PLASMA LEVELS OF PROLACTIN AND GONADOTROPINS DURING THE REPRODUCTIVE CYCLE OF WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS*)

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ABSTRACT.—Plasma concentrations of prolactin, LH, and FSH were measured in free-living pairs of *Zonotrichia leucophrys pugetensis* throughout the natural breeding season, and during a photoperiodically induced cycle of gonadal development and regression in both sexes of captive *Z. l. gambelii* under controlled conditions. In free-living male *Z. l. pugetensis* plasma levels of FSH, which correlate well with changes in testicular weight reported previously, are higher than in females. Although only females of this species incubate, maximal levels of prolactin are observed in both sexes during late incubation. This is consistent with observations in other avian species and suggestive of a role for prolactin in incubation and associated parental behavior. The temporal association of elevated FSH with high levels of prolactin in females may represent a mechanism for maturation of ovarian follicles for the next clutch in this race, which typically raises as many as 3 broods per season. In the laboratory study on *Z. l. gambelii*, prolactin secretion in both sexes appears to have been induced photoperiodically in the absence of other environmental stimuli associated with incubation. The time course and magnitude of plasma prolactin levels were similar in both sexes, although levels were considerably lower than values obtained from incubating birds during the field study. Plasma levels of LH and FSH in females increased rapidly in response to photostimulation and began to decline after one week, whereas in males the pattern of increase and decrease of both gonadotropins was more gradual. *Received 12 November 1985, accepted 6 October 1986.*

THE endocrine correlates of the various events of the annual cycle of the White-crowned Sparrow (*Zonotrichia leucophrys*) have been investigated extensively (for reviews see Farner 1980, Wingfield and Farner 1980). With the exception of prolactin, changes in circulating concentrations of the known reproductive hormones have been measured in feral birds. Among other roles in the control of the annual cycle, avian prolactin has been proposed to function in incubation, molt, and premigratory fattening (for reviews see Meier 1975, de Vlaming 1979, Dyachenko 1982, Goldsmith 1983). Seasonal changes in pituitary prolactin content have been reported in a number of passerine species, including *Zonotrichia leucophrys* (Meier and Farner 1964, Meier et al. 1965), *Z. albicollis* (Meier 1975), *Fringilla coelebs* (Dyachenko 1972, 1974a, 1977, 1982), and *Passer domesticus* (Dyachenko 1974b, 1982), although these changes are not necessarily reflected in changes in circulating levels of the hormone. Recently, however, prolactin has been measured under natural conditions in the plasma of two passerine species [European Starling (*Sturnus vulgaris*), Dawson and Goldsmith 1982, 1985; Pied Flycatcher (*Ficedula hypoleuca*), Silverin and Goldsmith 1983). In both cases high prolactin levels were associated temporally with parental behavior and with the concurrent regression of the reproductive system at the end of the breeding season.

We measured and compared plasma concentrations of prolactin in free-living male and female *Z. l. pugetensis* throughout the natural breeding season, and during a photoperiodically induced cycle of gonadal development and regression in captive *Z. l. gambelii* under controlled conditions. Circulating levels of luteinizing hormone (LH) and follicle-stimulating

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TABLE 1. Sample sizes, dates, and characteristics of stages of the reproductive cycle of female *Zonotrichia leucophrys pugetensis*. The total number of banded females was 28, from which we collected 57 blood samples that could be placed in one of the categories below. *n* is the sample size.

