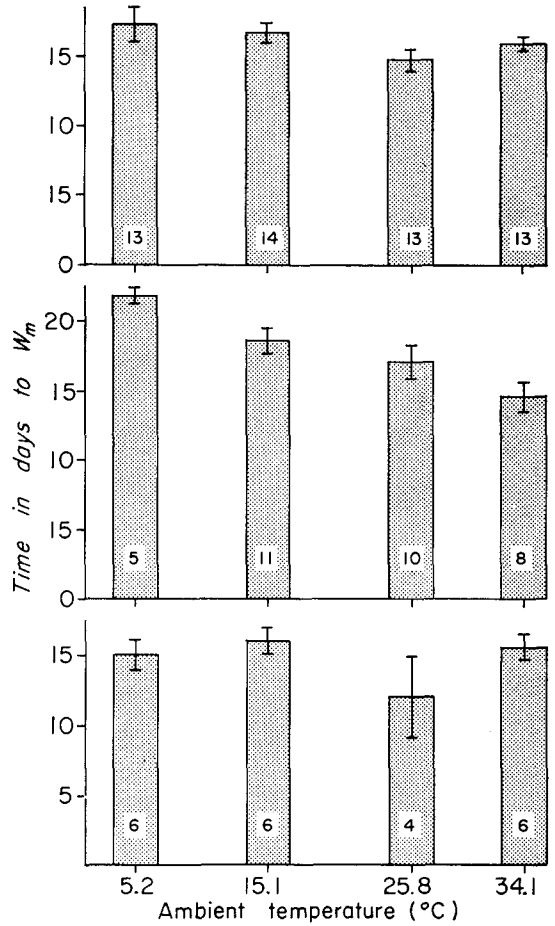
FIGURE 3. The rate of photoperiodically induced fattening [expressed as the number of days to reach maximum weight (W_m)] as a function of ambient temperature. Conventions are as in fig. 1. Upper set = male *Z. l. gambelii*; middle set = female *Z. l. gambelii*; lower set = female *Z. l. pugetensis*.

maximum weight attained was least at 34.1°C (fig. 2), a temperature that is rarely encountered by either race under natural conditions in spring. The rate of fattening (fig. 3) was greater in male than in female *gambelii* except at the high temperature. Furthermore, the rate of weight increase of the female *gambelii* was influenced more by T_E than that of the males (fig. 3).

Body weight of birds in the thermoperiod series increased exponentially. Differences in response among groups, however, were not significant.

ZUGUNRUHE

Nocturnal activity as a function of ambient temperature is presented in figure 4 as the number of 10-min intervals during the daily dark period during which a bird exhibited motor activity. The time of onset of *Zugunruhe* is an inverse function of ambient tem-

perature from 5.2–25.8°C. Onset of *Zugunruhe* occurred earlier in male than in female *gambelii*. The data from the 34.1°C treatment group are excluded from this figure because both diurnal and nocturnal locomotor activity are depressed or suppressed at this unnaturally high temperature. Indeed, most individuals failed to exhibit any nocturnal activity at 34.1°C.

MOLT

The time of onset of molt in the temperature series was advanced in the low temperature group (5.2°C). Thus, by day 19, 80% of the male *gambelii* in the 5.2°C group were in moderate to heavy body molt and 60% of the female *gambelii* in this group were exhibiting heavy molt; a few of the *pugetensis* females at this temperature were molting lightly. Molt had not yet begun at this time in the higher temperature groups. Intense prenuptial-type
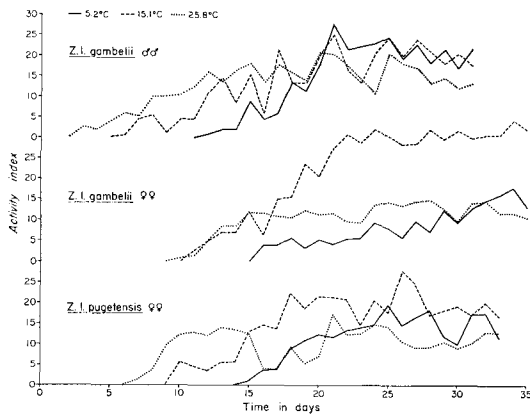
FIGURE 4. Intensity of *Zugunruhe* as a function of ambient temperature. Activity is expressed as the number of 10-min intervals during the daily dark period (Series I, temperature as variable) during which a subject exhibited any activity; each curve represents the mean for five birds.

