

ENDOCRINE RESPONSES OF WHITE-CROWNED SPARROWS TO ENVIRONMENTAL STRESS

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ABSTRACT.—Field and laboratory investigations were conducted to assess the effects of selected stressors on White-crowned Sparrows (*Zonotrichia leucophrys gambelii* and *Z. l. pugetensis*). Within a few minutes after capture during the non-breeding winter phase, the birds' plasma corticosterone increased, whereas their already low levels of luteinizing hormone (LH) and dihydrotestosterone (DHT) declined further. In contrast, in the summer, or breeding phase, corticosterone levels increased much more slowly (sometimes not at all in females) during the first hour after capture. Plasma levels of LH in breeding birds were unaffected by capture and handling, as were levels of DHT in males and estrogen in females. In some cases, however, circulating levels of testosterone declined in males.

In photostimulated, caged, male *Z. l. gambelii* circulating levels of corticosterone, LH, and DHT appeared to be unaffected by ambient temperatures between 5° and 32°C, but the level of testosterone was significantly depressed at 32°C.

Capture, transport for 250 km, and subsequent caging of male and female *Z. l. gambelii* in autumn and winter within 24 h increased plasma corticosterone, and decreased LH and DHT. As the birds acclimated to captivity, a decrease in levels of corticosterone was followed by transient elevations of LH and DHT after which concentrations of these hormones stabilized at capture levels. Males transferred from outdoor aviaries and held one, two, or three per cage on short days also developed elevated concentrations of corticosterone and depressed levels of LH and DHT. Corticosterone decreased within two weeks in birds held one or two per cage, and within three weeks in those housed three per cage. As corticosterone levels decreased, transient increases occurred in LH and DHT, with the highest levels in birds held three per cage.

For more than half a century feral passerine birds have been used in investigations in both laboratory and field. Recently techniques have been developed to examine changes in endocrine status and in condition of the reproductive system of individually marked breeding birds in the field (Wingfield and Farner 1976, 1977, 1978a, b). However, relatively little consideration has been given to the development and effects of stress under the conditions of investigation. Although capture, handling, laparotomy, transport, and confinement in captivity are presumably stressful, we know of no attempt as yet to assess the role of these procedures as stressors in feral avian species. Such assessments are obviously critical for interpreting data on endocrine and gonadal function derived from such species in both the field and laboratory. In addition, they should provide insights into the underlying mechanisms of responses and adaptations of natural populations to stressful disturbances or alterations of the environment.

Using a system first described six years ago

(Wingfield and Farner 1976), we have assessed the effects of selected assumed stressors on the plasma concentrations of corticosterone, luteinizing hormone, and sex steroid hormones in White-crowned Sparrows (*Zonotrichia leucophrys*).

MATERIALS AND METHODS

BIRDS

The investigations described here are based primarily on *Z. l. gambelii*, a long-distance migrant that breeds at high latitudes or altitudes. This race normally produces only a single brood per season although pairs renest after early loss of clutch or brood (Wingfield and Farner 1978b). For some comparative purposes we present a few data from *Z. l. pugetensis*, a short-distance migrant that breeds at lower latitudes and altitudes and produces two or three broods per season (Lewis 1975, Wingfield and Farner 1977, 1978a).

Blood samples were collected from breeding *Z. l. pugetensis* on Camano Island, Island

County, Washington (48°10'N, 122°30'W) in spring and summer 1974 and 1975, and from breeding *Z. l. gambelii* near Fairbanks, Alaska (64°50'N, 147°48'W) in the summer of 1976. Most of the birds were banded and released after blood sampling, laparotomy, and weighing in conjunction with investigations of the endocrinology of the annual cycles of these two races. Birds were also taken from wintering flocks of *Z. l. gambelii* in the Sunnyside Game Refuge, 5 km southeast of Mabton, Yakima County, Washington (46°50'N, 120°0'W) in the period 1974–1980. The latter were held in bur-lap-covered cages (1 × 0.5 × 0.5 m), 40–50 per cage, and provided with food and water ad libitum for several hours while being transported to Seattle. Here, at the University of Washington, they were placed either in large outdoor aviaries under natural conditions of daylength and ambient temperature, or in small cages (40 × 26 × 22 cm) in controlled environment chambers at 20°C and 55% relative humidity. Food and water were again provided ad libitum.

Blood samples were collected from the basilic vein into heparinized microhematocrit capillary tubes both in the field and the laboratory. In the laboratory all samples were collected 2–4 h after “lights on” (10:00–12:00), and in the field most samples were taken during the morning (06:00–13:00).

Plasma from these samples was stored at –20°C until analyzed. (Details concerning blood sampling, centrifugation, and transport of samples collected in the field have been described by Wingfield and Farner [1976].) In some cases, hematocrit was estimated in order to assess the effects of serial sampling of blood from individual sparrows. Birds in laboratory experiments were weighed periodically, whereas those in field studies were weighed only at each capture.

ASSAY OF PLASMA LEVELS OF HORMONES

Luteinizing hormone (LH) was measured by the post-precipitation, double-antibody radioimmunoassay for avian LH of Follett et al. (1972) modified for use on plasma from White-crowned Sparrows (Follett et al. 1975). The assay has been in routine use in this laboratory for over seven years. All samples were assayed in duplicate and aliquots of plasma pooled from several sparrows were assayed at three dilutions in each assay as a measure of inter-assay variation.

By radioimmunoassay or competitive-protein-binding, we measured 17B-hydroxy-5 α -androstane-3-one (dihydrotestosterone or DHT), testosterone, estrone, estradiol-17B, and

corticosterone. Each plasma sample was equilibrated with approximately 2,000 cpm of the H³-steroid to be measured, as an internal standard for recovery determinations, and extracted with 5–10 volumes of dichloromethane. Extracts were dried under a stream of nitrogen, solubilized in 10% ethyl acetate in isooctane, chromatographed on Celite-glycol micro-columns, and the partially purified steroid hormones then assayed. For details of these techniques, see Wingfield and Farner (1975).

After plasma had been removed for radioimmunoassay of LH, the remaining volume of each sample from serially sampled birds in laboratory experiments was generally insufficient for the measurement of sex steroid hormones. In these cases, we measured the corticosterone in the sample after chromatographing it on thin-layer silica gel plates (see Wingfield and Grimm 1977). Dichloromethane extracts were chromatographed in chloroform:methanol:water (90:10:1, v/v/v) for 15 cm and areas of extract lanes next to lanes containing corticosterone standards eluted in dichloromethane:methanol, 9:1, v/v (Wingfield and Grimm 1977). Purified extracts were then assayed for corticosterone as described by Wingfield and Farner (1975).

In all steroid assays, two 1-ml aliquots of distilled water and 0.5-ml aliquots of pooled plasma were taken through the entire assay procedure. Assay of distilled water measured non-specific interference in the assay system. Such interference was below the sensitivity of the standard curves. Assay of the pooled plasma gave a measure of inter-assay variation, which was less than 13%. All of these values are within the ranges given by Wingfield and Farner (1975).

