TEMPORAL SYNERGISM OF CORTICOSTERONE AND PROLACTIN IN REGULATING ORIENTATION IN THE MIGRATORY WHITE-THROATED SPARROW (*ZONOTRICHIA ALBICOLLIS*)

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The White-throated Sparrow (*Zonotrichia albicollis*), like most migratory birds in the North Temperate area, migrates northward to breeding grounds in the spring and southward to wintering quarters in the fall. Nocturnal migrants, such as the White-throated Sparrow, rely on various environmental cues (stellar, lunar, magnetic, and others) for purposes of orientation (Sauer and Sauer 1960; Mewaldt and Rose 1960; Emlen 1967). Whether the seasonal changes in orientation result from seasonal changes in the cues or from physiological differences in the birds during the spring and fall migratory periods has been debated for many years.

Current theories which hold that seasonal changes in migratory orientation are determined by the physiological conditions of the bird stem from rationale developed by Rowan (1932). By artificially manipulating the daily photoperiod, Rowan simulated seasonal changes in daylength and induced the spring physiological state of migratory readiness in the Common Crow (*Corvus brachyrhynchos*), a diurnal migrant, during October and November. Upon release, some of the birds flew northward from the experimental site in Edmonton, Canada, whereas all of the control birds in the fall physiological condition flew southward. Rowan concluded that the seasonal differences in orientation between spring and fall migration resulted from changes in the physiological conditions of the birds. This conclusion has been corroborated in a nocturnal migrant, the Indigo Bunting (*Passerina cyanea*), tested in orientation cages (Emlen 1969).

Investigations of the White-throated Sparrow in our laboratory have demonstrated that physiological conditions associated with various seasons of the year can be induced by daily injections of corticosterone and prolactin administered at specific times. For example, in photorefractory and photosensitive birds maintained in continuous light, conditions of the vernal migratory period (gonadal growth and heavy fat stores) may be induced and augmented by daily injections of prolactin administered 12 hr after injections of corticosterone, and the conditions of the fall migratory period (heavy fat stores) may be induced by prolactin injections given 0–4 hr after injections of corticosterone (Meier and Martin 1971; Meier et al. 1971a). In addition, in caged birds, adrenal corticoids and prolactin synergize in several temporal patterns to induce nocturnal locomotor restlessness, an index of migratory activity (Meier 1969; Meier and Martin 1971). Accordingly, we performed several experiments to test whether the temporal patterns of hormones that produce the physiological conditions similar to those found during the spring and fall migratory periods might also regulate the orientation of these birds in a predictable manner. A portion of this study was reported at the symposium of the International Society for the Study of Biological Rhythms held at Little Rock, Arkansas, in November 1971.

MATERIALS AND METHODS

White-throated Sparrows were collected with mist nets from wintering flocks near Baton Rouge, Louisiana. They were maintained outdoors initially in screened aviaries and later brought indoors for experimental treatment. Indoors the birds were housed (2–3 per cage) in metal wire cages (23 × 36 × 28 cm) and the temperature was maintained at 25 ± 4°C. During captivity, the birds were supplied with an abundant amount of cracked corn and poultry grower crumbles. In Experiments 1, 2, and 3, Emlen's "footprint technique" was employed to record orientational tendencies (Emlen and Emlen 1966). The orientation cage was composed of a cone of white blotting paper with the smaller end (6 inches diameter) set in an aluminum pan. A thin cellulose sponge, moistened with black printer's ink, was set in the aluminum pan within the cone. The top of the paper cone was capped by a flat piece of ¼-inch hardware cloth. The activity of a bird was indicated by ink smudges on the sloping sides of the cage. The greatest density of ink occurs in the section of the cone that lies in the direction of the

bird's intended movement. A shield was placed around each orientation cage to block out peripheral "landmarks" and horizon glows; however, the shield still allowed a clear view of the sky to within 35° of the horizon. All the tests were performed on the roof of a one-story building between 21:00 and 24:00 (Exps. 1 and 2), 21:00 and 01:00 (Exp. 3), or from 20:00 to 03:00 (Exp. 4) (sunset occurred between 18:00 and 19:00 during the experimental periods). The tests were performed on clear nights. The principal glow of the city was to the north; the test site was on the southern edge of Baton Rouge.