molt was, in fact, observed only at 5.2°C; many individuals at higher temperatures exhibited little or no molt. No differences in the timing of prenuptial molt were observed among the groups in the thermoperiod series. The birds of Group I, however, exhibited a generally more intense and more complete molt than either of the other two groups.

THYROID WEIGHT

There was a significant increase in thyroid weight of both males and females at 5.2 and 15.1°C, but not at the higher temperatures. The initial mean thyroid weight (±95% confidence limits) of the *gambelii* males ($N = 9$) was 1.49 (±0.15) mg. Thyroid weight increased steadily in the 5.2 and 15.1°C groups, reaching a mean value of 2.06 (±0.29) mg ($N = 10$) by day 31 of photostimulation. Initial thyroid weights of the *gambelii* females ($N = 8$) averaged 1.29 (±0.12) mg, and the initial weights of the female *pugetensis* ($N = 4$) averaged 1.55 (±0.09) mg. Final weights of the *gambelii* females in the two low temperature groups ($N = 11$) averaged 1.65 (±0.07) and those of the *pugetensis* ($N = 12$) were 2.27 (±0.17).

GENERAL DISCUSSION

TEMPERATURE MODULATION OF PHOTO-PERIODICALLY INDUCED FUNCTIONS

Gonads. Our data confirm and extend those of earlier investigations of the effect of ambient temperature on experimentally induced gonadal growth of White-crowned Sparrows by Farner and Mewaldt (1952, 1953), who demonstrated also that elevated environmental temperatures do not bring about testicular

growth when the photoperiod is of nonstimulatory duration.

Assuming that the empirical relationship between photoperiodically induced testicular growth and ambient temperature is approximately linear, the slope constant, m (in days⁻¹ degrees⁻¹), of the generalized form of equation (1),

$$k = m\,T_E + d, \qquad (2)$$

may be used as a comparative measure of the "sensitivity" of photoperiodically induced testicular growth to constant ambient temperature. Thus, data obtained by Farner and Mewaldt (1953) from the two groups of Z. l. *gambelii* that were photostimulated by 15L 9D at 1°C and 22°C, respectively, give a value of m that does not differ significantly from our value of 0.0004 (see equation 1). While the data are not strictly comparable, it appears that the temperature dependence of testicular growth in *Junco hyemalis* that were photostimulated at 12L 12D (Engels and Jenner 1956) and *Sturnus vulgaris* that were photostimulated at 14L 10D (Burger 1948) is somewhat greater than in Z. l. *gambelii*. We estimate that $m = 0.0007$ in the *J. hyemalis* and about 0.001 in the *S. vulgaris*. That such temperature effects are small is illustrated by the fact that in *gambelii* an increase of light period by 1 hr (from 17L 7D to 18L 6D) would increase the testicular growth rate by about as much as increasing the T_E by 30°C. The rates of photoperiodically induced testicular and ovarian growth of the House Sparrow (*Passer domesticus*) (Kendeigh 1941) and the testicular growth of the Great Tit (*Parus major*) (Suomalainen 1937) are apparently little affected by ambient temperature.

It is notable that a daily thermoperiodic cycle of substantial amplitude (p. 281) has no effect on the rate of testicular growth in Z. l. *gambelii*. Although our experiments, described above, were of limited scope, it does seem safe to conclude that amplitude of the daily thermoperiod is not used as information in any significant manner in the control scheme.

