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SEASONAL AND AGE-RELATED CHANGES IN PLASMA TESTOSTERONE LEVELS IN MOUNTAIN WHITE-CROWNED SPARROWS[1]

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Abstract. Plasma levels of testosterone (T) were measured by radioimmunoassay in Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) males of known age and natural history during four consecutive reproductive seasons in the Sierra Nevada of California. Because nesting occurred comparatively early in all of these seasons and mean schedules varied by only 11 days, data were lumped to show the seasonal pattern of T. This pattern was unimodal with a maximum coinciding with the period of competition for territories and mates and with mate guarding. This was followed by a decrease toward a minimum that coincided with the period of parental care and, eventually, postnuptial molt. When these data were analyzed by stage of the reproductive season (rather than calendar date) and by age, two unexpected results emerged. First, T levels decreased significantly between the stages of nest building and laying. Female mates should have been fertilizable and soliciting copulations during both of these stages and intermale conflicts associated with mate guarding should have been frequent. In both situations, high T levels would be predicted by current paradigms. Second, T levels were considerably lower in yearling males than in older males prior to the laying stage. Reasons for this age-related difference are unknown but it was observed that yearling males tended in all comparison intervals to have lower body masses, shorter wings, and shorter testis and cloacal protuberance lengths than older males—they were smaller birds. Yearling males were also less successful in obtaining mates than older males but, once paired, reared just as many offspring.

Key words: Testosterone; hormones; reproductive cycles; age effects; Zonotrichia leucophrys; *altitude.*

INTRODUCTION

In recent years field endocrine studies have greatly expanded our understanding of how hormones interact with social and ecological factors to affect the timing, sequence, and frequency of reproductive activities. Among the more interesting data have been those obtained on plasma levels of the male sex steroid, testosterone (T). Several investigators have found that plasma T concentrations vary by an order of magnitude or more in seasonally breeding birds. These fluctuations can defy straightforward interpretation, but usually follow predictable patterns that can be related directly and causally to changes in territorial aggression and sexual behavior (see reviews by Wingfield and Ramenofsky 1985, Wingfield and Moore 1987, Wingfield et al. 1987). Maxima in T concentrations appear to be reliably associated with two important periods of male activity. First, they are high early in the season, coincident with frequent aggressive encounters among males striving to establish and maintain territories. Second, they are high when males are mate guarding. The latter escalation in T levels in mated males may be caused by an increase in encounters with neighbor males seeking access to the sexually receptive females that are being guarded. The increase in plasma T and guarding behavior may also be induced by stimuli received from soliciting females. For example, in both free-living and captive White-crowned Sparrows (*Zonotrichia leucophrys*), T levels of males were considerably increased when solicitation displays were prolonged in their mates by estrogen implants (Moore 1982, 1983). Under natural conditions the female-induced change in the male's hormones are thought to cause an increase in his aggressive behaviors including territorial defense and mate guarding (Moore 1984). Guarding itself can be linked closely to female solicitations of copulation (see review by Birkhead 1987). It should be noted that high T levels in males are required for normal sexual behavior, including copulation, in many species but not in all (Balthazart 1983, Crews and Moore 1986). In the male White-crowned Sparrow, for

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example, castrates exhibited mounting behavior when exposed to estrogenized, soliciting females (Moore and Kranz 1983).

T levels tend to be low during periods of parental care and social stability (Hegner and Wingfield 1987), but they can increase quickly such as when territorial boundaries are disturbed and a resident male is challenged by a conspecific (Wingfield 1985a). Loss of a nest also destabilizes the status quo and can cause T levels to escalate when renesting occurs and females cycle through another period of sexual activity. An important principle to emerge from these and other recent field studies is that concentrations of peripherally circulated hormones are highly labile and can change through nearly their full physiological range within minutes to hours (Harding and Follett 1979, Harding 1981, Wingfield 1985a).