Group	Stage in cycle	*n*	Dates of sample
A[a]	Soon after arrival; may or may not be mated; follicles not yolky (=1 mm); no brood patch	3	3–30 Apr
B[a]	Follicles not yolky; follicular hierarchy beginning to develop	8	21 Apr–10 May
C[a]	Yolk deposition evident; probably still preoviposition; no brood patch	2	29 Apr
D	Oviposition; egg in oviduct or presence of large yolky preovulatory follicles; brood patches in various stages of development but not fully vascularized or edematous	7	29 Apr–20 May
E[b]	Incubating; frequently flushed from nest; brood patch fully vascularized and edematous	16	29 Apr–27 May
F[c]	Feeding nestlings; often seen foraging with mate or delivering food to nest; brood patch beginning to regress	7	21 May–20 June
G[c]	Mate is caring for fledglings from first brood while female prepares for next clutch; follicles previtellogenic; brood patch regressed	3	14–19 July
H	Laying second or third clutch	2	12–18 June
I	Incubating second or third clutch	5	26 June–14 July
J	Both members of pair feeding nestlings (as in F)	0	
K	Mate caring for fledglings (as in G) from second or third brood	0	
L[d]	Ovary regressed; brood patch dry and scaly; no sign of fledglings; molt not yet begun	3	16–18 July
M[d]	Early postnuptial molt of primary remiges	1	18 July

[a] For statistical analysis and presentation of data, female stages A–C were combined into a "preoviposition" group ($n = 13$).
[b] Stage E was divided into "early incubation" ($n = 11$) and "late incubation" ($n = 4$) groups.
[c] Stages F and G were combined into a "feeding young" group ($n = 10$).
[d] Stages L and M were combined into a "postnuptial molt" group ($n = 4$).

hormone (FSH) also were monitored as indicators of reproductive status and to reveal temporal relationships between levels of prolactin and gonadotropins.

METHODS

Field investigations on Zonotrichia leucophrys pugetensis.—The birds were from a breeding population in the vicinity of Hart's Lake (ca. 47°N, 123°W), Pierce Co., Washington. The study site was in an extensive clear-cut forest with a 7-yr regrowth composed primarily of Douglas fir, alder, grasses, and forbs, a type of habitat heavily populated by *Z. l. pugetensis*. The birds were captured with mist nets, mostly between 0500 and 1000, from 21 April, at the termination of vernal migration, to 19 July 1981. We employed the field methods described by Wingfield and Farner (1976). Within 10 min after capture a blood sample of 0.3–0.6 ml was drawn from a wing vein; the bird was then laparotomized to permit identification of sex and stage of development of gonads and reproductive tract, examined for development of brood patch or cloacal protuberance, banded with a numbered aluminum band supplied by the U.S. Fish and Wildlife Service and an individually distinctive combination of colored plastic leg bands, weighed, and released.

After centrifugation, plasma samples were frozen individually and maintained at −20°C until transported on dry ice by air to Bristol.

The reproductive status of each bird was established by one or more of the following criteria: (1) direct observation of stage of gonadal development via laparotomy; (2) observation of external characteristics, such as extent of development of incubation patch or cloacal protuberance; (3) observation of behaviors associated with reproductive function; and (4) inference of reproductive state on capture date from confirmed state at an earlier or later date, e.g. a female known to be incubating 10 days before capture and later seen foraging with young fledglings was presumed to have been feeding nestlings on the capture date. These observations permitted the establishment of reproductive stages for both sexes (Tables 1 and 2). Because breeding was not closely synchronized within the population, analysis of results on the basis of these stages was essential.

Laboratory studies on Zonotrichia leucophrys gambelii.—The experimental birds were captured with mist nets during autumnal migration in 1981 in the Sunnyside Game Refuge near Mabton (ca. 46°50'N, 120°W), Yakima Co., Washington. In Seattle they were held temporarily in large aviaries under natural conditions of ambient temperature and day length. On 2 December 1981 and 15 January 1982, 24 females and 17 males, respectively, were transferred, two of the same sex per cage, into small (40 × 26 × 22 cm)

TABLE 2. Sample sizes, dates, and characteristics of stages of the reproductive cycle of male *Zonotrichia leucophrys pugetensis*. The total number of banded males was 36, from which we collected 91 blood samples that could be placed in the categories below. *n* is the sample size.