OBSERVATIONS AND EXPERIMENTS

FIELD INVESTIGATIONS

Blood samples were taken from males and females of both *Z. l. gambelii* and *Z. l. pug-etensis*. Some baseline samples were obtained by cardiac puncture within 1–2 min after the bird was shot. Most of the birds, however, were captured in Japanese mist-nets and samples were taken up to 120 min after capture.

COMBINED FIELD AND LABORATORY INVESTIGATIONS

To examine the effects of capture, handling, transport, and caging, we collected blood samples from male and female *Z. l. gambelii* at the Sunnyside Game Refuge in winter (October–January), at intervals during transport of them to the laboratory, and during their acclimation to captivity. These samples were assayed for LH and corticosterone; and in some

cases, for DHT and testosterone. In captivity, birds were exposed to natural daylength (outdoor aviaries) or to photoperiods in environmental chambers that equalled the natural daylength at that time.

In one experiment, we collected serial blood samples from 12 males and 8 females at 0, 0.5, 2, and 24 h after capture; and at three-day intervals thereafter until day 20 of captivity. Immediately after removing the first blood sample, we laparotomized these birds to determine their sex.

In another experiment, we captured 104 male *Z. l. gambelii* at the Sunnyside Game Refuge in January and took blood samples from groups of them. Each individual was sampled only once to avoid the possible effects of repeated sampling. The first group was sampled within 6 min of capture; samples from the others were taken at 2 and 24 h and then at intervals of three days for 33 days post-capture.

LABORATORY INVESTIGATIONS

Short-term effects of handling on plasma levels of corticosterone. In general, 2–5 min are required to either capture a bird in a cage or remove one from a mist-net, and to collect a blood sample. It is possible that plasma concentrations of corticosterone may change over this very brief period. To investigate this, we procured blood samples from captive male *Z. l. gambelii* 40–350 s after handling. Birds were housed two per cage in light- and sound-proof boxes at ca 20°C (one cage per box) in four groups, eight per group. Group 1 consisted of photorefractory (PR) birds held on a photoregime of 20L 4D; subjects in group 2 were also PR, but subjected to 8L 16D. Group 3 contained photosensitive (PS) birds held on 20L 4D; group 4 also consisted of PS birds, but they were held on 8L 16D. As the box was opened, the time taken to collect a blood sample (three capillary tubes, approximately 150 μ l) was measured with a stopwatch to the nearest 5 s.

Effects of crowding and social position on plasma levels of LH, androgen, and corticosterone. Male *Z. l. gambelii* were housed one ($n = 6$), two ($n = 10$), or three ($n = 12$) per cage with food and water ad libitum, on a photoregime of 8L 16D and at 23°C. Blood samples were collected on days 0, 7, 14, 21, and 28. In cases in which birds were held two or three per cage, the dominant and subordinate individuals were identified by daily observations of supplanting behavior at the food cup.

Effects of environmental temperature on plasma levels of LH, androgens, and corticosterone of photostimulated males. Three groups of male *Z. l. gambelii* were housed one or two

per cage on a daily photoregime of 8L 16D at 23°C. On day 0 of the experiment, the daylength was increased to 20L 4D and after 31 days of this treatment, a time when plasma levels of testosterone are highest (see Lam and Farner 1976), blood samples were obtained. Group 1 was then transferred to a chamber with an ambient temperature of 5°C ($n = 7$) and group 2 to a chamber at 32°C ($n = 7$). To control for the possible stress of moving cages from one chamber to another, group 3 ($n = 6$) was removed and then replaced in the chamber at 23°C. After four days (day 35 of 20L 4D), blood samples were collected and the birds returned to an ambient temperature of 23°C. Final blood samples were then collected on day 39 of the experiment.

STATISTICS

Unless otherwise stated, data within groups were subjected to an analysis of variance and levels of significance determined by the Newman-Keuls multiple range test for unequal samples. Comparisons among groups were made with the Student's *t*-test, unpaired, and the Mann-Whitney *U*-test. Paired *t*-tests were used to examine changes in the concentrations of hormones, or changes in body mass and hematocrit within the same group.

RESULTS

PLASMA LEVELS OF HORMONES FOLLOWING CAPTURE IN THE FIELD

No statistically significant changes in circulating levels of LH, DHT, testosterone, estradiol or corticosterone were observed over the first 10 min after capture in *Z. l. gambelii* and *Z. l. pugetensis* ($P > 0.1$, Figs. 1 and 2). However, time and corticosterone levels showed a significant positive correlation through the first 60 min in male *Z. l. gambelii* ($r = 0.388$, $P < 0.01$) whereas for the same interval the correlation between time and testosterone levels was negative ($r = -0.367$, $P < 0.01$).

Among male and female *Z. l. gambelii* captured on breeding and wintering areas, no significant changes in levels of LH were detectable up to 12 h after capture (Figs. 1 and 2). Similarly, levels of estrogen did not change significantly over the same period (Fig. 2). However, in males, circulating levels of corticosterone increased significantly between 3 and 10 min after capture in winter, and between 11 and 20 min in the breeding season (Fig. 1; $P \leq 0.01$ in both cases). Also in females in winter, the blood levels of corticosterone were elevated after 10 min of capture ($P < 0.01$) with highest levels at 120 min after capture (Fig. 2; $P < 0.001$). In contrast, plasma levels of corticosterone in breeding females did not

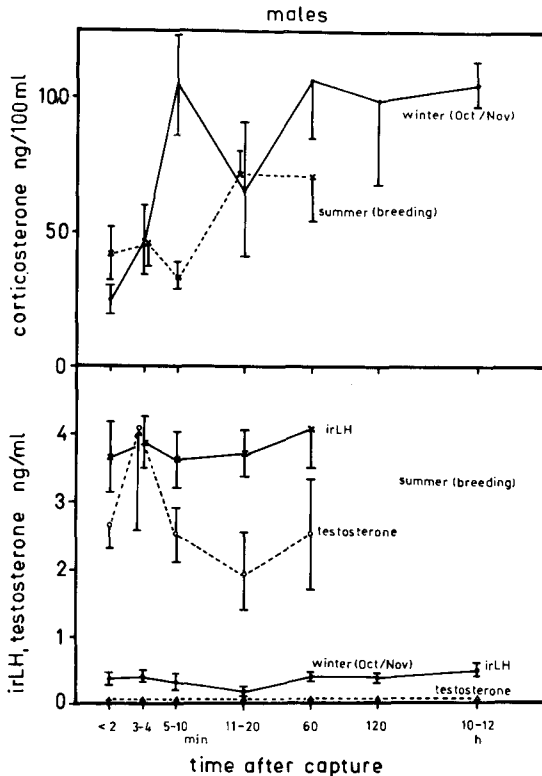


FIGURE 1. Plasma levels of corticosterone, irLH, and testosterone in male *Z. l. gambelii* as functions of time after capture in the field. Vertical lines in this and other figures represent standard errors of the means.

change over 30 min post-capture (Fig. 2). In breeding *Z. l. pugetensis* no significant changes in plasma levels of LH, DHT, testosterone, estrogen, or corticosterone occurred up to 29 min post-capture.