Under the conditions of our investigation, there was no significant effect of ambient temperature on either the rate or precision of the photoperiodic ovarian response in either *gambelii* or *pugetensis*. These data, together with those of Lewis (1971), suggest that the slow phase of ovarian development is under strict photoperiodic control (see also Farner and Lewis 1971), whereas vitellogenesis and the culminative stages of ovarian development are doubtless under complex environmental control (Lewis and Orcutt 1971). However,

there is no definitive evidence that environmental temperature is normally a part of the complex of stimuli that times the culminative stages. Short-term effects of ambient temperature on ovulation and egg-laying do occur (Koskimies 1950; Winkel 1970). It is by no means clear, however, that such effects are direct, since even short-term changes in T_E produce many changes in the microenvironment of the bird (e.g., Koskimies 1950). Particularly relevant to the results of our investigation are the observations of Oakeson (1954) at Mountain Village, Alaska. She noted that Z. l. gambelii initiated nest-building and egg-laying in 1950 (a year not considered severe by "old timers") under conditions that were "far from clement." Between the day of the first egg and the day on which the young of the first pair noted to nest were fledged, there were snow flurries, much rain, one hailstorm, and 4 nights when the temperature dropped to freezing or below. Nesting success was high under these conditions.

Lewis (1971; and unpubl. data) found that the time of first ovulations in a population of pugetensis that breeds on Camano Island, Washington, bears a close temporal relationship to the time of arrival of the females. Thus, the most important environmental modifiers of breeding onset are those that determine the time of arrival of the females and thereby indirectly determine the time of first ovulations. It is possible that environmental temperature on the wintering grounds could affect the onset of oviposition indirectly by its effect on the time of initiation of migration and hence the time of arrival at the breeding area. There is evidence that such a mode of control may be effective in other migrants (Goodacre and Lack 1959; Koskimies 1950; Stauber and Ullrich 1970).

Oviduct. The oviductal responses (fig. 1) indicate that the ovaries of photostimulated birds were active endocrine glands in all groups. However, the fact that ovarian growth is not measurably influenced by T_E suggests that perhaps ovarian weight is not a sensitive measure of the secretory state of that organ. Under field conditions for which data are adequate (Kern 1972; Lewis 1971), the annual cycle in weight of the oviduct closely parallels that of the ovary.

Zugunruhe and fattening. Z. l. gambelii and Z. l. pugetensis are nocturnal migrants. Both the vernal and autumnal premigratory and migratory periods are characterized by hyperphagia and the resultant deposition of fat (Blanchard 1941; Farner 1955; King and Farner 1963). A similar fattening occurs in captive gambelii, and generally in pugetensis, maintained in outdoor aviaries (King and Farner 1963; Mewaldt et al. 1968). A nocturnal restlessness (Zugunruhe) that is generally oriented toward the normal direction of migration is also observed in such captives at the time when migration would otherwise take place; this is accompanied by fattening (Farner et al. 1957; King and Farner 1963; Mewaldt et al. 1964). This characteristic migratory state can be induced experimentally in photosensitive birds by photostimulation as in the present investigation, but fails to develop when birds are retained on constant short daily photoperiods. Experimentally induced vernal nocturnal activity is similar in gambelii and pugetensis, differing primarily with respect to the earlier onset of Zugunruhe in male pugetensis (Lewis 1971). The onset of experimentally induced Zugunruhe is earlier in males than in females of both races (fig. 4). In general, experimentally induced fattening is substantially greater in gambelii than in pugetensis (see fig. 2; Lewis 1971). This correlates well with differences in distances and rates of migration between the two races. Fat deposition does not occur in the nonmigratory race Z. l. nuttalli and nocturnal activity occurs only to a limited extent (Mewaldt et al. 1964; Mewaldt et al. 1968). These differences in response are very similar to those that would be projected if photoperiodic information is assumed to be of primary importance in the control of the timing of these functions (Farner and Lewis 1971, 1972; Lewis 1971).

