THE EFFECT OF DIET ON PHOTOPERIOD-INDUCED LIPID DEPOSITION IN THE WHITE-THROATED SPARROW

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In a previous paper (Odum and Perkinson, 1951) it was shown that White-throated Sparrows (*Zonotrichia albicollis*) undergo two periods of lipid deposition while on their winter range, one during midwinter and the other just prior to northward migration in late April and early May. Between these periods a relatively lean period occurs during the prenuptial molt of March and early April. Actual extractions of lipids from various parts demonstrated that "winter fat" differed in body distribution as compared with "migratory fat," the latter showing a characteristic peritoneal concentration. Wolfson (1945, 1953, 1954) has shown that marked fat deposition can be induced in various migratory fringillids by increased photoperiods, the assumption being that the induced deposition represents the premigratory type. Characteristically, premigration lipid deposition occurs rapidly, the bulk of fatty material often being laid down within a few days. This poses interesting questions in regard to food and water intake.

The experiment described in this paper was designed (1) to compare the lipid deposition of birds on a high fat diet with a similar group on a low fat diet, (2) to determine the amount of food and water consumed by the experimental groups and a control group, and (3) to determine if the fat deposits induced in midwinter by increased photoperiods are quantitatively similar to "migratory fat" which normally occurs in the spring premigration period.

METHODS

White-throats were captured during October and November, 1952, and kept under natural day-length conditions until November 27, which is well beyond the end of the autumn refractory period (Miller, 1948; Wolfson, 1952). The birds were then divided into three groups as follows: group A—12 birds exposed to increased photoperiods and placed on a high fat diet; group B—12 birds exposed to the same increased photoperiods as group A but given a low fat diet; group C—9 control birds exposed to natural photoperiods and fed a mixed diet. Birds of group A were fed on "Pecano" which consists of bits of pecan meats that remain after shelling in pecan packing plants, and which has a lipid content of about 60 per cent. Group B were given unmixed canary seeds which are low in fat, while group C had access to both Pecano and seeds. All three groups were also given Gaines dog meal to insure adequate amounts of minerals and vitamins. The composition of the three food items by per cent was as follows:[1]

	Pecano	Seeds	Dog food
Fat	60	6	7
Protein	10	17	25
Carbohydrate	17	55	48
Fiber	4	5	4
Ash	2	6	8
Moisture	7	11	8
Calories per gram	6.5	3.4	3.5

[1]Analyses of Pecano and seed made by Dairy Nutrition Laboratory, University of Georgia, and dog food courtesy of Gaines Division of General Foods Corporation.

Each group was kept in a separate screen wire cage $3 \times 2\frac{1}{2} \times 3$ feet. Groups A and B were placed in a small basement laboratory room where they were exposed to daylight plus an extra period of light from a 75-watt bulb controlled by a poultry time switch. Birds of group C were kept in an adjoining room and exposed to normal daylight only.

Control birds, of course, were exposed to naturally increasing photoperiods during the latter half of the experiments, and they also received, inadvertently, some artificial light on several occasions when lights were turned on in the control room at night. Nevertheless, the difference between the response of controls and experimentals was quite marked. Two birds in group A were lost during the experiment and rats killed four birds in group C so that the numbers of birds completing the experiments were 10, 12, and 5, respectively. Birds in each group were nearly equally divided as to sex.

After correspondence with Dr. Albert Wolfson, who very kindly gave us the benefit of his experience in experiments of this type, it was decided to employ a light schedule which would be moderately forcing, that is, one that might be expected to bring about a full response in about two months. Beginning on November 28, when the day-length was 12 hours, 15 minutes of extra light was added daily until a 16-hour day was reached on December 16. This long photoperiod was then continued until the end of the experiment (fig. 1).

At intervals of three or four days birds were weighed in the early evening just after the light went off in the experimental room. Food consumption was measured by placing a known weight of food in each cage and then weighing the food remaining at the end of one to three 24-hour periods. The cages were equipped with hardware-cloth bottoms so that it was possible to recover spilled food in pans under the cages. At best, however, measurements of food consumption were considered to be only approximate. A somewhat more precise measurement of water consumption was made possible with the use of self-feeding water bottles. Hygrothermograph records revealed that the temperature of the laboratory rooms averaged 68°F., varying only between 62° and 72°, while the relative humidity varied between 50 and 80 per cent with an average of about 60 per cent.