PLASMA LEVELS OF LH AND STEROID HORMONES FOLLOWING CAPTURE IN THE FIELD, UNILATERAL LAPAROTOMY, AND ACCLIMATION TO CAPTIVITY

After capture, body weights were low, but then increased over the next 20 days in both male and female *Z. l. gambelii* (Figs. 3 and 4; $P < 0.001$ and $P < 0.01$, respectively). Although hematocrit decreased during the first day post-capture (Figs. 3 and 4; $P < 0.001$ and $P < 0.025$ in males and females respectively), by day 20 it had returned to levels recorded at capture ($P < 0.005$ and $P < 0.05$ between days 1 and 20 respectively). As expected under winter conditions, plasma levels of LH were low throughout the period of observation except for a transitory increase between 8 and 14 days after capture ($P < 0.005$ and $P < 0.025$ for males and females, respectively). In addition, circulating LH decreased slightly but significantly in males during the first day of captivity

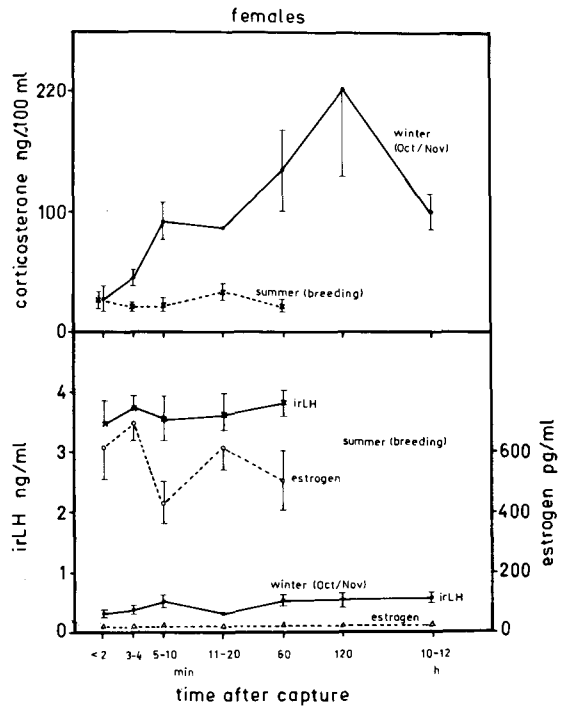


FIGURE 2. Plasma levels of corticosterone, irLH, and estrogen (estradiol and estrone combined) in female *Z. l. gambelii* as functions of time after capture in the field.

(Fig. 3; $P < 0.05$). Plasma levels of corticosterone were generally high over the first 24 h of captivity (Figs. 3 and 4; $P < 0.025$ in males), but then decreased between days 4 and 14 ($P < 0.05$ in both sexes) when levels of LH were high.

Among 104 males captured at Sunnyside Game Refuge in January and sampled in groups to avoid possible effects of repeated operations, body weight and plasma levels of LH decreased over the first day (Fig. 5; $P < 0.001$ and $P < 0.05$, respectively) and hematocrit declined after five days ($P < 0.001$). Circulating corticosterone levels increased between 6 min and 2 h ($P < 0.025$), but no further significant changes occurred over the next 33 days. Both body weight and hematocrit had recovered to original levels by day 33 ($P < 0.001$ and $P < 0.01$, respectively). As in birds subjected to serial sampling (Figs. 3 and 4), plasma levels of LH increased to a transient maximum at day 21 (Fig. 5; $P < 0.005$), and by day 33 had declined to the levels at capture. Since each bird was sampled only once, we collected enough plasma for assays of DHT and testosterone. Although no changes in testosterone were detected, plasma levels of DHT increased between days 8 and 14. Thereafter, the levels of DHT were similar to those measured during the 24 h after capture.

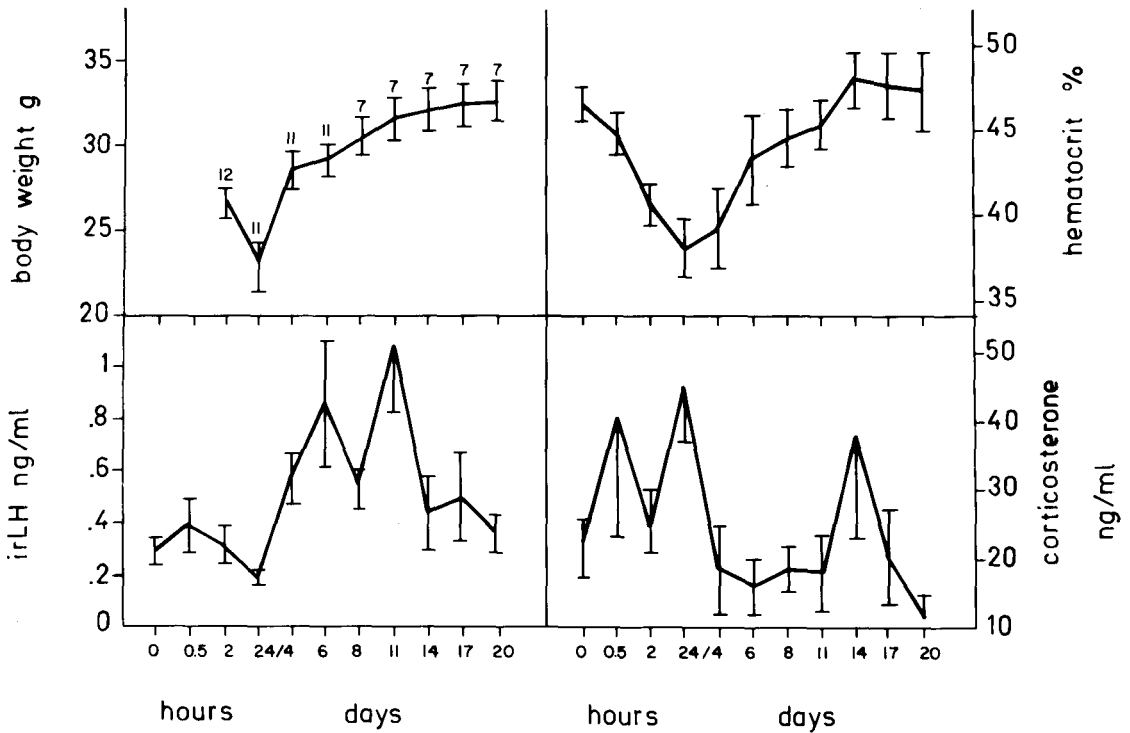


FIGURE 3. Body weight, hematocrit, and plasma levels of corticosterone and irLH in male *Z. l. gambelii* as functions of time after capture in the field, unilateral laparotomy, and acclimation to captivity. Each bird was serially sampled and numbers on the curve in the upper left panel indicate sample size. All birds were subjected to 10L 14D to mimic autumn daylength.