Group	Stage in cycle	*n*	Dates of sample
N	In breeding area for up to 4 weeks; no evidence of arrival of females; numerous territorial encounters; small to medium cloacal protuberance	16	10–29 Apr
O	Female arrival; pairing observed or likely to have occurred; medium to large cloacal protuberance	21	27 Apr–11 May
P	Mated to ovipositing female (see Table 1, group D)	4	11–20 May
Q	Mated to incubating female; probably all first brood (see Table 1, group E)	6	11–19 May
R	No information on breeding status of mate, though 10 females known to be incubating at this time; all have large cloacal protuberance	5	20–28 May
S[a]	Feeding nestlings; probably all first brood (see Table 1, group F)	5	19 May–3 June
T[a]	Caring for fledglings (see Table 1, group G)	3	12 June–19 July
U	Mated to female laying second or third clutch (see Table 1, group H)	1	3 June
V	No information on status of mate; breeding activity of population is highly asynchronous at this time; most males are "wanderers" captured while intruding on known territories, although no territorial encounters were observed; usually never seen or caught again	24	3–28 June
W	Known or presumed to be mated, though no sign of fledglings; molt not yet begun	4	14–18 July
X	Early postnuptial molt of primary remiges (see Table 1, group M)	2	16–18 July

[a] For statistical analysis and presentation of data, male stages S and T were combined into "feeding young" group ($n = 8$).

cages in two constant-condition environmental chambers at 20°C and 55% relative humidity. Light was provided from fluorescent lamps at an intensity of not less than 400 lux at the floor of each cage. The initial photoregime was 8L:16D, which is nonstimulatory to the hypothalamo-hypophysio-gonadal axis (Farner and Lewis 1971). Food (Purina Startena) and water were available *ad libitum*. On 16 January (females) and 14 February (males) (day 1 of the experiment) the photoregime was changed to 20L:4D. Beginning on day −7 (females) or day −6 (males), and at intervals of 10–12 days for 90–94 days, a blood sample was drawn from each bird between 1200 and 1700 (females) or 1000 and 1500 (males) as described above. We made no quantitative observations on gonadal growth and molt because these had been well documented previously for this photoregime (e.g. Farner and Wilson 1957; Farner et al. 1966; Kern 1970, 1972; Farner and Lewis 1971, 1973).

Statistics.—For the field investigation on *Z. l. pugetensis*, heterogeneity in hormone levels throughout the sampling period was tested by the Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956). To identify significant differences between breeding stages selected a priori for each sex, we used Dunn's multiple-comparison test, which is based on Kruskal-Wallis rank sums (Siegel 1956). To test for significant differences in plasma levels of FSH among groups of males selected a posteriori, we employed the Mann-Whitney *U*-test (Bruning and Kintz 1968). Using LH levels and testicular weights taken from an earlier study (1974) on the same population (Wingfield and Farner 1978), Spearman rank-order correlations (Bruning and Kintz 1968) were computed between levels of LH and FSH and between testicular weight and levels of both LH and FSH during comparable breeding stages of males. Data also were analyzed as a function of time of day at which the samples were drawn.

Data from the laboratory investigation on *Z. l. gambelii* were analyzed initially by the Kruskal-Wallis one-way analysis of variance by rank (Klugh 1974). To detect significant differences in direction of change between hormone levels on consecutive sampling dates, we employed the Wilcoxon sign test (Bruning and Kintz 1968).

Radioimmunoassays.—The methods employed were described in detail by Hiatt (1983). LH was measured by the homologous chicken LH assay described by Follett et al. (1972) as adapted for use on plasma samples of *Z. leucophrys* by Follett et al. (1975). FSH was assayed by a heterologous system based on that described by Hendrick et al. (1971), subsequently modified by Follett (1976) and Croix et al. (1974) and adapted for use on samples from *Z. leucophrys* (Wingfield et al. 1980). This method utilizes an antiovine FSH antiserum and iodinated FSH (NIADDK preparation I-1). The radioimmunoassay for prolactin, also a heterologous method, was that of McNeilly et al. (1978), as modified by Goldsmith and Hall (1980). The validity of the current avian prolactin radioimmunoassays is still a subject for discussion (e.g. El Halawani et al. 1984), but in a recent direct comparison, a close agreement was found between the heterologous assay and a homologous turkey prolactin radioimmunoassay (Burke and Papkoff 1980) in mea-