In order to present and analyze the data in a quantitative manner, each cone was divided into eight sectors of 45 degrees each, and each sector was given a value based on the intensity of ink smudges compared to a standard with values ranging from 1 to 20 (see Emlen and Emlen 1966). The larger values represented greater intensities of ink smudges. Thus, the higher relative values indicate the directions of the intended movements of the birds.

In Experiment 4, orientation was determined with a modification of the activity-orientational cage first used by Kramer (1957). In our cages, the floor consisted of eight movable sections of hardware cloth anchored at the center of the cage and slanted so as to rest on individual microswitches. Each microswitch was connected to a recording pen of an Esterline-Angus event recorder. When the bird's weight depressed a floor section, the microswitch was activated and the disturbance was recorded. The chart speed of the recorder was 3.81 cm/hr.

Experiment 1. The birds were brought indoors in January 1971, and maintained in continuous dim light (0.25 lumens/m² at perch level) supplied by an incandescent bulb. The birds were kept in continuous dim light in order to avoid photoperiodic entrainment of endogenous rhythms that may be involved in orientation and thereby interfere with the rhythms set up by hormonal treatment. Beginning on 1 March, the birds were injected subcutaneously (s.c.) with corticosterone and prolactin in three different relations. Ovine prolactin (25 µg in 0.02 ml 0.85% saline) was injected in the leg daily at 4, 8, or 12 hr (Groups A, B, and C, respectively) after the time (08:00) of corticosterone injections (25 µg in 0.02 ml 0.85% saline). Corticosterone was injected on alternate days at 08:00 because a single injection sets up circadian rhythms of responses to prolactin that persist for at least several days in conditions of continuous light (Meier and Martin 1971; Meier et al. 1971a, b). Several control groups were included. One group (Group D) consisted of birds maintained in large, outdoor holding aviaries with no treatment. Another group (Group E) consisted of untreated birds held indoors with the experimental birds. A third control group (Group F) was injected with prolactin 12 hr after injections of physiological saline given in place of corticosterone. There were three birds in each group. Because most daily rhythms adjust to a change in photoperiodic regimen within one week, we provided 10 days of hormone treatment before testing for orientation. The orientation was tested between 21:00 and 24:00 on 11, 12, and 13 March 1971.

Experiment 2. This experiment was performed during the vernal migratory season in May and involved four of the same groups of birds that were used in Experiment 1. The experimental treatment was changed among the groups so that the group which received prolactin injections 4 hr after the administration of corticosterone in the first test was given prolactin at 12 hr after the injection time of corticosterone (08:00) in the second test. Similarly, those birds that received prolactin 12 hr after corticosterone in the first test were injected with prolactin 4 hr after the injection time of corticosterone in the second test. The two remaining control groups were identical to those (Groups D and F) used in Experiment 1. There were three birds in each group. Lighting, orientation apparatus, hormonal dosages, and feeding were the same as in Experiment 1. The injections were initiated on 2 May, and the orientation was tested between 21:00 and 24:00 on 8, 9, and 10 May 1971.

Experiment 3. The birds were brought indoors in January 1972, and maintained in continuous dim light as in Experiments 1 and 2. Injections were begun on 28 February. Ovine prolactin (25 µg/injection) was injected (s.c.) in the leg daily at 4, 8, or 12 hr (Groups A, B, and C, respectively) after the time (08:00 of corticosterone injections which were administered on alternate days. Groups D and E received injections of saline at 4 and 12 hr, respectively, after the time (08:00) of corticosterone injections. Group F was untreated. There were five birds in each group which were tested twice on two of three nights (10, 11, 12 March), between 21:00 and 01:00.