Given the circumstances and complexities of hormone-behavior interactions alluded to above, it would seem axiomatic that accurate natural history information must accompany hormone data if the latter are to be reliably interpreted. We have tried to achieve this in the study, reported herein, of seasonal changes in T in *Z. l. oriantha* on their breeding grounds in the Sierra Nevada. This bird is an intracontinental migrant that winters primarily in Mexico and summers in subalpine meadows and riparian tracts in mountains of the western United States and Canada. The montane habitat utilized is usually above 2,500 m elevation but some summering populations are known from much lower locations (see King and Mewaldt 1987). Birds arrive at our Tioga Pass study area (elevation = 3,000 m ± 200 m) in May and leave in late September and early October. We started working on *Z. l. oriantha* at this location in 1968 (continuously since 1978) and data are reported from individuals of known age and reproductive histories.

In the study population, clutch initiations occur almost exclusively in June and July. Modal clutch size is four and usually only one brood is produced. In years of medium to light snowpack, nesting sites are readily available and *Z. l. oriantha* begin reproduction rather soon after their arrival at Tioga Pass (Morton et al. 1972, Morton 1978). Under such conditions one would expect that the maxima in plasma T associated with territorial disputes and with mate guarding would be temporally closely adjacent. In heavy snow years these events should be widely spaced because onset of nesting is held in abeyance while the birds wait for nesting sites. Thus, depending on snowpack, two distinctive seasonal patterns for plasma T levels in this population would be predicted, one tending to be unimodal and the other bimodal.

Age-related differences in T levels have now been reported for the Red-winged Blackbird, *Agelaius phoeniceus* (Beletsky et al. 1989). In this polygynous species, yearling males do not hold territories and their plasma T levels are lower than those of older, territory-holding males. Hormonal differences with age have not been noted in monogamous species such as the White-crowned Sparrow, however. Passerines with the latter type of mating system commonly breed at 1 year of age and appear to function, even in their first reproductive cycle, similarly to older birds. We had no expectations, therefore, that endocrine profiles of males would vary with age in *Z. l. oriantha.*

Although field endocrine studies have now been conducted during the breeding season on about two dozen species of wild birds, none of these has resided at high altitude and seldom, if ever, were individuals of known age. Since montane environments provide only a brief summer season, often with inequable weather conditions, we expect hormonal responses of birds of known age and histories breeding at such locations to provide much useful information on how environmental factors act in both the proximate and ultimate sense to control reproductive cycles and to affect their outcome.

METHODS

Detailed records on individuals have been kept on the study population since the summer of 1978 when we began routinely trapping and banding all birds on the study area. We have also attempted to find all nests and identify their owners. In most seasons we were dealing with 35 to 40 nesting pairs. Thus, a rich backlog of information was already in place when the endocrine studies began in 1985. In the four consecutive seasons that we obtained hormone data, 1985–1988, similar ecological conditions prevailed. Snowpack was moderate to light and no major storms sufficient to disrupt nesting occurred. Reproductive schedules, as measured by mean date of clutch initiations, varied by only 11 days. The mean dates were 15 June 1985, 23 June 1986, 12 June 1987, and 22 June 1988. Since schedules in this population can vary interannually by at