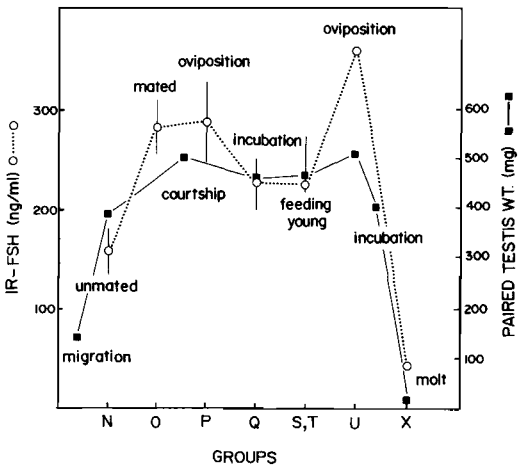

Fig. 1. Plasma levels of immunoreactive follicle-stimulating hormone (ir-FSH; ng/ml ± SEM) and testicular weights (from Wingfield and Farner 1978) of male *Zonotrichia leucophrys pugetensis* during the breeding season. The labels "oviposition" and "incubation" refer to plasma samples collected from males during periods when their mates were engaged in oviposition or incubation, respectively. Group designations (N-X) refer to stages in cycle in males from Table 2.

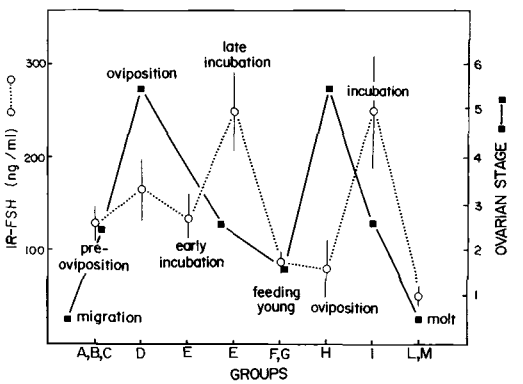

Fig. 2. Plasma levels of ir-FSH (ng/ml ± SEM) in relation to ovarian stage (from Wingfield and Farner 1978) of female *Zonotrichia leucophrys pugetensis* during the breeding season. Ovarian stages: 1 = follicles 0.5 mm in diameter; 2 = 0.5–1.0 mm; 3 = 1–2 mm; 4 = 3–5 mm, vitellogenic; 5 = 5 mm, about to ovulate; 6 = egg in oviduct, recently ovulated follicle apparent. Group designations (A-M) refer to stages in cycle in females from Table 1.

surements of samples from breeding Spotted Sandpipers (*Actitis macularia;* Oring et al. 1986). For the present study plasma samples and pituitary extracts from White-crowned Sparrows produced dilution curves that were parallel to that of the ovine prolactin standard.

Duplicate 20-μl plasma samples were measured in each of the three assay systems. The results are expressed in terms of the standard hormone preparations: chicken LH fraction IRC2, NIADDK rat FSH RP1, and NIADDK ovine prolactin P-S12.

Results

Field investigations on Zonotrichia leucophrys pugetensis.—Plasma concentrations of FSH in males (Fig. 1, stage N), upon their arrival in the breeding area in early April, were already elevated ($P < 0.05$, compared with postbreeding levels). According to earlier observations, males at this time are in the early stages of testicular development and have very small or undetectable cloacal protuberances (Lewis 1975b, Wingfield and Farner 1978). By the time maximal testicular weight was attained, when the females had arrived and courtship had begun, plasma FSH in the males had increased further ($P < 0.05$), and levels remained high during courtship, laying of the first clutch, incubation of the eggs, and feeding of the young. The particularly high FSH concentration in the one male caught while his mate was laying a second clutch (Fig. 1, stage U) suggests levels may increase again at this time, but concentrations had declined markedly by the time of the postnuptial molt (stage X). In Fig. 1 the mean plasma levels of FSH are compared with testicular weights determined in an investigation on birds in the same population in 1974 (Wingfield and Farner 1978). A Spearman rank-order correlation indicated a statistically significant relationship between testicular weight and FSH ($r_s = 0.94$, $P < 0.05$), but not LH ($r_s = 0.83$, $P = 0.1$). No significant correlation was found between LH and FSH concentrations ($r_s = 0.77$, $P > 0.1$).