At the end of the experiment when a full response in the experimentals had been obtained, as indicated by a marked increase in body weight, all birds were sacrificed. Subcutaneous, peritoneal, and total body lipids were extracted in exactly the same manner as had been done previously with birds from the wild population (Odum and Perkinson, 1951).

RESULTS

Changes in body weight are shown in figure 1. There was an initial drop in body weight in all three groups of birds and then a slight rise. Between January 10 and February 1 birds in the two experimental groups (A and B), in contrast to those in the control group (C), increased markedly in weight. A similar pattern of weight change was obtained by Wolfson (1952) in White-throated Sparrows using a more forcing light schedule (beginning in mid-January) of 5:1, or a continuous photoperiod of 20 hours; in these cases a full response was obtained in about a month as compared with over two months in the present experiment. As indicated in figure 1 both the timing and the amplitude of the response, as far as weight changes were concerned, were similar in groups A and B; birds increased in weight as readily on a high fat as on a low fat diet. However, as will be noted below, group A birds did become a little fatter.

An essentially normal prenuptial molt occurred in both experimental groups coincident with the weight increase as shown in figure 1. No sign of molt was observed in any of the control birds. In nature the prenuptial molt occurs in March or early April prior to the premigration weight increase; that is, birds in nature do not get fat and molt at the same time. In our experiments the birds were able to telescope both of the energy demanding changes when they were subjected to strong light stimulus in the presence of abundant food which could be obtained with a minimum of exercise. Farner and Mewaldt (1955:115) also report that "molt and weight responses, which are sequential under natural conditions in spring, can develop simultaneously under experimental conditions" in the White-crowned Sparrow (*Z. leucophrys gambelii*). It should be borne in mind that we are here considering the prenuptial molt, which is a partial molt involving the body but not the flight feathers, and not the complete postnuptial or annual molt which normally occurs, or may be experimentally induced, on short or decreasing photoperiods (Lesher and Kendeigh, 1941).

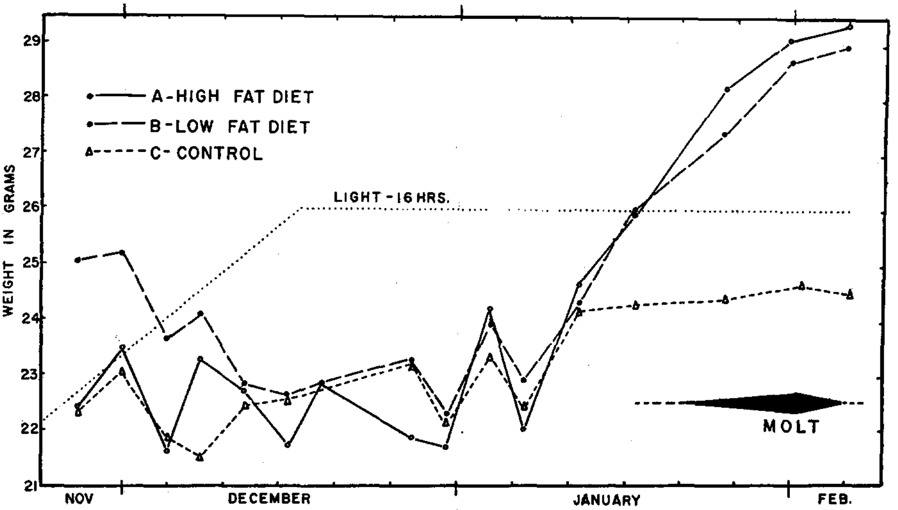

Fig. 1. Changes in weight of two experimental groups and one control group of White-throated Sparrows. Light schedule and time of molt for experimental groups shown.

It would appear that physiological changes which occur prior to northward migration do not represent chain reactions in the sense that one change (molt) must necessarily precede another change (fat deposition). It may be a matter of different hormone thresholds, the molt occurring at a lower level of pituitary stimulation. In wild birds once the molt is underway, the fat deposition might well be delayed because of the energy demands of feather growth even though the threshold for fat deposition had been reached in the meantime. This might explain why fat deposition in wild birds begins so rapidly after the molt is completed.

In nature, males increase in weight sooner than and migrate ahead of females by as much as two weeks (Odum, 1949). In figure 2 the average weights of the 11 males and the 11 females which made up the two experimental groups are shown. Weight changes in the two sexes, throughout the two and a half month experiment, almost exactly paralleled each other, but males reached the peak a few days before the females. Thus, even with the forcing light schedule the difference in response between the sexes is evident.

