ENDOCRINE RESPONSES TO INCLEMENT WEATHER IN NATURALLY BREEDING POPULATIONS OF WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS PUGETENSIS*)

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Abstract.—Plasma levels of luteinizing hormone (LH), testosterone, and corticosterone were measured in relation to periods of inclement versus fair weather during the reproductive season of the Puget Sound White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). In 1974, cool stormy weather in spring delayed the onset of breeding by one month and also prolonged the period of elevated circulating levels of LH and testosterone, compared with the fair spring of 1975. Inclement weather in 1974 did not appear to be stressful, as indicated by body weights and plasma levels of corticosterone. In late May 1980, however, a storm occurred after nesting activities had begun and all pairs sampled were feeding young. In this case, plasma levels of corticosterone were greatly elevated above those of birds sampled at the same time in the warm spring of 1979 and also above those of birds sampled in spring of both 1974 and 1975. In addition, fat depots were virtually exhausted in birds sampled during the storm of 1980, suggesting that these birds were stressed. Most pairs lost their brood in May 1980, presumably to starvation, and renested after amelioration of environmental conditions in June.

These data suggest that although storms may modify the onset and temporal progression of the reproductive cycle, they are stressful to adults only when the nesting phase is in progress. Thus, the underlying mechanisms by which inclement weather delays the onset of breeding or disrupts the nesting once underway are likely to have different endocrine bases. *Received 29 March 1982, accepted 31 August 1982.*

Aseasonal storms occasionally disrupt the nesting activity of birds that breed at higher latitudes and altitudes. For example, periods of unseasonably cold weather, prolonged precipitation, or storms may reduce the trophic resources available to Chaffinches (*Fringilla coelebs*) to an extent that adults cannot find sufficient food for themselves and their nestlings. The latter may die of starvation, or, in some cases, the nest may be damaged or destroyed (Newton 1964, 1973). In Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) aseasonal snowfall may cover food resources without destroying nests. Under these conditions, breeding pairs often abandon nests, and sometimes the territory, to forage widely. As conditions ameliorate and food is again available, they return to their territories and begin a second nesting effort (Morton et al., 1972, Morton 1976). In these instances, it is tempting to suggest that aseasonal storms somehow depress circulating levels of luteinizing hormone (LH) and sex steroid hormones, which regulate sexual and territorial behavior (e.g. Adkins-Regan 1981, Harding 1981; see also Wingfield and Farner 1980), and elevate plasma levels of corticosterone, which mobilizes energy reserves (see Holmes and Phillips 1976, Siegel 1980 for reviews).

Although renesting after the loss of a clutch or brood involves well-characterized endocrine changes (Donham et al. 1976, Wingfield and Farner 1979), the effects of inclement weather and the mechanisms through which it disrupts the nesting phase are by no means clear. Storms, concomitant decreases in ambient temperature, and restricted availability of food may be stressful, especially for individuals that are incubating or feeding young. Indeed, several laboratory investigations of reproductively mature birds have shown that a variety of stresses alter temporal patterns of secretion of LH, depress plasma levels of sex steroid hormones, and elevate circulating titers of corti-

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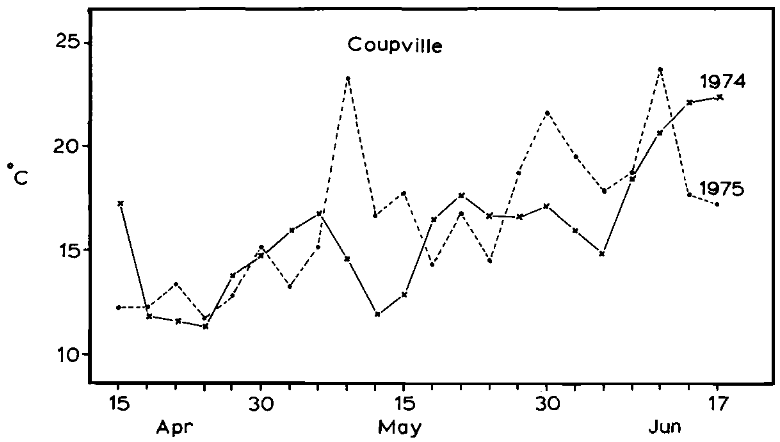