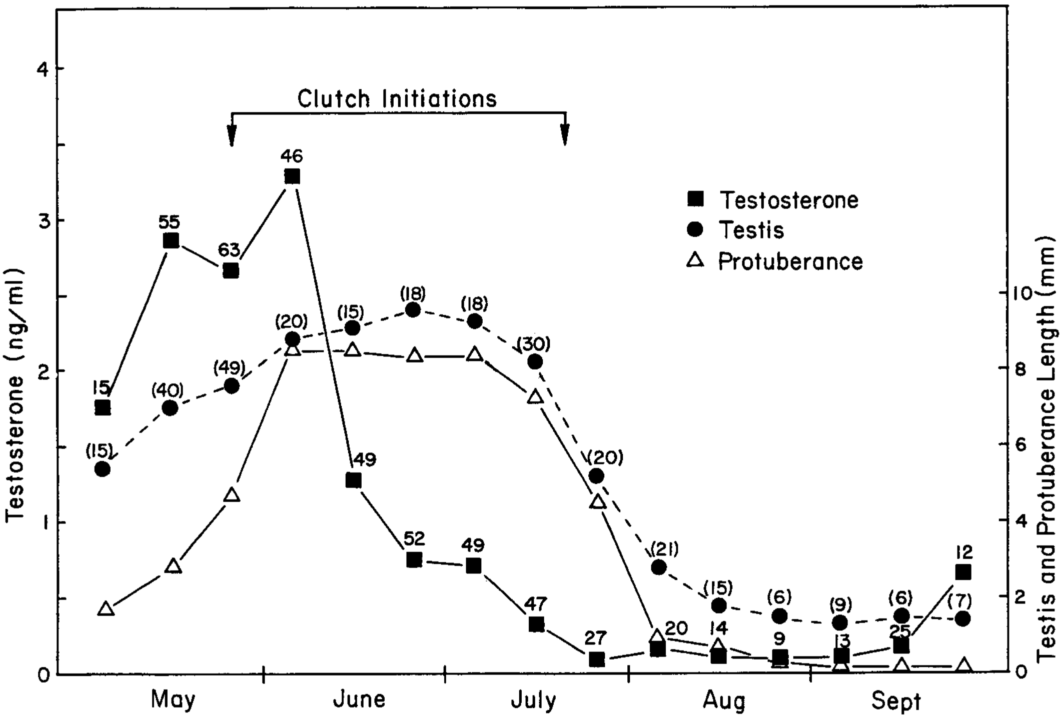

FIGURE 1. Seasonal pattern of plasma testosterone and testis and cloacal protuberance lengths in *Zonotrichia leucophrys oriantha* at Tioga Pass. Data are combined for the years 1985 to 1988. Sample sizes for testosterone means are without parentheses and those for testis and protuberance means are with parentheses. Arrows delimit the interval during which clutches were initiated.

least a month (Morton 1978), we felt justified in combining data from all four of these seasons when presenting information in this report.

Blood samples, taken from a wing vein into heparinized capillary tubes, were kept on ice for 1 to 4 hr and then centrifuged. Plasma (100 μl to 200 μl) was aspirated from the tubes and stored frozen until later analysis in the laboratory. Many individuals were sampled serially throughout the summer but usually at intervals of 1 week or longer. Cloacal protuberances were measured with a ruler to the nearest millimeter, as were left testis lengths during laparotomies. The latter were performed at 3-week intervals or longer on repetitively captured individuals. Wing length (relaxed chord) was measured to the nearest millimeter with a ruler and body mass to the nearest 0.1 g with a Pesola scale. Plasma T concentrations were measured by radioimmunoassay after separation of samples on celite : glycol columns. This technique effectively separates T from other steroids (see Wingfield and Farner 1975, 1976 for details). The mean recovery value for T was 63.2% (SD = 13.9%). LH was measured by the double-antibody radioimmunoassay of Follett et al. (1972).

Data are reported only for birds thought to be engaged in their first reproductive cycle of the season. We recognize that important changes in T regulation can occur during renesting, but our data on this phenomenon are too few to report at this time (see Wingfield 1988 for review).

RESULTS

The seasonal pattern of plasma T in *Z. l. oriantha* was essentially unimodal and involved large changes in titers (Fig. 1). For example, the mean concentration was 1.76 ng/ml in 15 males captured in early May soon after their arrival on the study area. This increased to 3.29 ng/ml by a month later when egg laying had commenced, then declined sharply to levels near 0.1 ng/ml until late September when it rose slightly to 0.66 ng/ml in 12 individuals just prior to their migration. This last mean increase was not quite significantly different from the immediately preceding mean ($t = 1.82$, $0.05 < P < 0.10$). Testis and cloacal protuberance lengths both increased through May, stayed at or near maximum through June and part of July, then decreased rapidly to minimal size and remained there (Fig. 1).