Experiment 4. Twenty White-throated Sparrows were brought indoors on 10 September 1971, and placed on a 16-hr daily photoperiod (04:00–20:00). The reproductive system was fully regressed in these birds. The intensity of light was 350–400 lumens/m² at perch level; the changes from light to dark and dark to light were abrupt. Ovine prolactin (25 µg/ inj.) was injected (s.c.) daily in the leg beginning on 10 September at 05:00, 09:00, or 13:00 (Groups A, B, and C, respectively). Because the daily increase in plasma concentration of corticosterone occurs within a few hours after the onset of dark in photorefractory White-throated Sparrows in late summer (Dusseau and Meier 1971) as well as in the fall in birds in migratory condition (Martin and Meier, Unpubl. Data), we infer that the groups received prolactin at approximately 8, 12, or 16 hr (Groups A, B, and C, respectively) after the time of the daily increase in plasma corticosterone. In addition to the groups that were treated with prolactin, several other groups were included for purposes of comparison and control. One control group (D) was injected with physiological saline (0.02 ml) instead of prolactin at 09:00. Another group (E) was also kept indoors but untreated. Group F was composed of untreated birds maintained in a large, outdoor aviary. There were three birds in Groups A, D, E, and F; six birds in Group B; and five birds in Group C. The birds were placed in the orientation cages early in the afternoon before the test night. The nocturnal orientation of the birds between 20:00 and 03:00 and other information are provided in table 4.

The results of all the experiments were subjected to an analysis of variance test for variable activity or for dependent variable activity when the experiment contained groups having unequal numbers.

RESULTS

Experiment 1. White-throated Sparrows maintained in outdoor holding aviaries have

TABLE 1. Effects of corticosterone and prolactin on orientation of nocturnal activity in White-throated Sparrows on 11, 12, and 13 March (Experiment 1).[a]

Direction	Group A			Group B			Group C			Group D			Group E			Group F		
	11	12	13	11	12	13	11	12	13	11	12	13	11	12	13	11	12	13
NW	2.3[b]	4.7	3.3	0.0	0.0	0.7	10.0	12.3	13.7	0.7	0.7	0.3	0.0	0.3	0.3	0.3	0.0	0.0
N	2.0	3.3	3.7	0.0	0.0	0.3	15.0	18.3	13.3	0.0	0.7	0.7	0.3	0.3	0.7	1.0	0.0	0.0
NE	1.0	3.7	3.0	0.3	0.0	0.3	13.3	20.0	14.7	0.0	1.0	0.3	0.3	0.0	0.7	0.0	0.0	0.3
E	0.7	4.0	2.7	0.3	0.0	0.3	14.3	14.0	12.3	0.0	0.3	1.0	0.0	0.0	0.0	1.3	0.0	0.3
SE	8.7	12.3	13.0	1.0	0.0	0.3	7.0	8.3	3.3	0.0	0.0	0.0	0.0	0.0	0.3	1.0	0.0	0.3
S	10.0	11.3	12.3	1.0	0.0	0.0	0.3	2.7	2.0	0.0	0.0	0.7	1.0	0.0	0.7	0.7	0.0	1.0
SW	19.0	19.0	14.7	1.0	0.0	0.3	1.3	2.3	1.0	1.0	0.0	0.3	0.0	0.3	0.7	1.0	0.0	0.7
W	14.0	13.0	11.3	0.0	0.0	0.3	3.7	5.7	3.7	0.0	0.0	0.0	1.3	0.0	0.7	1.7	0.0	0.3

[a] Groups A, B, C, D, and E were maintained indoors in constant dim light except at the times of testing under the open sky (21:00–24:00). Groups A, B, and C were injected daily with prolactin at 4 (A), 8 (B), or 12 (C) hr after the time (08:00) of corticosterone injections. Group D received prolactin injections 12 hr after injections of saline and Group E was untreated. Group F was composed of untreated birds kept outdoors. Each group was composed of three birds; each bird was tested on 3 successive nights (11, 12, and 13 March 1971).
[b] The activity was estimated by comparing the intensity of the ink blotches on each directional segment of the orientation cone with a set of standards that had designated values from 0 to 20. The higher relative values indicate the more frequent choices of intended movement.

low levels of body fat and no increase in gonadal weights early in March. Of the birds maintained indoors in continuous dim light, there was no apparent increase in fat stores nor of body weight in Groups B, E, and F. However, the birds in those groups that received daily injections of prolactin at 4 (Group A) or 12 (Group C) hr after the time of corticosterone injections were obviously fatter within one week. These results agree with those of previous studies of the White-throated Sparrow (Meier and Martin 1971; Meier et al. 1971a).