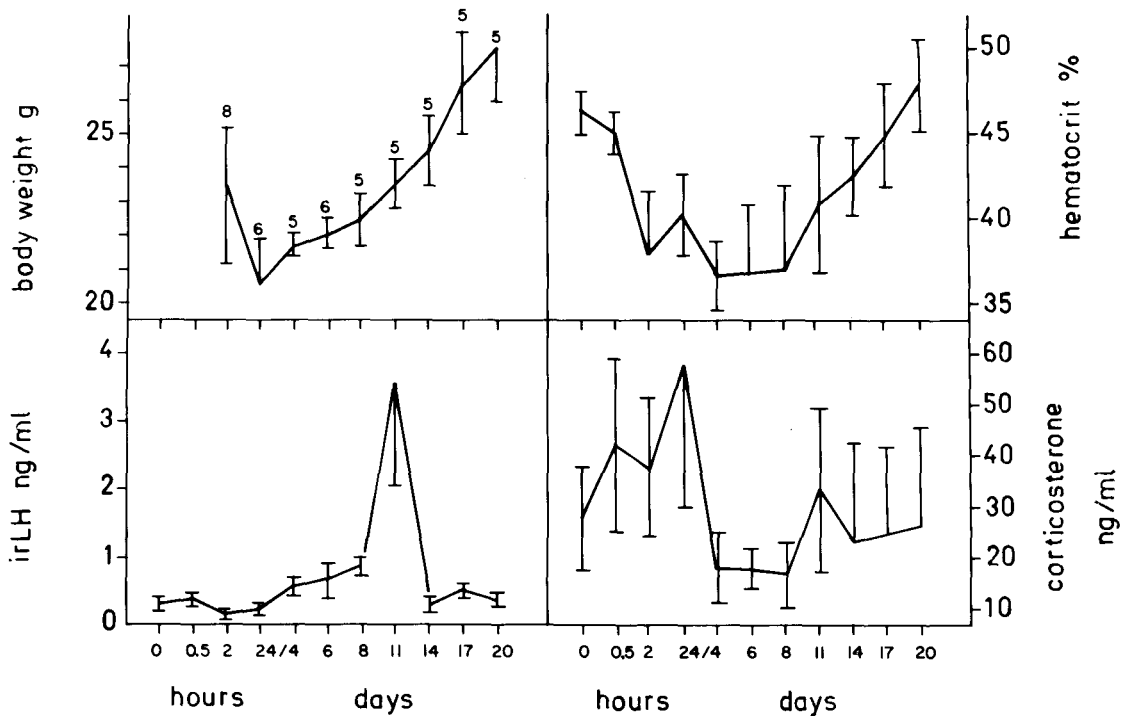


FIGURE 4. Body weight, hematocrit, and plasma levels of corticosterone and irLH in female *Z. l. gambelii* as functions of time after capture in the field, unilateral laparotomy, and acclimation to captivity. Each bird was serially sampled. Numbers on the curve in the upper left panel indicate sample sizes. All birds were subjected to 10L 14D to mimic autumn daylength.

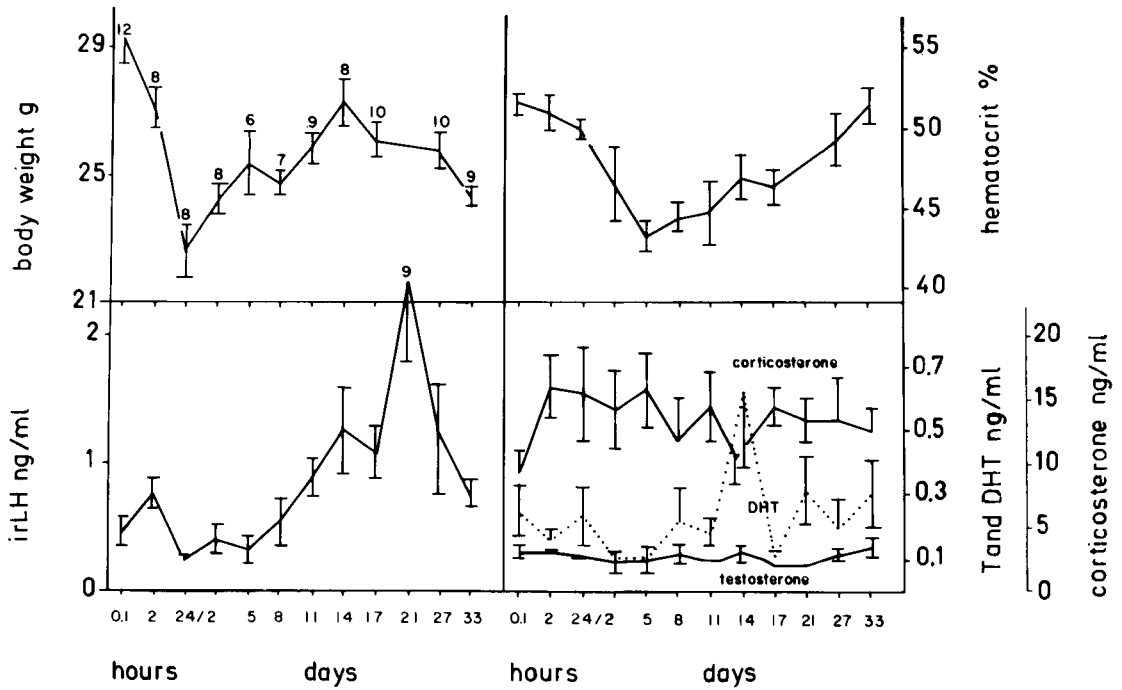


FIGURE 5. Body weight, hematocrit, and plasma levels of corticosterone, irLH, DHT, and testosterone in male *Z. l. gambelii* as functions of time after capture in the field, unilateral laparotomy, and acclimation to captivity. To avoid effects of serial sampling, only a single sample was taken from each bird. Numbers on the curve in the upper left panel indicate the size of each group. All birds were held in outdoor aviaries and subjected to natural winter days.

SHORT-TERM EFFECTS OF CAPTURE AND HANDLING ON PLASMA LEVELS OF CORTICOSTERONE

Plasma levels of corticosterone showed no change over a period of 350 s in PR birds held on 20L 4D, although levels may have tended to increase in PR birds held on 8L 16D and in PS birds on 20L 4D. Only in PS birds on short days did circulating levels increase significantly (after 150 s, $P < 0.02$), although there was a decrease by 300 s.