These data on seasonal trends, although interesting, do not adequately describe the functional relationships involved. To facilitate that purpose, we separated the data such that samples from males were defined as being in nine functionally distinct categories or stages. These were: (1) arrival—the day when birds were handled for the first time each season but confined to May captures only; (2) prenesting—included birds sampled after arrival but before their mates had begun building nests, must often have included individuals engaged in competition for mates and territories; (3) nest building—the mate was known to be building a nest or to have a nest completed but not yet laid in; (4) laying—the mate was laying, usually over a period of 4 days; (5) incubating—the time from clutch completion to hatching of the last egg, usually a span of 12 days; (6) with nestlings—chicks were present in the nest, usually a 9-day span; (7) with fledglings—period when young were out of the nest but still dependent, presumed to be until they were 21 days of age; (8) molting—beginning with dropping of the first primary and ending with completion of the postnuptial molt about 7 weeks later; (9) molt completed—birds were in fresh plumage, usually exhibiting premigratory fattening.

The pattern of plasma T levels resulting from this analysis (Fig. 2) resembled closely that already expressed in Figure 1. Of note, however, was that T concentrations decreased sharply between the stages of nest building and laying ($t = 6.79$, $P < 0.001$). A subsample of plasma from these birds was analyzed for LH concentration but there was no significant difference between them (nest building: LH = 3.1 ng/ml ± 0.8, $n = 5$; laying: LH = 3.3 ng/ml ± 1.3, $n = 12$; $P > 0.05$).

Intrigued by this information, we attempted to learn more about interstage changes by separating the data according to male age (Fig. 3). This showed that in the early stages of the season, old males (age = 2 years or older) tended to have higher T levels than young males (age = 1 year). During the nest-building stage, but no other, the difference was significant ($t = 2.38$, $P < 0.05$). Next, we analyzed our routinely taken field rec-

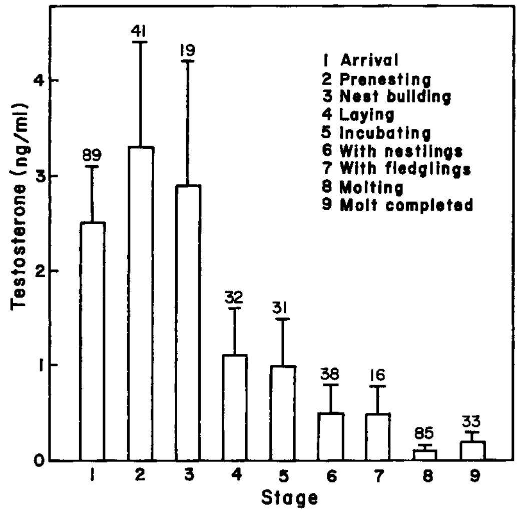

FIGURE 2. Mean plasma concentrations of testosterone in male *Zonotrichia leucophrys oriantha* according to functional stages. Lines extend 2 SE above the mean and numbers indicate sample sizes.

ords to see if other measurements varied with age. These showed that yearlings were smaller than older males. Their wings were shorter and their body mass was smaller (Table 1). Testes and cloacal protuberances of yearling males also tended to be shorter throughout the season than those of older males (Fig. 4). During the period of sexual activity, May through July, mean lengths for these organs were always lower in yearlings than in older males and according to a Mann-Whitney *U*-test, the difference was significant ($\alpha = 0.05$) for both testes and protuberances in five of the nine sample intervals. Analysis of our nesting records revealed that in those males known to be mated and have a nest there was no age-related difference in reproductive success, as measured by number of young fledged per season (Table 1). There was an age-related difference in ability to obtain a mate, however. Of 237 yearling males handled on our trapping rounds, 97 (41%) were known to have nests. Of 179 males aged 2 years or older, 101 (56%) were known to have nests. These differences were highly significant ($\chi^2 = 9.82$, $P < 0.005$).

DISCUSSION

When presented by calendar date, changes in plasma T concentrations associated with the reproductive cycle (Fig. 1) matched closely the pattern one would expect in a single-brooded, sea-