Plasma levels of FSH in the females were generally higher from the time of arrival on the breeding grounds and throughout the breeding season than during postnuptial molt (Fig. 2). Concentrations were in fact highest during the incubation periods of the first and second clutches ($P < 0.05$, compared with mean level during molt), when the ovaries are known to be partially regressed (Wingfield and Farner 1978). For most of the breeding season, apart from incubation, FSH concentrations were about twice as high in male *Z. l. pugetensis* as in females (Figs. 1 and 2).

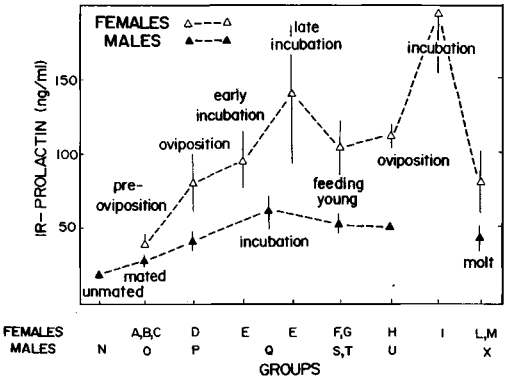

Fig. 3. Plasma levels of immunoreactive prolactin (ir-PRL; ng/ml ± SEM) of male and female *Zonotrichia leucophrys pugetensis* during the breeding season. Group designations refer to stages in cycle in females (A–M) from Table 1, and in males (N–X) from Table 2.

Prolactin concentrations (Fig. 3) increased steadily in the plasma of birds of both sexes during the early part of the breeding season, reaching highest values during incubation ($P < 0.05$, compared with prebreeding levels). Levels remained high in the females during the second nesting cycle, with the highest concentrations occurring during the second incubation phase. Prolactin levels were consistently about twice as high in females as in males.

Laboratory investigations on Zonotrichia leucophrys gambelii.—In males plasma levels of LH increased relatively more rapidly than those of FSH (Fig. 4). Both reached maxima between 30 and 45 days, declining thereafter, as an effect of photorefractoriness, to initial levels. The increase in circulating concentrations of prolactin either was delayed or occurred very slowly during at least two weeks after the onset of photostimulation. Levels were significantly ($P < 0.001$) elevated after 45 days, and maximal concentrations occurred between 45 and 65 days of photostimulation. Prolactin concentrations had decreased slightly by 90 days of photostimulation but were still significantly higher ($P < 0.05$) than at the onset of photostimulation (Fig. 4).

Plasma levels of LH and FSH of females increased more rapidly after onset of photostimulation than did those of males (Figs. 4 and 5). Maxima occurred at about one week, whereafter they declined to initial levels by the end of the experiment. Presumably, the early decreases in levels of these two hormones reflect the absence in cages of essential supplementary nonphotoperiodic information (e.g. presence of territorial male, availability of nesting materials; see Farner 1964, Wingfield and Farner 1980). In contrast to the higher levels of FSH measured in males relative to females in the field investigation on *Z. l. pugetensis*, FSH levels in females were somewhat higher than in males in the laboratory study. Otherwise, the temporal course of increase and subsequent decrease in plasma levels of both gonadotropins in females was generally similar to that in males (Fig. 4). Prolactin concentrations in the females showed changes similar to those of males. Levels remained low for the first 17 days, increased significantly by 28 days ($P < 0.01$), and reached maximal levels after 50–70 days of photostimulation ($P < 0.001$, compared with levels before onset of photostimulation). Compared with the males, however, the females showed a more pronounced decline in prolactin concentration ($P < 0.01$) at the end of the experiment.