EFFECTS OF AMBIENT TEMPERATURE ON PLASMA LEVELS OF HORMONES

Circulating levels of LH and corticosterone did not differ significantly among the groups after four days of exposure to 5, 23, or 32°C (analysis

of variance with respect to time within a group; and Mann-Whitney *U*-test across treatments, Table 1). However, plasma levels of testosterone were significantly higher in controls held at 23° than in those held at 32° ($P < 0.05$, Mann-Whitney *U*-test).

EFFECTS OF GROUPING ON PLASMA LEVELS OF HORMONES

Levels of corticosterone were highest in all birds at day 0 (Fig. 7) and decreased to a low at day 14 in those either caged alone ($P < 0.01$) or in pairs ($P < 0.05$). Plasma levels of corticosterone in sparrows held three per cage also declined, but more slowly, with lowest levels being reached only at day 21 ($P < 0.01$).

Circulating levels of LH showed transitory

TABLE 1. Effects of environmental temperature on plasma levels of irLH, DHT, testosterone (T), and corticosterone (C) in artificially photostimulated male *Z. l. gambelii*.¹

Temperature group	n	Day 31				Day 35				Day 39			
		irLH	DHT	T	C	irLH	DHT	T	C	irLH	DHT	T	C
5°C	7	2.36 ± 0.49	327 ± 26	209 ± 17	13.47 ± 1.78	2.51 ± 0.29	362 ± 78	654 ± 266	13.14 ± 2.47	2.39 ± 0.45	164 ± 44	292 ± 112	13.25 ± 2.21
		23°C	6	1.87 ± 0.16	286 ± 92	430 ± 250	12.16 ± 1.37	2.28 ± 0.15	514 ± 84	963 ± 301*	12.01 ± 2.30	1.70 ± 0.22	209 ± 56
32°C	7	2.20 ± 0.17	299 ± 38	279 ± 65	15.77 ± 2.28	2.33 ± 0.43	305 ± 81	302 ± 128	13.60 ± 2.17	2.09 ± 0.49	133 ± 34	287 ± 67	25.39 ± 6.32

¹ Values in the tables are $\bar{x} \pm SE$. Titrers of irLH and C are in ng/ml; DHT and T in pg/ml.
² The decline in plasma testosterone by day 39, especially in the 23°C (control) group, is typical of a normal photoperiodically induced cycle of testicular development in White-crowned Sparrows (see Lam and Farner 1976, Wingfield and Farner 1980).
 * $P < 0.05$, 23°C vs. 32°C (Mann-Whitney *U*-test).

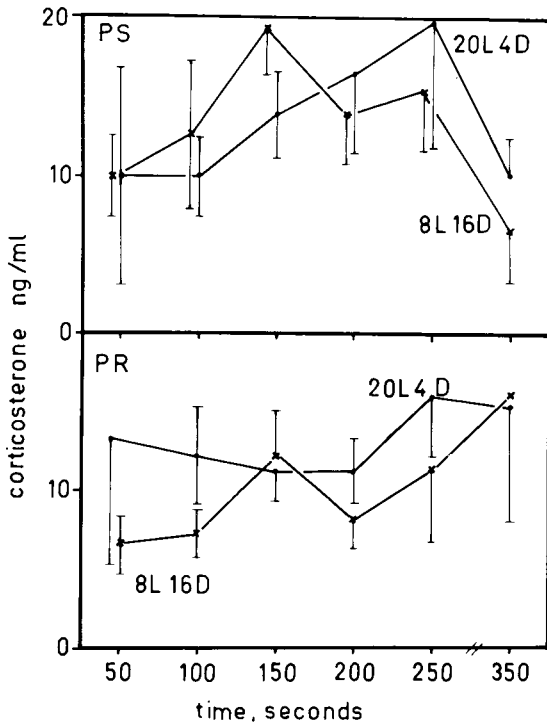


FIGURE 6. Short-term effects of handling on plasma levels of corticosterone in male *Z. l. gambelii*. Upper panel = photostimulated (PS) birds, lower panel = photorefractory (PR) birds.

increases in all groups by day 21 ($P < 0.01$ in all cases). The pattern of change was similar to that of birds captured in the field (Figs. 1–3). Furthermore, the highest levels of LH were attained in birds grouped three per cage ($P < 0.05$). Plasma levels of DHT were low on day 0, but increased significantly at least initially ($P < 0.05$). Since blood levels of testosterone were generally below the sensitivity of the assay system, we cannot assess the effect of grouping on this hormone.

We found no significant differences in plasma levels of LH, DHT, testosterone, or corticosterone between dominant and subordinate birds.

DISCUSSION

The increase in plasma levels of corticosterone that occurred in White-crowned Sparrows during the winter months following their capture in the field, and during routine laboratory procedures is consistent with the effects of a variety of stressors on several domestic avian species (for reviews see Frankel 1970, Freeman 1971, Holmes and Phillips 1976, Siegel 1980), and generally consistent with recent studies of plasma corticosterone in domestic fowl (*Gallus domesticus*; Edens and Siegel 1975, Nir et al. 1975, Etches 1976, Beuving and Vonder 1978, Scanes et al. 1980), domestic Turkey

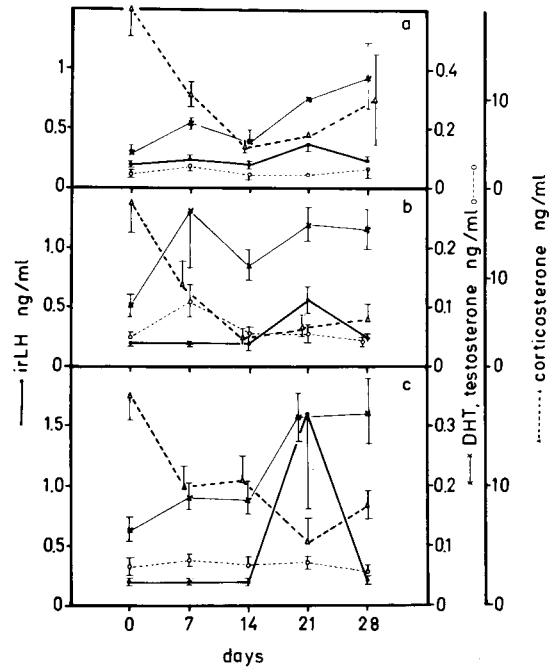


FIGURE 7. Effect of grouping male *Z. l. gambelii* on plasma levels of corticosterone (open triangles), irLH (closed circles), testosterone (open circles), and DHT (crosses). a = one bird per cage; b = two birds per cage; c = three birds per cage. All birds were held on short day lengths (8L 16D).

(*Meleagris gallopavo*; Brown and Nestor 1973, El-Halawani et al. 1973, Simensen et al. 1978), domestic Mallard (*Anas platyrhynchos*; Assenmacher 1973, Allen et al. 1975, Landsberg and Weiss 1976, Harvey et al. 1980), and domestic pigeon (*Columba livia*; John and George 1973, Jeronen et al. 1976). However, changes in circulating levels of corticosterone in White-crowned Sparrows are conspicuously lower than those of domesticated species. In some cases, e.g., in the breeding season, stress induces at most a sluggish increase in levels of corticosterone in contrast with conspicuous increases in winter (Figs. 1 and 2).