Following 11 days of hormone treatment, the activity and orientation of the birds were tested between 21:00 and 24:00 on 11, 12, and 13 March (table 1). There was little or no nocturnal activity in birds that were maintained in outdoor aviaries (Group D). Of the birds kept indoors, only those injected with prolactin at 4 (Group A) or 12 (Group C) hr after the time of corticosterone injections exhibited nocturnal activity when tested in

activity cages or orientation cages. However, the orientation of the 4- and 12-hr groups were very different from one another ($P < 0.01$). The activity was oriented in a north-northeast direction in the 12-hr group (Group C) and in a south-southwest direction in the 4-hr group (Group A). Although the moon has often been cited as causing interference in the orientation of caged birds, most of the birds tested in this experiment did not appear to be affected even though the tests were performed on the 3 nights following full moon and the moon was visible to the birds at least during a portion of the test periods. One bird of Group A exhibited intense activity in a narrow sector to the southwest which appeared to be lunar taxis.

Experiment 2. In early May, the birds that were maintained in an outdoor aviary were fat, and the nocturnal activity was intense and oriented in a north-northeast direction (table 2). Following a week of hormone or control injections, the activity and orientation of the

TABLE 2. Effects of corticosterone and prolactin on orientation of nocturnal activity in White-throated Sparrows on 8, 9, and 10 May (Experiment 2).[a]

Direction	Group A			Group B			Group C			Group D		
	8	9	10	8	9	10	8	9	10	8	9	10
NW	7.3[b]	5.0	7.3	8.0	7.7	6.3	1.3	0.3	1.0	18.0	16.7	17.0
N	3.0	2.3	2.3	15.3	16.7	17.3	1.3	0.3	0.3	20.0	17.7	20.0
NE	4.3	1.7	2.0	17.7	15.7	18.7	0.3	0.0	0.7	19.3	18.3	19.3
E	10.0	6.3	4.0	7.3	8.7	8.7	0.3	1.3	0.3	11.7	12.0	11.3
SE	13.0	13.0	12.0	1.7	0.7	2.0	0.7	0.3	0.7	5.3	3.7	2.7
S	15.0	15.0	16.0	0.7	1.3	1.7	0.3	1.0	0.3	2.7	3.7	2.7
SW	15.0	13.3	15.0	1.3	1.3	1.0	0.3	0.3	1.3	3.7	1.3	1.7
W	12.0	10.3	11.0	3.7	2.3	2.0	0.7	0.3	0.3	11.0	8.3	6.7

[a] Groups A, B, and C were maintained indoors in constant dim light except during the times of testing under the open sky (21:00–24:00). Groups A and B were injected with prolactin at 4 (A) or 12 (B) hr after the time of corticosterone injections (08:00). Group C received prolactin injections 12 hr after injections of saline. Group D was composed of untreated birds kept outdoors. Each group was composed of three birds; each bird was tested on 3 successive nights (8, 9, and 10 May 1971).
[b] See table 1.

TABLE 3. Effects of corticosterone and prolactin on orientation of nocturnal activity in White-throated Sparrows on 10, 11, and 12 March (Experiment 3).[a]

Direction	Group A	Group B	Group C	Group D	Group E	Group F
NW	1.3[b]	1.1	9.8	0.2	0.2	0.2
N	1.3	0.4	14.2	0.2	0.4	0.4
NE	1.1	0.2	12.2	0.6	0.2	0.6
E	1.3	0.8	6.6	1.0	1.0	0.4
SE	4.0	0.2	2.6	0.6	0.0	0.6
S	5.0	0.0	0.4	0.2	0.6	0.4
SW	5.4	0.4	0.2	0.2	0.2	0.4
W	3.2	0.8	5.0	0.2	0.6	0.0

[a] All groups were maintained in continuous dim light except at the times of testing under the open sky (21:00–01:00). Groups A, B, and C were injected daily with prolactin at 4 (A), 8 (B), or 12 (C) hr after the time (08:00) of corticosterone injections. Groups D and E received saline injections at 4 or 12 hr after corticosterone injections, respectively. Group F received no treatment. Each group was composed of five birds; each group was tested on 2 of the 3 test nights.
[b] See table 1. The activity indexes are the means of five birds tested on 2 nights.