DISCUSSION

In view of the known role of FSH in the development and maintenance of testicular size in birds, it is not surprising that the plasma levels of this hormone in *Zonotrichia leucophrys pugetensis* (Fig. 1) correlate well with the temporal course of testicular weight during the breeding season as reported by Wingfield and Farner (1978) for the same population. Because of small sample sizes, however, adequate documentation was possible only during the first of two or three broods that this subspecies may produce over a breeding season. We observed higher levels of FSH in males, in comparison with females, in the breeding season as reported by Dawson and Goldsmith (1982) for *Sturnus vulgaris* and by Silverin and Goldsmith (1983) for *Ficedula hypoleuca*. The same sex difference in FSH concentration also applies to at least some galliform and anseriform birds (Follett 1976, Goldsmith 1982a, Hissa et al. 1983, Dittami et al. 1985).

The attainment of maximal levels of prolactin in both sexes of *Z. l. pugetensis* during late incubation is consistent with observations on other passerine birds [*Ficedula hypoleuca*, Silverin and Goldsmith 1983; *Sturnus vulgaris*, Daw-

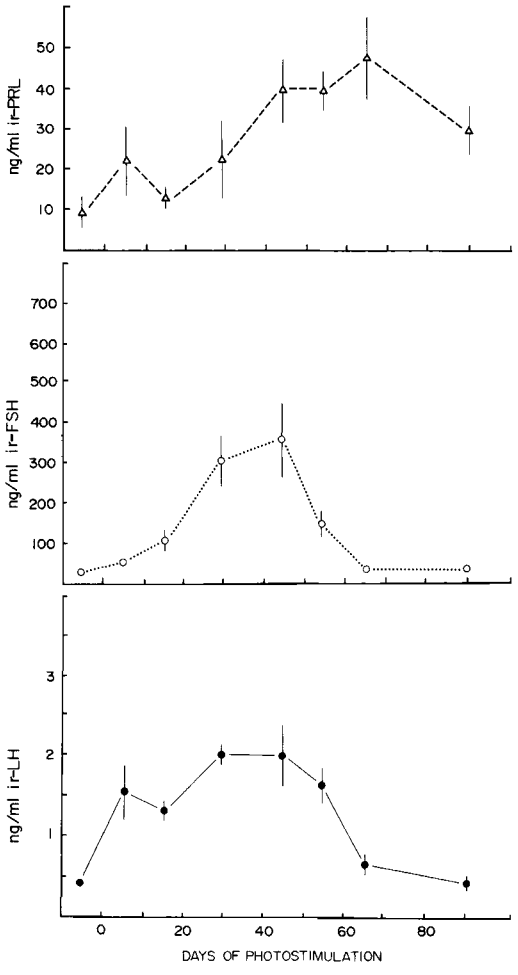

Fig. 4. Plasma levels of ir-PRL, ir-FSH, and immunoreactive LH (ir-LH) (ng/ml ± SEM) following changes in photoregime from 8L:16D to 20L:4D in photosensitive male *Zonotrichia leucophrys gambelii.*