The lipid levels of experimental and control birds are compared with those of wild birds in table 1. It is evident that birds subjected to increased photoperiods very closely resembled normal premigratory birds both in the total amount of fat and its distribution within the two major deposits. This was especially true of birds in group A, which accumulated a somewhat larger total amount of fat than birds on the low fat diet. The difference in subcutaneous lipids of the two experimental groups was significant at the 95 but not at the 99 per cent level while differences in abdominal lipids were not significant (table 2).

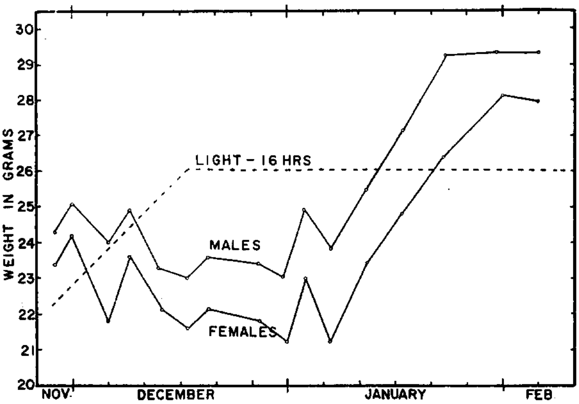

Fig. 2. Comparison of weight changes of 11 males and 11 females from the two experimental groups subjected to long photoperiods as shown.

Normal winter birds accumulate considerable fat in the subcutaneous region but comparatively little in the abdominal region (see table 1). Note that both groups of experimental birds had the characteristic concentration of abdominal lipids of normal premigratory birds. Control birds, on the other hand, resembled normal winter birds in having a low percentage of abdominal fat, and they were also less fat generally.

Table 1

Extracted Lipids in Grams in Experimentally Induced Lipid Deposition as Compared with Seasonal Variation in Wild Birds

	No. birds	Average body weight	Subcutaneous lipids	Per cent body weight	Abdominal lipids	Per cent body weight	Total lipids	Per cent body weight
Wild Series[1]								
Post migration (fall)	23	26.3	0.615	2.34	0.118	0.45	1.804	6.88
Winter	15	29.9	1.551	5.19	0.266	0.89	3.608	12.05
Molt (early spring)	27	27.1	0.597	2.20	0.097	0.36	1.688	6.25
Premigration (late spring)	19	30.4	2.076	6.83	0.599	1.97	4.806	16.66
Experimental Series								
A (high fat diet)	10	29.4	2.156	7.33[2]	0.663	2.25[3]	4.911	16.70
B (low fat diet)	12	29.0	1.614	5.57[2]	0.624	2.15[3]	4.266	14.71
C (control)	5	24.8	1.029	4.15	0.240	0.97	2.594	10.46

[1] Data from Odum and Perkinson (1951) table 2.
[2] Difference between A and B significant at 95 per cent level ($T = 2.28$; $P = 0.04$).
[3] Difference between A and B not significant.

It appears from these data that the normal spring premigratory deposition was quantitatively duplicated in amount and body distribution by the manipulation of the single environmental factor, namely light, and that the amount of fat in the diet had little effect on the magnitude of the deposition. A high fat diet did not cause the birds to become any fatter than normal premigratory birds in nature.

The caloric value of food consumed during the experiment is shown in table 2. No correction has been made for unmetabolized food in the excreta. In a later experiment it was found that food utilization efficiency did not differ between the two diets. In the experimentals, average calories used per bird per day paralleled changes in weight (compare fig. 1 and table 2). The first increase in food consumption coincided or slightly preceded the first evident increase in weight, and the maximum food consumption occurred during the period of rapid increase in weight between January 10 and 30. It is also evident from table 2 that birds in group A consumed more energy than birds in group B. However, birds of group B started at a lower level at the onset of the experiment so that the rate of increase was about the same for both groups.