birds maintained indoors were tested between 21:00 and 24:00 on 8, 9, and 10 May. As in Experiment 1, injections of prolactin 4 hr after the time of corticosterone injections (Group A) induced nocturnal restlessness oriented to the south-southwest, whereas injections of prolactin administered 12 hr after the time of corticosterone injections (Group B) induced nocturnal activity oriented to the north-northeast. The vector means of Groups A and B are statistically different ($P < 0.01$). Although the combined activities of Group A were oriented southward on all 3 nights, the orientation of one of the birds was random. Injections of prolactin at 12 hr after injections of saline in place of corticosterone (Group C) were ineffective in inducing significant amounts of nocturnal activity. In addition, this treatment (Group C) did not elicit fattening whereas injections of prolactin at 4 or 12 hr after corticosterone injections (Groups A and B) did produce heavy fat stores as well as intense nocturnal activity. There was no evidence of lunar taxis in any of the tests. The moon was visible during portions of the test periods. Full moon occurred on 10 May.

Experiment 3. Noticeable increases in fat stores occurred only in the groups that received prolactin at 4 (Group A) or at 12 (Group C) hr after injections of corticosterone. The fat stores appeared to be greater in Group C than in Group A.

Only the groups treated with prolactin at 4 (Group A) or at 12 (Group C) hr after injections of corticosterone exhibited significant amounts of activity in the orientation cones (table 3). The orientation was to the south-southeast in Group A and to the north

in Group C. The differences in direction are statistically significant ($P < 0.01$). The moon was not visible to any of the birds during these tests. The third quarter was on 8 March.

Experiment 4. In the first three experiments, daily rhythms of corticosterone and prolactin were simulated in birds kept in continuous dim light by injecting both hormones in various temporal relations. Because daily rhythms of endogenous adrenal corticoids are present in the White-throated Sparrow on natural photoperiods (Dusseau and Meier 1971), and because the corticoid rhythms are entrained by the photoperiod, we decided to test whether injections of prolactin alone might synergize temporally with a daily rhythm of endogenous corticosterone and induce oriented nocturnal activity in birds maintained on a 16-hr daily photoperiod. Both fattening (Meier and Davis 1967) and nocturnal activity (Meier 1969) have been induced in White-throated Sparrows by daily injections of prolactin alone administered at specific times of day. The principal objective of the present experiment was to determine whether northward orientation could be induced by prolactin in birds exposed to a fall sky. Because northward orientation in birds under a spring sky was induced by injections of prolactin at 12 hr after the time of corticosterone injections, an attempt was made to produce a comparable interval between the daily increase in plasma concentration of corticosterone and the daily injection of prolactin. Consequently, one group of birds maintained on a 16-hr photoperiod (04:00–20:00) was injected at 09:00 and two others were injected at 4 hr before or 4 hr afterward. The daily increase in plasma concentration of corticosterone is believed to occur during the first few hours after the onset of dark (see Materials and Methods). Thus, we estimated that the daily increase in plasma corticosterone would probably occur at about 21:00 under the conditions of the present experiment.

White-throated Sparrows that are retained in outdoor holding aviaries on the southern wintering area are subjected to shorter photoperiods during the summer compared to those experienced by feral birds on the northern breeding areas, and the sequence of seasonal events is delayed (Meier et al. 1969). The appearance of the fall migratory condition appears to have been delayed by a little more than a month in the present experiment. The birds maintained outdoors were lean and exhibited no nocturnal restlessness when tested in early November. They became fat during

November and exhibited nocturnal restlessness oriented to the south-southwest when tested later in the month (table 4).

All the untreated birds maintained indoors on a 16-hr daily photoperiod were also lean and exhibited no nocturnal restlessness in late October and early November (table 4). The responses of the groups treated with prolactin varied depending on the time of injection. The group that received prolactin at 09:00 was most responsive. After 2 weeks of daily injections, the birds were heavy with fat stores, there was some cloacal protuberance (evidence of gonadal activity), and all the birds were especially active at night with their peak of activity around midnight. In addition, the nocturnal activity was oriented predominantly northward. The group that was injected with prolactin at 13:00 (Group C) also responded to the treatment but not so well as the group treated at 09:00. There was no cloacal protuberance and variable amounts of fattening. Two of the heavier birds exhibited moderate to intense nocturnal activity that was oriented northward. Light nocturnal activity oriented northward was found in another bird. Two birds were apparently unaffected by the hormonal treatment. The group injected with prolactin at 05:00 (Group A) was completely unresponsive with respect to cloacal protuberance, fat stores, and nocturnal activity. A control group that received saline injections at 09:00 (Group D) instead of prolactin was similarly unaffected. The nights when the moon was visible are listed in table 4.