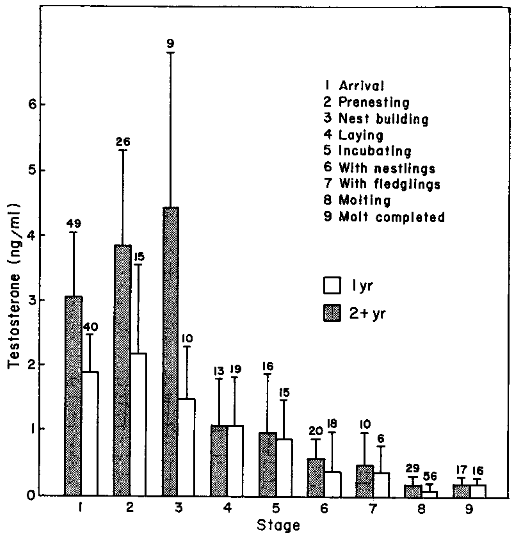

FIGURE 3. Mean plasma concentrations of testosterone in male *Zonotrichia leucophrys oriantha* according to functional stages and age. Lines extend 2 SE above the mean and numbers indicate sample sizes.

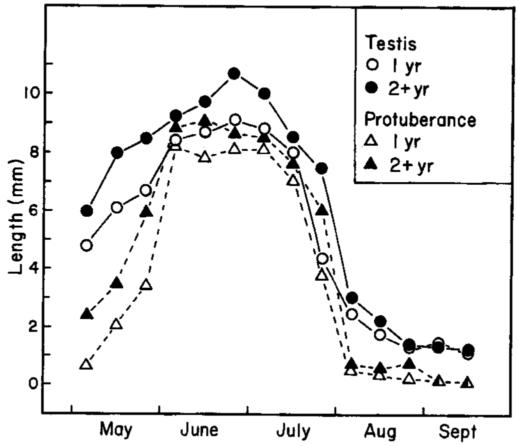

FIGURE 4. Seasonal pattern of testis and cloacal protuberance lengths in *Zonotrichia leucophrys oriantha* of known age. Data are combined for the years 1985 to 1988. Sample sizes for each of the plotted means varied between seven and 28 from May through July and between three and 14 in August and September.

sonally breeding migratory species experiencing no major perturbations induced by weather (see for example, Farner and Wingfield 1978, 1980; Moore 1982; Wingfield 1983, 1984a, 1984b, 1984c, 1985b; Wingfield and Farner 1978a, 1978b, 1979; Wingfield et al. 1983; Silverin 1984; Silverin et al. 1986). T levels were already elevated when the birds arrived at the breeding area. They increased thereafter and remained high for a period of time that coincided broadly with that of territorial establishment and defense and of mate guarding. They then declined in concert with the onset of the parental phase of reproduction (incubation, followed by the feeding of dependent young) and remained low through the period of postnuptial molt and premigratory fattening.

Interestingly, for the population, mean T levels decreased sharply even during the period of clutch initiations. Also, testis and cloacal protuberance lengths, although showing great seasonal changes, were not in phase with plasma T levels (Fig. 1). The latter was expected because plasma T levels usually increase and may even peak maximally during the early portion of testicular growth in both captive (Kerlan and Jaffe 1974, Moore 1982) and free-living birds (Wingfield and Farner 1979; Wingfield 1984a, 1985b). Thereafter T typically decreases and remains low and is mostly sequestered within the testis, in keeping with its role in spermatogenesis, but can be quickly secreted to the bloodstream in large quantities if the social climate is sufficiently disrupted such that prolonged aggressive interactions occur (Wingfield 1984a, 1985a).

T levels, when analyzed by functional relationships, were highest during the prenesting stage (Fig. 2). The temporal limits of data in this stage encompassed the period when territories were being established and stabilized. Later, during nest building, T remained high and this seems reasonable because males should have been mate guarding. The decrease in T immediately thereafter as females began laying was a distinct surprise, however. Laying females are fertilizable (Sturkie and Opel 1976) and should also be guarded by their mates in order to prevent cuckoldry. Furthermore, under existing paradigms, these guarding males should have high T levels (Moore 1982, 1983; Runfeldt and Wingfield 1985; Ball and Wingfield 1987; Wingfield et al. 1989). That they do not suggests to us that major changes in the social climate must have occurred at about the time nest construction ended. These changes might have involved decreases in solicitations by females and/or decreases in aggressive encounters with other males. There are indications in a few other studies that plasma T levels decreased in mated males before or during egg lay-

TABLE 1. Bodily measurements and reproductive success (number of young fledged/season) of male *Zonotrichia leucophrys oriantha.*