Similarly, pen-raised and feral California Quail (*Lophortyx californicus*) responded only slightly to cold, caging, and treatment with cortisol and ACTH, which elicit marked responses in domestic species (Flickinger 1966a). However, plasma levels of corticosterone in very young chickens (Newcomer 1959, Freeman and Manning 1979, Freeman and Flack 1980), and also in laying hens (Etches 1976) did not increase following handling and restraint, suggesting that even among domestic avian species there is variation in adrenal responses to stress.

The apparent lack of an adrenal response to stress in some species, or individuals, could indicate either that they were maximally

stressed at the onset of the experiment, or that they responded rapidly to handling, before a blood sample could be withdrawn. Our results, however, make the latter appear unlikely, since corticosterone usually did not increase within 350 s following handling (Fig. 6).

Seasonal changes, as yet of unexplained origin, in responses of White-crowned Sparrows to stress are noteworthy. In *Z. l. gambelii*, adrenocortical tissue regresses during the breeding season (Lorenzen and Farner 1964), which is consistent with our observations here that the adrenal response to stress diminishes during this season. We suggest for *Z. l. gambelii*, which breeds at high latitudes and altitudes with brief summers, that the reduced adrenal response to acute environmental stress may be adaptive in permitting the normal progression of reproductive function. This is consistent with the rapid amelioration of environmental conditions in spring, the brief duration of episodes of inclement weather, and the requirement for maximal fitness that the reproductive effort begin as early as possible to avoid overlap with the first autumnal storms. Such a mechanism may also operate for *Z. l. pugetensis*, which begins nesting in the often cool and wet springs of the Pacific Northwest. On the other hand, if a severe stressor such as an unseasonal storm should occur and persist for several days, then one would predict a marked endocrine response (Wingfield 1980). Indeed, severe and chronic restriction of food for at least 24 h causes plasma corticosterone to increase and testosterone to decrease in sexually maturing or mature *Z. l. gambelii* (R. A. Lewis, P. W. Mattocks, Jr., J. C. Wingfield, and D. S. Farner, unpubl.), which is also consistent with observations on domestic avian species (Assenmacher et al. 1965, Assenmacher 1973, Wilson et al. 1979, Scanes et al. 1980).

Environmental temperature had little effect on the plasma levels of hormones in our experimental White-crowned Sparrows (Table 1), although marked effects have been described in adrenal and reproductive function in other species, e.g., California Quail (Flickinger 1959), domestic fowl (Edens and Siegel 1975, Huston 1975, Nir et al. 1975, Etches 1976), and domestic pigeon (Riddle and Honeywell 1924). Our data concerning the effects of ambient temperature on testosterone secretion (Table 1) are consistent with those of Lewis and Farner (1973) who found that testicular growth in *Z. l. gambelii* was relatively unaffected by ambient temperature. Thus, as already noted, the relative insensitivity of gonadal, as well as adrenal, function to low temperatures may be

adaptive in species that breed at high latitudes and altitudes.

It is apparent that *Z. l. gambelii* adapts well to captivity, at least with respect to hematocrit and plasma levels of hormones (Figs. 3–5). After an initial loss of body weight, our experimental birds, especially those captured in October, recovered well.

In birds captured in October (Figs. 3 and 4), the initial decrease in hematocrit was undoubtedly the result of serial blood sampling. However, in those taken in January (Fig. 5) a decrease was noted that could not be attributed thereto. We do not know why it occurred, especially since hematocrit later recovered to capture levels despite repeated blood sampling (approximately 250 μ l) at intervals as brief as three days. Kern et al. (1972) were also able to collect blood at three-day intervals from *Z. l. gambelii* without affecting hematocrit. DeGraw et al. (1979) found that the hematocrit of free-living *Z. l. gambelii* dropped significantly in January. However, in our investigations, hematocrit declined to a low value by days 3–4 and recovery was apparent 6–10 days later, suggesting that seasonal changes per se are probably not responsible.

The transient increase in plasma LH of White-crowned Sparrows during the period of adaptation to captivity (Fig. 5) is curious. Because we know of no way to provide genuine controls, this phenomenon is difficult to explain. However, in other experiments conducted in this laboratory (e.g., Follett et al. 1975, Lam and Farner 1976, Mattocks et al. 1976), no such transitory increases were found in White-crowned Sparrows already adapted to captivity and held on short days. The maximum levels of LH (Figs. 3–5) in our captives were substantially above normal winter levels in free-living birds and similar to those measured in summer in this species (Wingfield and Farner 1977, 1978a, b), and to those of birds on an artificial photoregime of 20L 4D (Follett et al. 1975). Since the transient increase in LH is usually accompanied by an increase in plasma levels of DHT, and since avian LH is known to be steroidogenic (e.g., Maung and Follett 1978), we conclude that the increase in LH is real and not an artifact produced by some nonspecific plasma protein or by cross reaction of the LH antiserum with thyroid-stimulating hormone (cf. Follett et al. 1972). It should be noted that although initial increases in LH and DHT are positively correlated, this relationship is not always maintained in the long term. This suggests that other factors may regulate LH and androgen levels of *Z. l. gambelii* (see also Wingfield and Farner 1980). The

reason why circulating levels of testosterone did not increase along with the increases in LH and DHT is less clear. However, during the winter DHT is apparently present in the plasma of White-crowned Sparrows in greater concentrations than testosterone in both males and females, whereas in summer, testosterone levels far exceed those of DHT (Wingfield and Farner 1977, 1978a, b).

Much has been written on the effects of population size and social hierarchies, i.e., social stresses, on the endocrine glands of mammals and, especially, of rodents. In general, isolation, increased population size, density, and a low position in a social hierarchy may increase adrenal weight and activity, as well as decrease body weight, and the size of testes and accessory glands (e.g., Christian 1960, Bronson 1979). Similarly, grouping domestic fowl leads to social conflict and smaller testes (Flickinger 1966b). The number of birds within a group rather than the density (i.e., space per bird does not appear to be important) seems to be influential in determining the intensity of social interactions. Within groups, dominant males have the largest testes, whereas the subordinate cocks have the smallest and, occasionally atrophic, testes. In wild flocks of Wood pigeons (*Columba palumbus*), subordinate members have lower body weights and reduced survivorship compared with dominant birds. Moreover, the adrenal cortex of subordinates is hypertrophied, the cortical cells displaying enlarged nuclei and increased RNA activity (Murton et al. 1971). These data suggest that social interactions do indeed have marked effects on the endocrine state of birds. Furthermore, Goetz (1974) demonstrated in Ring-necked Pheasants (*Phasianus colchicus*) that penning, handling, and crowding induce elevated levels of corticosterone, especially in females. In our investigation, plasma levels of corticosterone were high when male *Z. l. gambelii* were first grouped, probably because of handling since levels did not differ significantly among the groups. However, the subsequent decline in plasma corticosterone as the birds acclimated to the experimental conditions was delayed in subjects in groups of three. The latter also had the highest levels of LH, although we found no difference between dominant and subordinate birds. Similarly, Balthazart et al. (1979) found no relationship between aggressiveness and plasma androgen levels in Japanese Quail (*Coturnix c. japonica*), and Rohwer and Wingfield (1981) found no correlation between plasma levels of DHT, testosterone, or LH and position in dominance hierarchies of wintering Harris' Sparrows (*Zonotrichia*