Table 2

Food Consumption in Calories per Bird per Day

	Series A Increased photoperiod, high fat diet	Series B Increased photoperiod, low fat diet	Series C (control) Normal photoperiod, mixed diet
Nov. 27–Dec. 5	17.8	14.2	13.6
Dec. 5–Dec. 11	14.0	11.4	14.6
Dec. 11–Dec. 18	11.5	12.3	12.6
Dec. 18–Dec. 24	16.9	14.0	12.9
Dec. 24–Dec. 31	19.4	14.6	15.1
Dec. 31–Jan. 7	24.3	18.3	15.8
Jan. 7–Jan. 12	22.0	18.1	16.5
Jan. 12–Jan. 18	26.0	18.4	17.1
Jan. 18–Jan. 25	24.8	19.6	17.9
Jan. 25–Jan. 30	26.1	25.0	18.0
Jan. 30–Feb. 4	22.8	22.4	17.1
Feb. 4–Feb. 8	23.3	18.5	17.6
Average	20.7	17.2	15.7

Water consumption during the experiment is summarized in table 3. In both experimental groups, in contrast to controls, there was an increase in water consumption, especially after fat deposition was well underway. The increase was more marked in birds on the high fat diet. The increase in water is presumedly related to the need for increased heat loss as birds become enveloped in a blanket of fat, especially since they were confined to cages in a relatively warm room.

It is well known that in rats certain hypothalamic lesions, which may be experimen-

Table 3

Water Consumption in Milliliters per Bird per Day

	Series A Increased photoperiod, high fat diet	Series B Increased photoperiod, low fat diet	Series C (control) Normal photoperiod, mixed diet
Nov. 29–Dec. 8	9.9	8.8	10.0
Dec. 8–Dec. 15	10.2	8.4	11.5
Dec. 15–Dec. 20	11.5	8.4	
Dec. 24–Jan. 1	8.1	10.0	12.7
Jan. 1–Jan. 6[1]	14.8	13.5	14.2
Jan. 6–Jan. 12	15.6	12.1	
Jan. 12–Jan. 22	13.2	12.8	12.1
Jan. 22–Jan. 31[2]	17.4	14.4	10.7
Jan. 31–Feb. 8[3]	27.5	17.3	13.2

[1] First evidence of increase in weight in experimentals.
[2] Rapid increase in weight in experimentals.
[3] Maximum lipid deposition in experimentals.

tally produced, cause the animals to become very obese. Appetite and food consumption increase, but Brobeck (1946) reports that even when food is restricted to that used by the normal rat the experimental rats may still get fat. He suggested that the habit of eating rapidly and a reduction in heat production allows conversion of more food energy to fat. Since water consumption increased in our experiment on birds, it might be assumed that heat production energy was not diverted into fat since birds were having to take more water to get rid of excess heat. A logical follow-up experiment, of course, would involve restricting food to 15 calories per bird per day, applying increased photoperiods, and then observing whether the birds were able to accumulate fat.

SUMMARY

An experiment was designed to compare photoperiod-induced lipid deposition of birds on high fat and low fat diets, to determine food and water consumption, and to determine if induced fat deposits are quantitatively similar to normal premigratory deposits.

Beginning in late November two groups of White-throated Sparrows, one on a high fat diet (pecans, 60 per cent fat) and the other on a low fat diet (seeds, 6 per cent fat), were subjected to gradually increased photoperiods up to 16 hours. A third, or control, group on a mixed diet was subjected to normal late fall and early winter photoperiods.

Both groups of experimental birds, in contrast to controls, increased markedly in weight between January 10 and February 1 while at the same time undergoing a prenuptial molt, demonstrating that these two energy-demanding events, which occur separately in nature, can be telescoped under conditions of forcing stimuli and ample food (fig. 1). Males increased in weight sooner than females as is normal in the field in spring (fig. 2).

The lipid levels in experimental birds sacrificed when maximum weight was obtained were very similar to normal premigratory birds (Odum and Perkinson, 1951) both as to total amount of fat and its distribution between subcutaneous and abdominal deposits. Controls resembled normal winter birds. Birds on the high fat diet accumulated somewhat more subcutaneous fat and more closely resembled normal premigratory birds than did those on the low fat diet. It is concluded that the normal spring premigratory deposition was quantitatively duplicated by the manipulation of the single factor of light and that the amount of fat in the diet had but little effect on the magnitude of the deposition (table 1).

Food consumption, calculated as calories consumed and uncorrected for fecal loss, in the experimentals increased from 11 to 17 calories per bird per day up to as high as 26 calories during the period of most rapid weight increase and molting (table 2).

Water consumption in experimentals increased rather markedly during the last stages of weight increase, especially in birds on the high fat diet, presumably due to the increased need for internal heat loss (table 3).

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