Previous experimental studies of vernal-type Zugunruhe have also suggested that environmental temperature affects the onset and intensity of Zugunruhe (for reviews see Eyster 1954; Kendeigh et al. 1960; Nisbet and Drury 1968). Eyster (1954), who studied three species of migratory finches, including two Z. l. leucophrys, found that Zugunruhe was inhibited by both extremely high and low temperatures. His limited data on Z. l. leucophrys revealed the greatest activity near 20°C; with increasing temperature to 33°C both nocturnal and diurnal activity was reduced. These results are similar to our own. The higher temperatures (33–35°C) at which migratory behavior in these several taxa of finches is seriously inhibited are considerably above the range experienced during the vernal migratory phase of the annual cycle. Thus, in effect, the induction of vernal migratory state would appear to be favored by warmer environmental temperatures under natural conditions.

The role of environmental temperature, like

that of other weather factors, in the initiation of migration is doubtless complex (see Lack 1960:30–34; Nisbet and Drury 1968). Nevertheless, a parsimonious and conservative evaluation of the available data on the environmental control of *Zugunruhe* and migration suggests that the White-crowned Sparrows are brought into vernal migratory state (*Zugdisposition*) primarily by photoperiodic information. In such a state the bird is sensitive to the stimuli that actually release and control migratory flights. The effect of photostimulation in altering the internal state of the bird is enhanced by relatively high temperatures within the range normally experienced by the birds during late winter and spring. The release of *Zugunruhe* under constant conditions, as in the present study, is probably spontaneous in the sense that photostimulation progressively increases motivation to the point where no specific external stimulus is necessary to release the behavior. In any event, it appears that photostimulation is both necessary and sufficient (Eyster 1954; Farner and Mewaldt 1955; Kendeigh et al. 1960) to produce vernal-type *Zugdisposition*, *Zugunruhe*, and migration in White-crowned Sparrows.

The thyroid gland. The increase in thyroid weight observed at 5.2 and 15.1°C is correlated with delayed onset of *Zugunruhe*. However, there was a lower rate of fattening and advanced onset of molt only at 5.1°C. Thyroid weight bore no clear relationship to the growth rate of gonads or oviducts. In *Z. l. gambelii*, thyroid activity is closely related to environmental temperature (Oakeson and Lilley 1957, 1960; Wilson and Farner 1960); there is little or no increase in thyroid activity during vernal migration (Oakeson and Lilley 1960; Wilson and Farner 1960). Stetson and Erickson (1971) found no change in thyroid weight as a result of photostimulation at 20°C. Wilson and Farner (1960) found no significant increase in thyroid activity of *Z. l. gambelii* males that were photostimulated at 26°C or 12°C relative to nonstimulated (short day) controls. Little is known about the relationship of thyroid weight and activity to ovarian development. Results of our investigation suggest, however, that if the thyroid plays a significant role in the control of ovarian growth and development, it does not do so during the slow (*i.e.*, previtellogenic) phase of growth.

SUMMARY

The results of a series of experiments indicate that environmental temperature has a slight, although significant, role in the control of the rate of photoperiodically induced vernal development of the testes of *Zonotrichia leucophrys gambelii*. However, our data give no reason to assume that it has any significant role as "predictive" information in the sense of day length. The amplitude of the daily cycle in environmental temperature per se appears not to be a significant source of information in the control of the rate of testicular growth.

In *gambelii* and *pugetensis*, environmental temperature appears to have no role in the control of the rate of development of the ovary up to the time of inception of vitellogenesis. If there is any direct modulation of the female gonadal cycle by ambient temperature, it occurs only during the culminative stages of ovarian development. The induction of vernal migratory state, as evidenced by the time of onset of *Zugunruhe* and the timing and extent of fattening, is favored by moderately high ambient temperature. Prenuptial or at least a prenuptial-like molt appears to be favored by low environmental temperature.

Our conclusions are tentative and do not preclude other indirect effects of winter and spring temperatures, or of short-term effects operating at or near the time of egg-laying. Nor do our data support or preclude possible indirect effects of ambient temperature in modifying the schedule of migration once under way.

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