Age (years)	Wing length (mm)				Body mass (g)*				Young fledged			
	$\bar{x}$	SD	n	P	$\bar{x}$	SD	n	P	$\bar{x}$	SD	n	P
1	79.48	1.76	155	<0.001	27.31	0.14	219	<0.001	2.34	1.88	114	>0.05
2+	80.81	1.64	74		28.13	0.15	199		2.33	1.76	178	

* Includes only data collected prior to onset of postnuptial molt.

ing but sample sizes were small (Silverin and Wingfield 1982, Dawson 1983, Silverin 1983). There are also indications that the timing and frequency of copulations in pairs do not always match closely the presumed fertilizable period of the female. Copulations (and mate guarding) may cease entirely between a pair before clutch completion as in Black-billed Magpies, *Pica pica* (Birkhead 1982), and Zebra Finches, *Poephila guttata* (Birkhead et al. 1988a, 1988b), or even before egg laying actually begins as in Pied Flycatchers, *Ficedula hypoleuca* (Haartman 1951, Lundberg and Alatalo 1988, see also review by Birkhead et al. 1987). At this point we do not have enough reliable observations of behaviors or of functional capabilities related to fertility in either sex to warrant further speculation. It is worth noting, however, that paternity exclusion data indicate that cuckoldry is common in our study population (Sherman and Morton 1988). The lack of change in LH concentration in our data between nest-building and laying stages was expected. Several studies have shown that plasma LH and T do not covary seasonally (e.g., Wingfield and Farner 1978b; Dawson and Goldsmith 1982; Dawson 1983; Moore 1983; Silverin 1984; Wingfield 1984a, 1985b).

Another surprise in our data was that mated yearling males had lower T levels early in the season than mated older males. They also had smaller body masses and shorter wing, testis, and cloacal protuberance lengths. These differences had no effect on reproductive success of *mated* birds, as measured by number of young fledged per season. Initial success at obtaining a mate would seem to be the real problem facing young males since they were not as likely to accomplish this feat as older males.

We have no explanation for the lower T levels in young males at this time. More information needs to be obtained about male-male and male-female interactions that affect T patterns and that also vary in their potency with factors such as age and territory quality. We also need to know if age affects the basic physiological capacities involved in hormone synthesis, secretion, and clearance. For example, do testes undergoing hypertrophy for the first time, as in yearlings, have different secretory characteristics than those that are recrudescing, as in older birds?

To summarize these age-related phenomena: yearling males did not compete for mates as well as older males and they had lower T Levels than older males during the prenesting stage when this competition was presumed to occur. These T level differences persisted through the nest-building stage when males were presumed to be guarding their mates. Interestingly, previous paternity studies in this population showed that cuckolded males were older than those that were not cuckolded (Sherman and Morton 1988). During stages associated with parental care, T levels did not differ with age. Ability to fledge young also was not age related.

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LITERATURE CITED

Ball, G. F., and J. C. Wingfield. 1987. Changes in plasma levels of luteinizing hormone and sex steroid hormones in relation to multiple-broodedness and nest-site density in male starlings. Physiol. Zool. 60:191–199.

Balthazart, J. 1983. Hormonal correlates of behavior, p. 221–365. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], Avian biology. Vol. 7. Academic Press, New York.

Beletsky, L. D., G. H. Orians, and J. C. Wingfield. 1989. Relationships of steroid hormones and polygyny to territorial status, breeding experience, and reproductive success in male Red-winged Blackbirds. Auk 106:107–117.

BIRKHEAD, T. R. 1982. Timing and duration of mate-guarding in magpies *Pica pica*. Anim. Behav. 30: 277–283.

BIRKHEAD, T. R. 1987. Sperm competition in birds. Trends Ecol. Evol. 2:268–272.

BIRKHEAD, T. R., L. ATKIN, AND A. P. MOLLER. 1987. Copulation behaviour of birds. Behaviour 101: 101–138.

BIRKHEAD, T. R., J. PELLATT, AND F. M. HUNTER. 1988a. Extra-pair copulation and sperm competition in the Zebra Finch. Nature 334:60–62.