FIG. 1. Temperature data (3-day means) for Coupeville, Whidbey Island, Island County, Washington (from U.S. Environmental Data Service). Coupeville is approximately 10 km west of the study sites on Camano Island.

costerone (e.g. Wilson et al. 1979, Scanes et al. 1980, Wingfield 1980, Wingfield et al. 1982; see Holmes and Phillips 1976, Siegel 1980 for review). As far as we are aware, however, there have been no investigations of the endocrine responses of naturally breeding populations of birds to the stressful effects of aseasonal storms.

In this communication we report the effects of low ambient temperature and stormy weather on plasma levels of hormones and reproduction in free-living populations of the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*).

Materials and Methods

Study areas and field techniques.—Male White-crowned Sparrows were captured in mist nets and baited live traps in the vicinity of Seattle, Washington (48°N), on study sites on Camano Island (Island County) in 1974 and 1975 and near Hart's Lake (Pierce County) in 1979 and 1980. Results of investigations at the former site have been published previously (Wingfield and Farner 1977, 1978a).

Immediately after a bird was captured, a blood sample (approximately 400 μl) was removed from the alar vein into heparinized capillary tubes. Each bird was then banded, color marked, and weighed, and

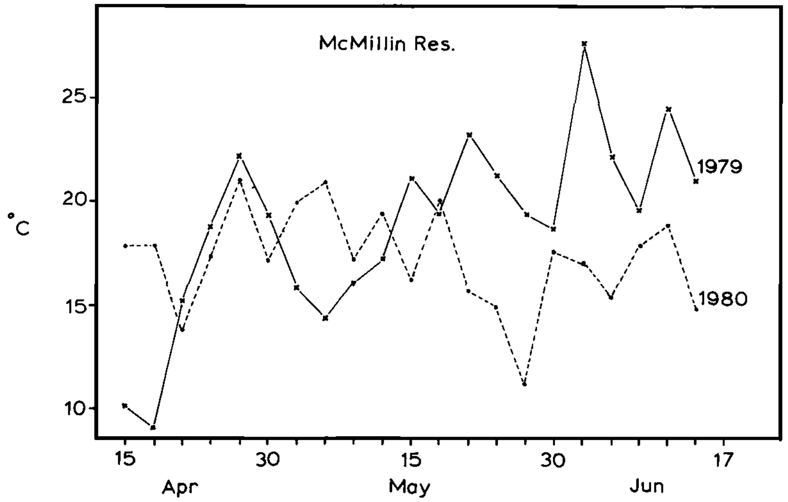

FIG. 2. Temperature data (3-day means) for McMillin Reservoir, Pierce County, Washington (from U.S. Environmental Data Service). McMillin Reservoir is approximately 25 km northeast of the study site at Hart's Lake.

TABLE 1. Breeding status in relation to weather of naturally breeding populations of White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*).

Year	Sample dates	Weather	Breeding activity
1974	30 April–20 May	Cold, heavy overcast, precipitation, frequent storms	Males on territory and paired, little further breeding activity
1975	30 April–20 May	Cool, sunny, no storms	Most females incubating
1974	20 May–6 June	Cold, heavy overcast and precipitation, frequent storms	Breeding delayed by storms, very few females with nests, little breeding activity
1975	20 May–6 June	Cool, sunny, no storms	All sampled pairs feeding nestlings First fledglings appear
1974	6 June–2 July	Warm and sunny	Feeding nestlings, first fledglings appear
1975	6 June–2 July	Warm and sunny	Nesting activity for second brood, incubation and feeding nestlings
1979	26 May–31 May	Warm and sunny	All sampled pairs feeding nestlings of fledglings
1980	27 May–30 May	Cold, heavy overcast and precipitation	All sampled pairs feeding nestlings or fledglings
1980	8 July–28 July	Warm and sunny	All samples pairs feeding nestlings or fledglings

its gonadal state was assessed during unilateral laparotomy (Wingfield and Farner 1976). In 1979 and 1980, estimates of subcutaneous fat depot in the furculum and abdomen were also made. All birds were then released for field observations and possible recapture. After centrifugation of blood samples in the field, the plasma samples were frozen on dry ice until returned to the laboratory where they were stored at −20°C until analyzed (Wingfield and Farner 1976).