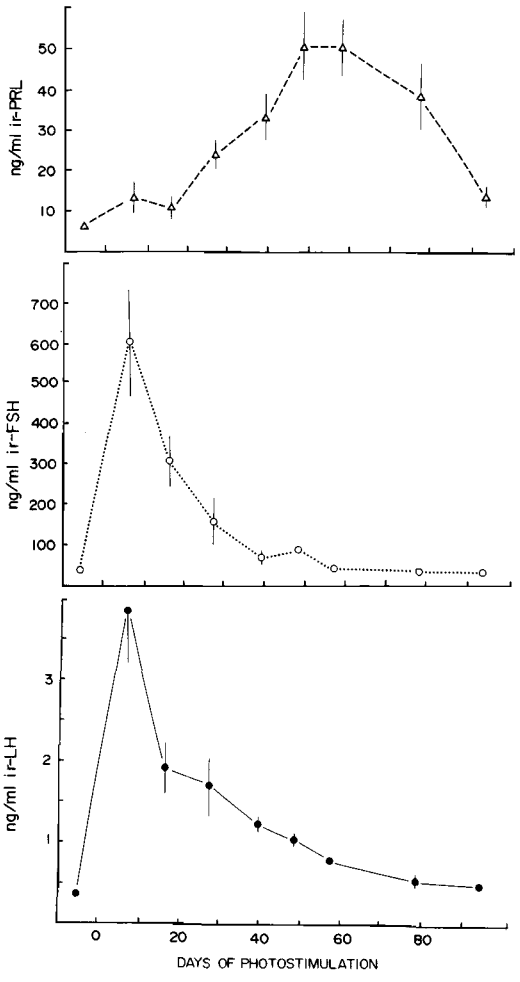

Fig. 5. Plasma levels of ir-PRL, ir-FSH, and ir-LH (ng/ml ± SEM) following changes in photoregime from 8L:16D to 20L:4D in photosensitive female *Zonotrichia leucophrys gambelii.*

son and Goldsmith 1982, 1985; and apparently female domesticated canaries (*Serinus canaria*), Goldsmith 1982b]. In female *Z. l. pugetensis* plasma levels of prolactin during the breeding season are conspicuously higher than those of males (Fig. 2) in a manner similar to *Ficedula hypoleuca* (Silverin and Goldsmith 1983). In the latter males do not incubate, but may feed the incubating female; they also participate in feeding young (von Haartman 1954, Creutz 1955, Curio 1959, Silverin and Wingfield 1982). In contrast, the difference in plasma levels of prolactin between the sexes in *Sturnus vulgaris* during the breeding season is much smaller (Dawson and Goldsmith 1982, 1985). This may be consistent with observations that males of this species at least occasionally incubate. It is of interest that both FSH and prolactin are elevated during incubation in female *Z. l. pugetensis.* Because pairs of this race apparently produce as many broods per season as environmental conditions permit (Lewis 1975a, Wingfield and Farner 1978), the high levels of FSH during incubation may represent a mechanism that causes maturation of ovarian follicles for the next clutch. The incidence of high FSH levels in incubating birds of species that are normally single brooded (European Starlings, Dawson and Goldsmith 1982; Pied Flycatchers, Silverin and Goldsmith 1983) may fa-

cilitate renesting after loss of clutch or brood. Two recent observations in breeding starlings support this idea: (1) plasma FSH levels are markedly reduced in females incubating eggs late in the season when renesting is no longer feasible (Dawson and Goldsmith 1985), and (2) in an unusually double-brooded British population, FSH levels were high (135 ng/ml) in females captured while feeding young from their first brood but much lower (27 ng/ml) in the same birds sampled while feeding their second brood (Dawson and Goldsmith 1985).

The temporal association of high circulating prolactin concentrations with incubation behavior has been demonstrated in a wide variety of avian species (Goldsmith 1983), although a causal relationship remains to be confirmed (Opel and Proudman 1980, Goldsmith 1983, Zadworny et al. 1985). Because it is also typical of altricial birds, including *Z. leucophrys*, that high circulating levels of prolactin continue during the rearing of young, it has been argued recently that the stimulus for release of the hormone during this phase of the breeding cycle may be provided by brooding newly hatched offspring in the nest (Silverin and Goldsmith 1984). Not all data, however, are consistent with simple prolactin-incubation and prolactin-brooding relationships. Notably, male birds of some species have high circulating levels of prolactin during the breeding season despite little or no role in incubation, as in the Pied Flycatcher (Silverin and Goldsmith 1983) and now *Z. l. pugetensis*. Furthermore, both males and females of these and other species exhibit high circulating concentrations of prolactin even if kept in cages and given no opportunity to form pair bonds or make nests (Ebling et al. 1982, Goldsmith unpubl. data, Figs. 4 and 5 above). Prolactin in this context may be involved in the physiological processes that characterize termination of the breeding season, i.e. photorefractoriness (Dawson and Goldsmith 1983, Dawson et al. 1986), either with gonadal regression per se or with one or more of the temporally related events such as molt and premigratory fattening (for a review of the effects of exogenous prolactin, see Meier and Ferrell 1978). The timing of maximum prolactin levels in the laboratory experiment on *Z. l. gambelii* is consistent with this view; high levels occurred just before the onset of the photorefractory condition (Figs. 4 and 5).