querula), although rank and plasma corticosterone titer were negatively correlated. On the other hand, androgen levels increased in both dominant and subordinate birds as agonistic interactions increased in frequency. Whether or not the transient increases of circulating LH and DHT in our birds are related to social interactions following grouping remains to be determined.

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LITERATURE CITED

- ALLEN, J. C., J. H. ABEL, JR., AND D. J. TAKEMOTO. 1975. Effects of osmotic stress on serum corticoid and plasma glucose levels in the duck (*Anas platyrhynchos*). *Gen. Comp. Endocrinol.* 27:209-216.
- ASSENMACHER, I. 1973. The peripheral endocrine glands, p. 183-286. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 3. Academic Press, New York.
- ASSENMACHER, I., A. TIXIER-VIDAL, AND H. ASTIER. 1965. Effets de la sous-alimentation et du jeûne sur la gonadostimulation du canard. *Ann. Endocrinol.* 26:1-26.
- BALTHAZART, J., R. MASSA, AND P. NEGRI-CESI. 1979. Photoperiodic control of testosterone metabolism, plasma gonadotropins, cloacal gland growth and reproductive behavior in the Japanese Quail. *Gen. Comp. Endocrinol.* 35:222-235.
- BEUVING, B., AND G. M. A. VONDER. 1978. Effect of stressing factors on corticosterone levels in the plasma of laying hens. *Gen. Comp. Endocrinol.* 35:153-159.
- BRONSON, F. H. 1979. The reproductive ecology of the house mouse. *Q. Rev. Biol.* 54:265-299.
- BROWN, K. I., AND K. G. NESTOR. 1973. Some physiological responses of turkeys selected for high and low adrenal responses to cold stress. *Poult. Sci.* 52:1948-1954.
- CHRISTIAN, J. J. 1960. Adrenocortical and gonadal responses of female mice to increased population density. *Proc. Soc. Exp. Biol. Med.* 104:330-332.
- DEGRAW, W. A., M. D. KERN, AND J. R. KING. 1979. Seasonal changes in the blood composition of captive and free-living White-crowned Sparrows. *J. Comp. Physiol. B* 129:151-162.
- EDENS, F. W., AND H. S. SIEGEL. 1975. Adrenal responses in high and low ACTH response lines of chickens during acute heat stress. *Gen. Comp. Endocrinol.* 25:64-73.
- EL-HALAWANI, M. E., P. E. WAIBEL, J. R. APPEL, AND A. R. GOOD. 1973. Effects of temperature stress on catecholamines and corticosterone of male turkeys. *Am. J. Physiol.* 224:384-388.
- ETCHES, R. J. 1976. A radioimmunoassay for corticosterone and its application to the measurement of stress in poultry. *Steroids* 28:763-773.
- FLICKINGER, D. P. 1959. Adrenal responses of California