Collection of samples in relation to weather.—In 1974 and 1975, blood samples were collected at least 4 days per week from mid-April to August as part of an investigation of the endocrine control of reproduction under natural conditions (Wingfield and Farner 1977, 1978a). The spring of 1974 (late April and May) was marked by continually inclement weather; heavy precipitation and strong winds (up to 60 km/h) prevailed in May, in contrast with the same period in 1975 (Fig. 1).

In 1979 and 1980, blood samples were collected at least 3 days per week from mid-April through early July as part of further investigations on the hormonal control of reproduction in birds (Moore and Wingfield 1980, Moore 1982). The springs of 1979 and 1980 (April–May) were mild, with no storms, and in both years breeding began in early May. In 1980, however, an intense storm accompanied by heavy precipitation occurred at the end of May, when most pairs were feeding nestlings or fledglings. Temperature data for McMillin Reservoir, 25 km northeast of Hart's Lake, are presented in Fig. 2.

Hormone assays.—Luteinizing hormone was measured by the double antibody, post-precipitation radioimmunoassay for avian LH as developed by Follett et al. (1972) and modified for use on plasma from Passeriformes by Follett et al. (1975). Plasma levels of testosterone were measured by the methods of Wingfield and Farner (1975), and corticosterone by a radioimmunoassay procedure following the chromatographic separation procedure described by Wingfield and Farner (1975). These assays have been used routinely in this laboratory for over 8 years (see Wingfield and Farner 1977, 1978a, b, 1980).

Statistics.—Differences between groups were determined by the Mann-Whitney *U*-test, one-tailed (Zar 1974).

RESULTS

As noted above, the ambient temperature was 5–10°C lower in early May 1974 than in 1975 (Fig. 1). Early May is usually the period of egg laying for the first clutch (Fig. 1, Table 1; see also, Wingfield and Farner 1977, 1978a). Temperatures in 1974 remained generally lower than those of 1975, except for a brief period in mid-May, and did not increase appreciably until June. This period of low temperature was accompanied by heavy overcast and frequent storms with precipitation (Table 1). In 1975 weather was generally sunny and without storms; all pairs studied were feeding nestlings or fledglings by early June. In 1974 breeding was delayed, with few females having nests by this time. Nestlings were not found until late June, and the first fledglings did not appear until 2 July 1974, in comparison with 4 June in 1975.

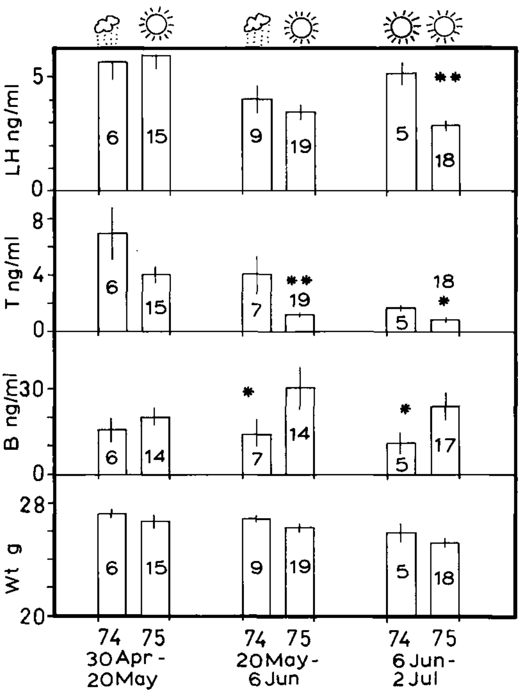

FIG. 3. Body weight, and plasma levels of LH, testosterone (T), and corticosterone (B) in male White-crowned Sparrows (*Z. l. pugetensis*) sampled during spring 1974 and 1975. The stylized rain cloud indicates the period of stormy weather, and the sun indicates periods of fair weather. Vertical lines are standard errors of means, and numbers within open bars indicate sample sizes. Asterisks indicate significant difference between 1974 and 1975, * = $P < 0.05$; ** = $P < 0.02$.