BIRKHEAD, T. R., K. CLARKSON, AND R. ZANN. 1988b. Extra-pair courtship, copulation and mate guarding in wild Zebra Finches *Taeniopygia guttata*. Anim. Behav. 36:1853–1855.

CREWS, D., AND M. C. MOORE. 1986. Evolution of mechanisms controlling mating behavior. Science 231:121–125.

DAWSON, A. 1983. Plasma gonadal steroid levels in wild starlings (*Sturnus vulgaris*) during the annual cycle and in relation to the stages of breeding. Gen. Comp. Endocrinol. 49:286–294.

DAWSON, A., AND A. R. GOLDSMITH. 1982. Prolactin and gonadotrophin secretion in wild starlings (*Sturnus vulgaris*) during the annual cycle and in relation to nesting, incubation, and rearing young. Gen. Comp. Endocrinol. 48:213–221.

FARNER, D. S., AND J. C. WINGFIELD. 1978. Environmental endocrinology and the control of annual reproductive cycles in passerine birds, p. 44–51. *In* I. Assenmacher and D. S. Farner [eds.], Environmental endocrinology. Springer-Verlag, Berlin.

FARNER, D. S., AND J. C. WINGFIELD. 1980. Reproductive endocrinology of birds. Annu. Rev. Physiol. 42:457–472.

FOLLETT, B. K., C. G. SCANES, AND F. J. CUNNINGHAM. 1972. A radioimmunoassay for avian luteinizing hormone. J. Endocrinol. 52:359–378.

HAARTMAN, L. VON. 1951. Successive polygamy. Behaviour 3:256–274.

HARDING, C. F. 1981. Social modulation of circulating hormone levels in the male. Am. Zool. 21: 223–231.

HARDING, C. F., AND B. K. FOLLETT. 1979. Hormone changes triggered by aggression in a natural population of blackbirds. Science 203:918–920.

HEGNER, R. E., AND J. C. WINGFIELD. 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male House Sparrows. Auk 104:462–469.

KERLAN, J. T., AND R. B. JAFFE. 1974. Plasma testosterone levels during the testicular cycle of the Red-winged Blackbird (*Agelaius phoeniceus*). Gen. Comp. Endocrinol. 22:428–432.

KING, J. R., AND L. R. MEWALDT. 1987. The summer biology of an unstable insular population of White-crowned Sparrows in Oregon. Condor 89:549–565.

LUNDBERG, A., AND R. V. ALATALO. 1988. Mate guarding in the polyterritorial Pied Flycatcher. Proc. XIX Int. Ornithol. Congr. (1986):428–434.

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.

MOORE, M. C. 1983. Effect of female sexual displays on the endocrine physiology and behaviour of male White-crowned Sparrows, *Zonotrichia leucophrys*. J. Zool. (Lond.) 199:137–148.

MOORE, M. C. 1984. Changes in territorial defense produced by changes in circulating levels of testosterone: a possible hormonal basis for mate-guarding behavior in White-crowned Sparrows. Behaviour 88:215–226.

MOORE, M. C., AND R. KRANZ. 1983. Evidence for androgen independence of male mounting behavior in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). Horm. Behav. 17:414–423.

MORTON, M. L. 1978. Snow conditions and the onset of breeding in the Mountain White-crowned Sparrow. Condor 80:285–289.

MORTON, M. L., J. L. HORSTMANN, AND J. 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.

RUNFELDT, S., AND J. C. WINGFIELD. 1985. Experimentally prolonged sexual activity in female sparrows delays termination of reproductive activity in their untreated mates. Anim. Behav. 33:403–410.

SHERMAN, P. W., AND M. L. MORTON. 1988. Extra-pair fertilizations in Mountain White-crowned Sparrows. Behav. Ecol. Sociobiol. 22:413–420.

SILVERIN, B. 1983. Population endocrinology and gonadal activities of the male Pied Flycatcher (*Ficedula hypoleuca*), p. 289–305. *In* S. Mikami, K. Homma, and M. Wada [eds.], Avian endocrinology: environmental and ecological perspectives. Japan Scientific Societies Press, Tokyo and Springer-Verlag, Berlin.