DISCUSSION

These studies further establish a basic role for the temporal synergism of adrenal corticoids and prolactin in regulating seasonal conditions in the White-throated Sparrow (Meier and Martin 1971; Meier et al. 1971a). A relation in which daily injections of prolactin are administered 12 hr following injections of corticosterone induces conditions found during the vernal migratory period: gonadal growth, heavy fat stores, and nocturnal restlessness directed northward. Moreover, when prolactin is given 12 hr after the probable daily increase in concentration of endogenous corticosterone, it induces similar physiological and behavioral responses.

Another relation in which prolactin injections are given 4 hr after injections of corticosterone induces conditions found during the fall migratory period: heavy fat stores and nocturnal restlessness directed southward. Injections of prolactin administered 8 hr after injections of corticosterone or after the prob-

TABLE 4. Hormonal control of the orientation of nocturnal activity of the White-throated Sparrow (*Zonotrichia albicollis*) in the fall.

Group[a]	Bird No.	Date of test	Direction of nocturnal activity[b]							
			NW	N	NE	E	SE	S	SW	W
A	4317	11/2[c]	0	0	0	1	0	0	0	0
	3643	11/2[c]	0	0	0	0	1	0	0	1
	4354	10/18	0	0	1	1	0	0	0	0
B	3635	10/24[d]	39	31	37	0	4	1	0	21
	4105	10/19	40	38	6	0	0	0	0	12
	4083	10/20	8	37	36	31	4	8	4	0
	4123	10/21	21	32	20	0	3	1	1	9
	3539	10/21	20	35	26	18	3	5	11	2
	4304	10/26[d]	8	23	27	0	7	1	3	6
C	4071	10/16	19	18	14	0	0	0	2	17
	4086	10/25[d]	18	37	33	0	8	0	4	4
	4090	10/18	3	8	3	0	0	0	0	4
	3632	10/22	1	2	1	3	1	2	2	0
	4318	10/26	2	14	17	0	4	4	2	1
D	3631	10/20	0	0	0	0	0	0	2	0
	4080	10/24[d]	0	0	1	0	0	1	1	0
	4223	10/31[c]	0	1	0	0	0	0	0	0
E	4328	10/19	1	0	1	0	0	0	0	1
	4344	10/22	0	0	0	0	1	1	0	0
	4345	11/3[c]	1	1	1	0	0	2	1	0
F$_1$	4305	11/4[c]	0	1	0	0	1	3	5	2
	4343	11/4[c]	0	0	0	0	0	3	2	1
	4326	11/3[c]	1	1	0	0	2	2	1	0
F$_2$	4305	11/22[d]	11	11	0	6	4	23	29	0
	4343	11/22[d]	33	0	0	0	0	10	49	41
	4326	11/24[d]	0	0	0	0	0	20	23	17

[a] A, B, and C received prolactin at 8, 12, and 16 hr, respectively, after the probable daily increase in concentration of plasma corticosterone (21:00); D received saline at 12 hr after daily rise in levels of endogenous corticosterone; E consisted of untreated birds maintained indoors; F$_1$ and F$_2$ were untreated birds maintained outdoors and tested in early (F$_1$) and late (F$_2$) November.

[b] One activity unit = a minimum of four perch registrations per 8-min interval.

[c] The moon was prominent and visible to the birds throughout most of the night.

[d] Moon visible only during a short interval of the night.

able daily increase in concentration of endogenous corticosterone induce conditions that are found during the summer photorefractory period: gonadal regression, low levels of body fat stores, and suppression of nocturnal restlessness.

Measurements of plasma corticosterone (Dusseau and Meier 1971) and pituitary prolactin (Meier et al. 1969) corroborate the conclusions that several seasonal conditions in the White-throated Sparrow are controlled by a temporal synergism of corticosterone and prolactin. During the vernal migratory period, there is a 12-hr interval between the daily rise in plasma corticosterone and the daily release of pituitary prolactin. During the summer postnuptial period, the interval is about 6 hr and from our data we hypothesize that

during the autumnal migratory period the interval is about 4 hr.