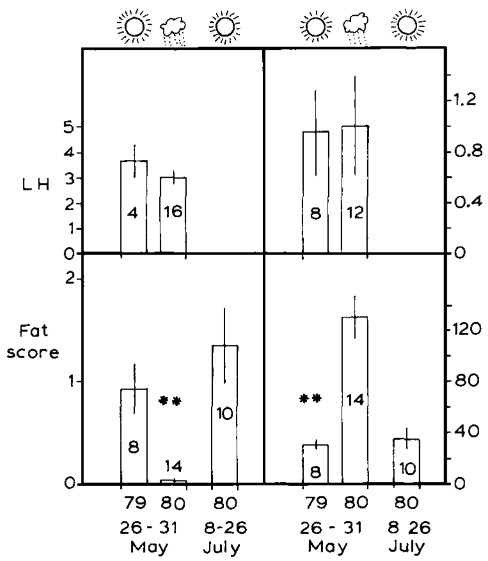

FIG. 4. Fat score and plasma levels of LH, testosterone (T), and corticosterone (B) in male White-crowned Sparrows (*Z. l. pugetensis*) sampled during spring and summer, 1979 and 1980. The stylized rain cloud indicates the period of stormy weather, and the sun indicates the periods of fair weather. Vertical lines are standard errors of means, and numbers within open bars indicate sample sizes. Asterisks indicate significant difference between 1979 and 1980, ** = $P < 0.001$.

There was a downward trend in both years in plasma levels of LH and testosterone in males from late April to June or July (Fig. 3), as is typical for White-crowned Sparrows through this period (Wingfield and Farner 1977, 1978a). Plasma levels of LH in males in June 1974 were higher than in males during the same period in 1975 ($P < 0.02$), and circulating levels of testosterone were also higher during May and June in 1974 ($P < 0.02$ and $P < 0.05$). Plasma levels of corticosterone had increased by late May and June 1975 when birds were feeding young ($P < 0.05$). There were no differences in body weight between the two years.

The weather in early spring in both 1979 and 1980 was warm and sunny, with temperatures usually remaining above 15°C (Fig. 2). In both years White-crowned Sparrows were feeding nestlings or fledglings by late May (Table 1). At this time in 1980, however, there was a precipitous decrease in temperature, to as low as 10°C below that recorded at the same time in 1979 (Fig. 2), accompanied by heavy overcast and precipitation (Table 1). In June, conditions ameliorated, temperatures remaining below those of 1979 but similar to those of June 1974 and 1975 (Fig. 1). During late May 1980, plasma levels of corticosterone were elevated greatly above those of birds sampled at the same time in 1979 and at the same stage of breeding ($P < 0.001$, Fig. 4). By July 1980, when birds were feeding nestlings of a second nesting attempt, corticosterone levels had declined ($P < 0.02$). Subcutaneous fat depots were virtually depleted in birds sampled during the storm of 1980 ($P < 0.001$) but were restored by July. No differences in plasma levels of LH and testosterone in males were observed between years.