SILVERIN, B. 1984. Annual gonadotropin and testosterone cycles in free-living male birds. J. Exp. Zool. 232:581–587.

SILVERIN, B., AND J. C. WINGFIELD. 1982. Patterns of breeding behaviour and plasma levels of hormones in a free-living population of Pied Flycatchers, *Ficedula hypoleuca*. J. Zool. (Lond.) 198:117–129.

SILVERIN, B., P.-A. VIEBKE, AND J. WESTIN. 1986. Seasonal changes in plasma levels of LH and gonadal steroids in free-living Willow Tits *Parus montanus*. Ornis Scand. 17:230–236.

STURKIE, P. D., AND H. OPEL. 1976. Reproduction in the male, fertilization, and early embryonic development, p. 331–347. *In* P. D. Sturkie [ed.], Avian physiology. Springer-Verlag, New York.

WINGFIELD, J. C. 1983. Environmental and endocrine control of avian reproduction: an ecological approach, p. 265–288. *In* S. Mikami, K. Homma, and M. Wada [eds.], Avian endocrinology: environmental and ecological perspectives. Japan Scientific Societies Press, Tokyo and Springer-Verlag, Berlin.

WINGFIELD, J. C. 1984a. Environmental and endocrine control of reproduction in the Song Sparrow, *Melospiza melodia.* Gen. Comp. Endocrinol. 56: 406–416.

WINGFIELD, J. C. 1984b. Environmental and endocrine control of reproduction in the Song Sparrow, *Melospiza melodia.* Gen. Comp. Endocrinol. 56: 417–424.

WINGFIELD, J. C. 1984c. Influence of weather on reproduction. J. Exp. Zool. 232:589–594.

WINGFIELD, J. C. 1985a. Short-term changes in plasma levels of hormones during establishment and defense of a breeding territory in male Song Sparrows, *Melospiza melodia.* Horm. Behav. 19:174–187.

WINGFIELD, J. C. 1985b. Influences of weather on reproductive function in male Song Sparrows, *Melospiza melodia.* J. Zool. (Lond.) 205:525–544.

WINGFIELD, J. C. 1988. Changes in reproductive function of free-living birds in direct response to environmental perturbations, p. 121–148. *In* M. H. Stetson [ed.], Proceedings in life sciences. Springer-Verlag, New York.

WINGFIELD, J. C., G. F. BALL, A. M. DUFTY, JR., R. E. HEGNER, AND M. RAMENOFSKY. 1987. Testosterone and aggression in birds. Am. Sci. 75: 602–608.

WINGFIELD, J. C., AND D. S. FARNER. 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. Steroids 26:311–327.

WINGFIELD, J. C., AND D. S. FARNER. 1976. Avian endocrinology—field investigations and methods. Condor 78:570–573.

WINGFIELD, J. C., AND D. S. FARNER. 1978a. The endocrinology of a natural breeding population of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). Physiol. Zool. 51:188–205.

WINGFIELD, J. C., AND D. S. FARNER. 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.

WINGFIELD, J. C., AND D. S. FARNER. 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.

WINGFIELD, J. C., AND M. C. MOORE. 1987. Hormonal, social, and environmental factors in the reproductive biology of free-living male birds, p. 148–175. *In* D. Crews [ed.], Psychobiology of reproductive behavior. An evolutionary perspective. Prentice-Hall, Englewood Cliffs, NJ.

WINGFIELD, J. C., M. C. MOORE, AND D. S. FARNER. 1983. Endocrine responses to inclement weather in naturally breeding populations of White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*). Auk 100:56–62.

WINGFIELD, J. C., AND M. RAMENOFSKY. 1985. Testosterone and aggressive behavior during the reproductive cycle of male birds, p. 92–104. *In* R. Gilles and J. Balthazart [eds.], Neurobiology. Springer-Verlag, Berlin.

WINGFIELD, J. C., E. RONCHI, A. R. GOLDSMITH, AND C. MARLER. 1989. Interactions of sex steroid hormones and prolactin in male and female Song Sparrows, *Melospiza melodia.* Physiol. Zool. 62: 11–24.