Consistent with the observations of Ebling et al. (1982), Dawson and Goldsmith (1983), and Dawson et al. (1986) on *S. vulgaris*, the results on *Z. l. gambelii* indicate that secretion of prolactin is photoperiodically induced. In European Starlings, the rate of prolactin increase is proportional to day length (Dawson and Goldsmith 1983) and occurs independently of the secretion of pituitary gonadotropins and gonadal steroids, which normally precede prolactin in a photoperiodically induced reproductive cycle (Goldsmith and Nicholls 1984). The fact that plasma levels of prolactin in female *Z. l. gambelii* (Fig. 5) continued to increase despite decreasing levels of LH and FSH may argue that these two hormones do not have a role in induction of prolactin secretion.

One striking feature of the data reported here concerns the relative concentrations of prolactin in the laboratory and field studies. Male and female *Z. l. gambelii* (laboratory experiment) and male *Z. l. pugetensis* (field study) achieved similar circulating prolactin concentrations of around 50 ng/ml. An attractive, although entirely speculative, explanation for the further increase in prolactin levels (to 100–150 ng/ml) in female *Z. l. pugetensis* breeding in the wild is that this represents an additional release of prolactin stimulated by breeding behavior (particularly incubation) superimposed on an underlying photoperiodically induced seasonal cycle. A similar argument has been proposed for the starling, in which male and female birds have higher prolactin concentrations during the breeding season in the wild than under laboratory conditions (Dawson and Goldsmith 1982, Ebling et al. 1982). Further experiments conducted in the field illustrate an interaction between seasonal (photoperiodic) and behavioral (nesting) stimuli in controlling prolactin release in free-living starlings (Dawson and Goldsmith 1985). For example, both male and female starlings permitted to reach the parental phase of their breeding cycle (incubation and feeding of young) showed higher prolactin levels than birds that were sampled at the same time of year but were still at the nest-building stage (caused artificially by repeated egg removal).

Although we found no trends in plasma levels of prolactin as a function of time of day of sampling, the restriction of capture times to morning hours could have obscured the detec-

tion of a diurnal rhythm. That such rhythms occur is suggested by the demonstration by Dyachenko (e.g. 1982) of seasonally changing diurnal cycles of concentrations of prolactin in the anterior pituitary glands of *Turdus philomelos, Fringilla coelebs, Passer hispaniolensis,* and *P. domesticus,* and earlier by Meier et al. (1969) in *Z. albicollis.* That these cycles in pituitary prolactin content may be reflected as cycles in plasma levels of the hormone becomes more probable because of the demonstration of diurnal cycles in plasma levels of LH that differ in photorefractory and photosensitive *Z. l. gambelii* (Wingfield et al. 1981), and by parallelism between pituitary and plasma concentrations of prolactin in *S. vulgaris* in experiments recently reported by Dawson et al. (1986).

It should be noted that seasonally changing phase relationships between entrained circadian rhythms in circulating levels of prolactin are a basic element of Meier's (e.g. 1975) model for the regulation of reproductive and migratory cycles in *Z. albicollis.* Doubtless because of obvious technical problems, the possible existence of diel or endogenous (circadian) rhythms in circulating prolactin have not been explored in passerine species. However, a recent investigation (Siopes and El Halawani 1986) on female domestic turkeys revealed no significant diel or circadian rhythms in circulating levels of this hormone.

Acknowledgments

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