Discussion

Abnormal weather conditions may delay the onset of breeding, despite the presence of functional or near functional gonads, or disrupt the nesting phase if breeding is already underway (for reviews see Marshall 1949, 1959; Lofts and Murton 1968; Farner and Lewis 1971; Newton 1973; Murton and Westwood 1977; Wingfield 1980; Wingfield and Farner 1980). Our results show that the delay in the onset of breeding caused by prolonged spring storms in 1974 was also accompanied by maintenance of elevated plasma levels of LH and testosterone, which normally decline from the initial spring peak during the onset of incubation and feeding of young (Wingfield and Farner 1977, 1978a, b). Thus, the extended period of elevated plasma levels of sex hormones in 1974 may have maintained sexual and territorial behavior so that nesting activities could begin immediately after amelioration of environmental conditions. The storms did not appear to stress the adult White-crowned Sparrows because plasma levels of corticosterone were lower than in birds sampled at the same time in 1975, when the birds were foraging intensively in order to feed young. Foraging to feed young itself may have been stressful, as suggested by the gradual increase in circulating levels of corticosterone in male *Z. l. pugetensis* during parental care (Wingfield and Farner 1977, 1978a). In 1980, however, the storm struck after the nesting phase had begun and was accompanied by a dramatic increase in plasma levels of corticosterone well above those measured in 1974 and 1975, and a decrease in subcutaneous fat depots, suggesting that these birds were stressed. Curiously, plasma levels of LH and testosterone were unaffected, probably because these levels had already declined from the initial spring peak (see Wingfield and Farner 1977, 1978a). Furthermore, these birds remained on territory (or at least in the immediate area) throughout the period of inclement weather, although nesting was generally unsuccessful, as no fledglings were observed until after a second nesting attempt in June and July.

The different endocrine responses to storms in 1974 and 1980 suggest the following explanation: If an unseasonable storm occurs early in spring, the onset of breeding is delayed even though the gonads may be functional or near functional, and plasma levels of LH and testosterone in males remain generally high. The effects of the storm do not appear to be stressful, because there are no young that require extra foraging by the adults. If storms and low temperatures occur late in spring during parental care, however, trophic resources decline at a time when both adults and a brood of young must be fed. In this case, the storm is stressful, as indicated by increases in plasma levels of corticosterone and depletion of fat stores. Thus, the underlying mechanisms by which inclement weather delays the onset of breeding or disrupts the nesting phase once underway are likely to have different endocrine bases.

Whether storms influence endocrine function through a direct effect of, for example, low temperature or an indirect effect on food resources has been a matter of conjecture (Wingfield 1980, Wingfield et al. 1982). In domestic birds low temperatures tend to depress testis growth (e.g. Huston 1975) and disrupt ovulatory cycles (e.g. Riddle and Honeywell 1924), even though food and water are provided *ad libitum*. Similar treatment also produces an elevation of circulating levels of corticosterone (Nir et al. 1975, Jeronen et al. 1976, Beuving and Vonder 1978). Low environmental temperature, however, has only a slight effect on photoperiodically induced gonadal growth in feral species (for review of early literature see Marshall 1949, see also Lewis and Farner 1973), on plasma levels of LH or testosterone, or on circulating levels of corticosterone in male *Z. l. gambelii* (Wingfield 1980, Wingfield et al. in press). Moreover, Rowan (1925) showed that male Dark-eyed Juncos (*Junco hyemalis*) housed in outdoor aviaries (in Alberta, Canada) under artificial long days and with free access to food developed functional gonads and came into full song in December, when ambient temperatures were as low as −47°C. Similarly, feral populations of crossbills (*Loxia curvirostra* and *L. leucoptera*) can breed at any time of the year if cone crops of pines (*Pinus* sp.), larches (*Larix* sp.), and spruce (*Picea* sp.) are sufficient (Bailey et al. 1953, Tordoff and Dawson 1965, Newton 1973).

Thus, if birds have free access to food, low environmental temperature appears to have little effect on reproductive function in feral species. Inanition can have rapid and dramatic effects on reproductive function, however, in both domesticated and feral avian species. For example, varying degrees of food restriction result in gonadal atrophy, decreased plasma levels of LH and testosterone, and increased concentrations of corticosterone (e.g. Assenmacher et al. 1965, Assenmacher 1973, Erb et al. 1978, Wilson et al. 1979, Harvey et al. 1980, Scanes et al. 1980, Wingfield 1980; R. A. Lewis, P. W. Mattocks, J. C. Wingfield, and D. S. Farner unpubl. results). Although low temperatures may result in more rapid depletion of energy stores, especially for nocturnal thermoregulation and for the feeding or brooding of young, these stores can be easily replaced if sufficient food is available (Ketterson and King 1977). Thus, it seems likely that inclement weather is stressful during breeding because it depresses food resources, especially in species such as the White-crowned Sparrow, which feeds its young almost entirely on insects.