Our results indicate that the nocturnal cue(s) existing during the vernal and autumnal migratory seasons can be utilized interchangeably by the bird to orient either northward or southward. They corroborate other evidence (Rowan 1932; Emlen 1969) that the same celestial cue(s) is employed by migrants during both migratory seasons. The manner in which the cue(s) is employed depends in part on the temporal relation of the daily rhythms of corticosterone and prolactin.

SUMMARY

Oriented nocturnal locomotor activity was induced in migratory White-throated Sparrows under the open night sky by injection of hormones. In experiments performed on birds maintained in continuous dim light before and during the vernal migratory season, injections of prolactin administered 4 hr after the time of injections of corticosterone induced locomotor restlessness oriented southward. Injections of prolactin given 12 hr after injections of corticosterone promoted northward orientation. In a study of another group of birds maintained on a 16-hr daily photoperiod in the fall, injections of prolactin 12 hr after the probable daily rise of plasma corticosterone stimulated nocturnal restlessness that was oriented northward. Injections of prolactin at 8 hr after the increase of either exogenous or endogenous corticosterone did not stimulate nocturnal activity. It is concluded that the orientation of migratory activity is controlled by a temporal synergism of corticosterone and prolactin.

ACKNOWLEDGMENTS

LITERATURE CITED

DUSSEAU, J., AND A. H. MEIER. 1971. Diurnal and seasonal variations of plasma adrenal steroid hormone in the White-throated Sparrow, Zonotrichia albicollis. Gen. Comp. Endocrinol. 16: 399–408.

EMLEN, S. T. 1967. Migratory orientation in the Indigo Bunting, Passerina cyanea. I. Evidence for use of celestial cues. Auk 84:309–342.

EMLEN, S. T. 1969. Bird migration: influence of physiological state upon celestial orientation. Science 165:716–718.

EMLEN, S. T., AND J. T. EMLEN. 1966. A technique for recording migratory orientation of captive birds. Auk 83:361–367.

KRAMER, G. 1957. Experiments on bird orientation and their interpretation. Ibis 99:196–227.

MEIER, A. H. 1969. Diurnal variations of metabolic responses to prolactin in lower vertebrates. Gen. Comp. Endocrinol. 2:55–62.

MEIER, A. H., J. T. BURNS, AND J. W. DUSSEAU. 1969. Seasonal variations in the diurnal rhythm of pituitary prolactin content in the White-throated Sparrow, Zonotrichia albicollis. Gen. Comp. Endocrinol. 12:282–289.

MEIER, A. H., AND K. B. DAVIS. 1967. Diurnal variation of the fattening response to prolactin in the White-throated Sparrow, Zonotrichia albicollis. Gen. Comp. Endocrinol. 8:110–114.

MEIER, A. H., AND D. D. MARTIN. 1971. Temporal synergism of corticosterone and prolactin controlling fat storage in the White-throated Sparrow, Zonotrichia albicollis. Gen. Comp. Endocrinol. 17:311–138.

MEIER, A. H., D. D. MARTIN, AND R. MACGREGOR, III. 1971a. Temporal synergism of corticosterone and prolactin controlling gonadal growth in sparrows. Science 173:1240–1242.

MEIER, A. H., T. N. TROBEC, M. M. JOSEPH, AND T. M. JOHN. 1971b. Temporal synergism of prolactin and adrenal steroids in the regulation of fat stores. Proc. Soc. Exp. Biol. Med. 137: 408–415.

MEWALDT, L. R., AND R. G. ROSE. 1960. Orientation of migratory restlessness in the White-crowned Sparrow. Science 131:105–106.

ROWAN, W. 1932. Experiments in bird migration. III. The effects of artificial light, castration and certain extracts on the autumn movement of the American Crow (Corvus brachyrhynchos). Proc. Natl. Acad. Sci. 18:659–664.

SAUER, E. G., AND E. M. SAUER. 1960. Star navigation of nocturnal migratory birds. Cold Spring Harbor Symp. Quant. Biol. 25:463–473.