- Quail subjected to various physiologic stimuli. Proc. Soc. Exp. Biol. Med. 100:23-25.
- FLICKINGER, G. L. 1966a. Effect of prolonged ACTH administration on the gonads of sexually mature chickens. Poul. Sci. 45:753-761.
- FLICKINGER, G. L. 1966b. Responses of testes to social interactions among grouped chickens. Gen. Comp. Endocrinol. 6:89-98.
- FOLLETT, B. K., D. S. FARNER, AND 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.
- FOLLETT, B. K., C. G. SCANES, AND F. J. CUNNINGHAM. 1972. A radioimmunoassay for avian luteinizing hormone. J. Endocrinol. 52:359-378.
- FRANKEL, A. I. 1970. Neurohumoral control of avian adrenal. Poul. Sci. 49:869-921.
- FREEMAN, B. M. 1971. Stress and the domestic fowl: a physiological appraisal. World's Poul. Sci. J. 27:263-275.
- FREEMAN, B. M., AND I. H. FLACK. 1980. Effects of handling on plasma corticosterone concentrations in the immature domestic fowl. Comp. Biochem. Physiol. 66A:77-81.
- FREEMAN, B. M., AND A. C. C. MANNING. 1979. Stressor effects of handling on immature fowl. Res. Vet. Sci. 26:223-226.
- GOETZ, R. C., JR. 1974. Handling and field stress in a transplanted F(1) Ring-necked Pheasant population as determined by corticosterone levels in plasma and adrenal glands. Ph.D. diss., Iowa State Univ., Ames.
- HARVEY, S., B. J. MERRY, AND 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., AND J. G. PHILLIPS. 1976. The adrenal cortex of birds, p. 293-420. In I. Chester-Jones and I. W. Henderson [eds.], General, comparative and clinical endocrinology of the adrenal cortex. Academic Press, New York.
- HUSTON, T. M. 1975. The effects of environmental temperature on fertility of the domestic fowl. Poul. Sci. 54:1180-1183.
- JERONEN, E., R. IOSMETSÄ, R. HISSA, AND A. PYORNILA. 1976. Effect of acute temperature stress on the plasma catecholamine, corticosterone and metabolite levels in the pigeon. Comp. Biochem. Physiol. 55C:17-22.
- JOHN, T. M., AND J. C. GEORGE. 1973. Effect of prolonged exercise on levels of plasma glucose, free fatty acids and corticosterone and muscle free fatty acids in the pigeon. Arch. Int. Physiol. Biochim. 81:421-426.
- KERN, M. D., W. A. DEGRAW, AND J. R. KING. 1972. Effects of gonadal hormones on the blood composition of White-crowned Sparrows. Gen. Comp. Endocrinol. 18:43-53.
- LAM, F., AND D. S. FARNER. 1976. The ultrastructure of the cells of Leydig in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*, in relation to plasma levels of luteinizing hormone and testosterone. Cell Tissue Res. 169:93-109.
- LANDSBERG, J.-W., AND J. WEISS. 1976. Stress and increase in corticosterone level prevent imprinting in ducklings. Behaviour 57:173-189.
- LEWIS, R. A. 1975. Reproductive biology of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis* Grinnell). 1. Temporal organization of reproductive and associated cycles. Condor 77:46-59.
- LEWIS, R. A., AND D. S. FARNER. 1973. Temperature modulation of photoperiodically induced vernal phenomena in White-crowned Sparrows (*Zonotrichia leucophrys*). Condor 75:279-286.
- LORENZEN, L. C., AND D. S. FARNER. 1964. An annual cycle in the adrenal gland of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. Gen. Comp. Endocrinol. 4:253-263.
- MATTOCKS, P. W., JR., D. S. FARNER, AND B. K. FOLLETT. 1976. The annual cycle in luteinizing hormone in the plasma of intact and castrated White-crowned Sparrows, *Zonotrichia leucophrys gambelii*. Gen. Comp. Endocrinol. 30:156-161.
- MAUNG, S. L., AND B. K. FOLLETT. 1978. The endocrine control by luteinizing hormone of testosterone secretion from the testis of Japanese Quail. Gen. Comp. Endocrinol. 36:79-89.
- MURTON, R. K., A. J. ISAACSON, AND N. J. WESTWOOD. 1971. The significance of gregarious feeding behaviour and adrenal stress in a population of Woodpigeons (*Columba palumbus*). J. Zool. 165:53-84.
- NEWCOMER, W. S. 1959. Adrenal and blood Δ^4 -3-ketocorticosteroids following various treatments in the chick. Am. J. Physiol. 196:276-278.
- NIR, I., D. YAM, AND M. PEREK. 1975. Effects of stress on the corticosterone content of the blood plasma and adrenal gland content of intact and bursectomized *Gallus domesticus*. Poul. Sci. 54:2101-2110.
- RIDDLE, O., AND 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. Am. J. Physiol. 67:337-345.
- ROHWER, S. A., AND J. C. WINGFIELD. 1981. A field study of social dominance, plasma levels of luteinizing hormone and steroid hormones in wintering Harris' Sparrows. Z. Tierpsychol. 57:173-183.
- SCANES, C. G., G. F. MERRILL, R. FORD, P. MAUGER, AND C. HOROWITZ. 1980. Effects of stress (hypoglycaemia, 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.
- SIMONSEN, E., L. D. OLSON, W. J. VANJONACK, H. D. JACKSON, AND M. P. RYAN. 1978. Determination of corticosterone concentration in plasma of turkeys using radioimmunoassay. Poul. Sci. 57:1701-1704.
- WILSON, E. K., J. C. ROGLER, AND R. E. ERB. 1979. Effect of sexual experience, location, malnutrition and repeated sampling on concentrations of testosterone in blood plasma of *Gallus domesticus* roosters. Poul. Sci. 58:178-186.
- WINGFIELD, J. C. 1980. Fine temporal adjustment of reproductive functions, p. 367-389. In A. Eppe and M. H. Stetson [eds.], Avian endocrinology. Academic Press, New York.
- 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. 1977. Zur Endokrinologie einer brutenden Population von *Zonotrichia leucophrys pugetensis*. Vogelwarte (Sonderheft) 29:25-32.
- WINGFIELD, J. C., AND D. S. FARNER. 1978a. The endocrinology of a naturally 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. 1980. Control of seasonal reproduction in temperate-zone birds. *Prog. Reprod. Biol.* 5:62-101.
- WINGFIELD, J. C., AND A. S. GRIMM. 1977. Seasonal changes in plasma cortisol, testosterone and oestradiol-17B in the Plaice, *Pleuronectes platessa* L. *Gen. Comp. Endocrinol.* 31:1-11.
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RECENT PUBLICATIONS

The Lesser Snow Geese of the eastern Canadian Arctic.—H. Boyd, G. E. J. Smith and F. G. Cooch. 1982. Canadian Wildlife Service. Occasional Paper Number 46. 23 p. Paper cover. No price given. Source: Printing and Publishing, Supply and Services Canada, Ottawa, Canada K1A 0S9. Population changes, including regional shifts during 1964-1979, have been described both for the eastern Canadian Arctic, and to a lesser degree for the Gulf Coast of the United States. Correlations with breeding and wintering weather conditions, hunting kill, and banding returns show that the geese are essentially managing themselves in regard to effective overall breeding population. Management implications of this observation are discussed. Breeding area map, figures and tables, black-and-white photographs; appendices; literature cited; also available in French.—J. Tate.

Proceedings of the Second International Swan Symposium.—Edited by G. V. T. Matthews and M. Smart. 1981. International Waterfowl Research Bureau. 396 p. Paper cover. Source: IWRB, Slimbridge, Glos., England. The Second International Swan Symposium, and an International Crane Symposium were held in Sapporo, Japan, in February 1980. The crane papers will be published elsewhere under the auspices of the International Crane Foundation. The swan papers published here are arranged geographically from New World to Old World whenever possible, within themes of: distribution and status, migration, breeding biology and population dynamics, behavior, feeding, hunting and management, mortality and disease, anatomy, weights and measurements, genetics, and contributions by "non-professional" researchers. Individual papers vary considerably in content, scope and completeness. The editors comment that considerable submitted material had to be cut to hold the volume within reasonable bounds. These proceedings represent a synoptic, but uneven update of the current state of world knowledge of swans that should prove quite useful to conservation as well as research. Numerous tables, figures and maps; pen-and-ink line drawings by Peter Scott; appendix of scientific names of birds mentioned.—J. Tate.

A Preliminary Inventory of Wetlands of International Importance for Waterfowl in West Europe and Northwest Africa.—D. A. Scott. 1980. International Waterfowl Research Bureau. 127 p. Paper cover. No price given. Source: IWRB, Slimbridge, Glos., England. Even though it is called preliminary, the value of this book to the international populations of water birds could be enormous. An ongoing wetlands census effort by numerous ornithologists from Western Europe and Northwest Africa has identified and initially evaluated approximately 544 areas potentially vital to the future of international water bird populations. By the definitions given, to be of international importance an area must: (1) regularly support 1% of the flyway population of one species; or (2) regularly support 10,000 ducks, geese, swans, or coots, or 20,000 waders; or (3) support an appreciable number of an endangered species of plant or animal. The survey covers 18 families and 134 species of water-dependent birds. Individual entries of wetlands provide name, location, habitats represented, usage by water birds, high-interest species and their maximum expected numbers, and breeding usage. References and tables; appendices of habitat types, scientific names, and data sheet.—J. Tate.

Some Results of Waterfowl Ringing in Europe.—A. C. Perdeck and C. Clason. 1980. International Waterfowl Research Bureau Special Publication Number 1. 21 p. Paper cover. No price given. Source: IWRB, Slimbridge, Glos., England. The main feature of this publication is 16 full-page computer-generated figures depicting four seasonal maps and one overall map of banding recoveries, and one graph of the data for a best-fit line on the overall map. In order to account for certain hunter-induced biases (the hunting season begins in July in southwest Europe), four map-pages are composites, or banding recoveries from birds found dead. This is a hi-tech presentation of data, but for the most part, interpretation and conclusions are left to the reader.—J. Tate.