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Literature Cited

Adkins-Regan, E. 1981. Hormone specificity, androgen metabolism, and social behavior. Amer. Zool. 21: 257–271.

Assenmacher, I. 1973. Reproductive endocrinology: the hypothalamo-hypophysial axis. Pp. 158–191 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., National Academy of Sciences.

———, A. Tixier-Vidal, & H. Astier. 1965. Effets de la sous-alimentation et du jêune sur la gonadostimulation du Canard. Ann. Endocrinol. (Paris) 26: 1–26.

Bailey, A. M., R. J. Niedrach, & A. L. Bailey. 1953. The Red Crossbills of Colorado. Publ. Denver Mus. Nat. Hist. 9: 1–64.

Beuving, G., & G. M. A. Vonder. 1978. Effect of stressing factors on corticosterone levels in the plasma of laying hens. Gen. Comp. Endocrinol. 35: 153–159.

Donham, R. S., C. W. Dane, & D. S. Farner. 1976. Plasma luteinizing hormone and the development of ovarian follicles after loss of clutch in female Mallards (*Anas platyrhynchos*). Gen. Comp. Endocrinol. 29: 152–155.

Erb, R. E., A. N. de Andrade, & J. C. Rogler. 1978. Interrelationships between diet and elevated temperatures (cyclic and constant) on concentrations of progesterone, estradiol-17B, and testosterone in blood plasma of laying hens. Poultry Sci. 57: 1042–1051.

Farner, D. S., & R. A. Lewis. 1971. Photoperiodism and reproductive cycles in birds. Pp. 325–370 *in* Photophysiology, vol. 6 (A. C. Giese, Ed.). New York, Academic Press.

Follett, B. K., C. G. Scanes, & F. J. Cunningham. 1972. A radioimmunoassay for avian luteinizing hormone. J. Endocrinol. 52: 359–378.

———, D. S. Farner, & P. W. Mattocks, Jr. 1975. Luteinizing hormone in the plasma of White-crowned Sparrows, *Zonotrichia leucophrys gambelii*, during artificial photostimulation. Gen. Comp. Endocrinol. 26: 126–134.

Harding, C. H. 1981. Social modulation of circulating hormone levels in the male. Amer. Zool. 21: 223–232.

Harvey, W. N., B. J. Merry, & J. G. Phillips. 1980. Influence of stress on the secretion of corticosterone in the duck (*Anas platyrhynchos*). J. Endocrinol. 87: 161–171.

Holmes, W. N., & J. G. Phillips. 1976. The adrenal cortex of birds. Pp. 293–420 *in* General, comparative and clinical endocrinology of the adrenal cortex (I. Chester-Jones and I. W. Henderson, Eds.). New York, Academic Press.

Huston, T. M. 1975. The effects of environmental temperature on fertility of the domestic fowl. Poultry Sci. 54: 1180–1183.

Jeronen, E., P. Isometsa, R. Hissa, & A. Pyornila. 1976. Effects of acute temperature stress on the plasma catecholamine, corticosterone and metabolite levels in the pigeon. Comp. Biochem. Physiol. 55C: 17–22.

Ketterson, E. D., & J. R. King. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). Physiol. Zool. 50: 115–129.

Lewis, R. A., & D. S. Farner. 1973. Temperature modulation of photoperiodically induced vernal phenomena in White-crowned Sparrows (*Zonotrichia leucophrys*). Condor 75: 279–286.

Lofts, B., & R. K. Murton. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool. London 155: 327–394.

Marshall, A. J. 1949. Weather factors and spermatogenesis in birds. Proc. Zool. Soc. 119: 711–716.

———. 1959. Internal and environmental control of breeding. Ibis 101: 456–478.

Moore, M. C. 1982. Hormonal response of free-living male White-crowned Sparrows to experimental manipulation of female sexual behavior. Horm. Behav. 16: 323–329.

———, & J. C. Wingfield. 1980. Hormone-behavior interactions during reproduction in White-crowned Sparrows (*Zonotrichia leucophrys*). Amer. Zool. 20: 788.

MORTON, M. L. 1976. Adaptive strategies of *Zonotrichia* breeding at high latitude or high altitude. Pp. 322–336 *in* Proc. 16th International Ornithological Congress (J. H. Frith and J. H. Calaby, Eds.). Canberra, Australian Acad. Sci.

———, J. L. HORSTMAN, & J. M. OSBORN. 1972. Reproductive cycle and nesting success of the mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. Condor 74: 152–163.

MURTON, R. K., & N. J. WESTWOOD. 1977. Avian breeding cycles. Oxford, Clarendon Press.

NEWTON, I. 1964. The breeding biology of the Chaffinch. Bird Study 11: 47–68.

———. 1973. Finches. New York, Taplinger.

NIR, I., D. YAM, & M. PEREK. 1975. Effects of stress on the corticosterone content of the blood plasma and adrenal gland of intact and bursectomized *Gallus domesticus*. Poultry Sci. 54: 2101–2110.

RIDDLE, O., & H. E. HONEYWELL. 1924. Studies on the physiology of reproduction in birds. XVIII. Effects of the onset of cold weather on blood sugar and ovulation rate in pigeons. Amer. J. Physiol. 67: 337–345.

ROWAN, W. 1925. Relation of light to migration and development changes. Nature 115: 494–495.

SCANES, C. G., G. F. MERRILL, R. FORD, P. MAUSER, & C. HOROWITZ. 1980. Effects of stress (hypoglycemia, endotoxin, and ether) on the peripheral circulating concentration of corticosterone in the domestic fowl (*Gallus domesticus*). Comp. Biochem. Physiol. 66C: 183–186.

SIEGEL, H. S. 1980. Physiological stress in birds. BioScience 30: 529–534.

TORDOFF, H. B., & W. R. DAWSON. 1965. The influence of day length on reproductive timing in the Red Crossbill. Condor 67: 416–422.

WILSON, E. K., J. C. ROGLER, & R. E. ERB. 1979. Effect of sexual experience, location, malnutrition and repeated sampling on concentrations of testosterone in blood plasma of *Gallus domesticus* roosters. Poultry Sci. 58: 178–186.

WINGFIELD, J. C. 1980. Fine temporal adjustment of reproductive functions. Pp. 367–389 *in* Avian endocrinology (A. Epple and M. H. Stetson, Eds.). New York, Academic Press.

———, & D. S. FARNER. 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. Steroids 26: 311–327.

———, & ———. 1976. Avian endocrinology—field investigations and methods. Condor 78: 570–573.

———, & ———. 1977. Zur Endokrinologie einer brutenden Population von *Zonotrichia leucophrys pugetensis*. Vogelwarte 29: 25–32.

———, & ———. 1978a. The endocrinology of a natural population of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). Physiol. Zool. 51: 188–205.

———, & ———. 1978b. The annual cycle of plasma irLH and steroid hormones in feral populations of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. Biol. Reprod. 19: 1046–1056.

———, & ———. 1979. Some endocrine correlates of renesting after loss of clutch or brood in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. Gen. Comp. Endocrinol. 38: 322–331.

———, & ———. 1980. Control of seasonal reproduction in temperate zone birds. Prog. Reprod. Biol. 5: 62–101.

———, J. P. SMITH, & D. S. FARNER. 1982. Endocrine responses of White-crowned Sparrows, *Zonotrichia leucophrys*, to environmental stress. Condor 88: 399–409.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice Hall.