LIPID DEPOSITION AND GONADAL RECRUDESCENCE IN RESPONSE TO PHOTOPERIODIC MANIPULATIONS IN THE SLATE-COLORED JUNCO

David W. Johnston

Stimulated by Rowan's epochal discoveries in the 1920's, many investigations have recently centered upon photoperiodic manipulations and their bearing upon the complexities of migration. Important among these have been experiments concerned with premigratory fat (lipid) deposition, a phenomenon noted as early as 1822 by Naumann (*fide* Farner, 1955). More recently, Odum and Perkinson (1951: 230) stated that "much concerning migration may be learned from a study of the lipid levels in a population," and, at present, there is a considerable body of literature relating to premigratory lipid deposition in birds, with fringillids of the genera *Zonotrichia* and *Junco* being the most commonly used by American investigators. Farner (1955) summarizes many of the experimental data relating to this subject, one aspect of which is that nonmigratory subspecies of a given species do not amass vernal lipid deposits although migratory subspecies usually do. These observations relate principally to the increasing photoperiod of the spring, and involve qualitative observations of lipid deposition.

About a decade ago Odum and his co-workers realized the need for quantitative data on lipids, especially if the bioenergetics of migratory flights were to be elucidated. Since that time, he, Farner, King, and others in this country have conclusively shown that White-throated and White-crowned sparrows (*Z. albicollis* and *Z. leucophrys*), as well as some other migrants, might increase their premigratory lipid contents to as much as 25 per cent of the body weight (Odum and Connell, 1956). Indeed, some birds were shown to have 30–40 per cent lipids while migrating. In the genus *Junco,* photoperiodic studies were begun by Rowan. These studies were continued by Wolfson, who, however, has been concerned chiefly with the role of various light periods in gonadal recrudescence and with subjective impressions of lipid deposits.

From an examination of this literature it is evident that many questions remained unanswered even in the widely used Slate-colored Junco (*J. hyemalis*). At least two questions were foremost as the present experiments were undertaken: (1) As far as gonads and total lipids are concerned, what would be the effect of a decreasing photoperiod? (2) How much lipid increase occurs in wild, premigratory, vernal juncos at the latitude of North Carolina as compared with birds exposed to a photoperiod increasing up to 16 hours per day? It is true that Wolfson's multifarious investigations had already dealt with some decreased photoperiod experiments, but his observations on lipids were not quantitative, pertained to juncos at a different latitude (Illinois), and represent a different migratory population.

METHODS

Juncos were trapped in mist nets at Winston-Salem, North Carolina, in mid-January 1960, and were immediately transferred to outdoor cages approximately 90 × 60 × 60 cm (3 × 2 × 2 feet). Ample scratch feed and water were supplied daily with periodic supplements of lettuce or cabbage or chickweed. Thirteen birds were retained as controls under natural light conditions. When the last of these were sacrificed on 4 May the day length had increased to 13 hours and 50 minutes. On 21 January photoperiodic manipulations were begun on two groups of birds. On this day there were 10 hours and 10 minutes of natural daylight. Thirteen other birds were exposed to artifical light increments (100-watt bulb inside the cage operated by a poultry timer) of 15 minutes a day until a 16-hour day was reached on 13 February. These birds are designated as 16L–8D, referring, respectively, to the number of hours of light and darkness in a 24-hour period.

In an additional group of 12 birds the photoperiod was reduced 15 minutes a day by covering the cage with a tight-fitting box. A six-hour day was reached by 6 February, and was maintained thereafter. Unfortunately, many of these 6L–18D birds accidentally escaped on 11 March, so another group of eight was begun on this same light schedule at that time. In the results, tables, and figures to follow no distinction has been made between these two groups of 6L–18D birds. The only difference would be the length of time during which they were on this photoperiod, and this difference was considered to be inconsequential, as evidenced by the uniformity of results for all birds on this short photoperiod. In general, the birds started on the 6L–18D schedule in January were sacrificed first (April) and those started in March, last (May).

So that comparisons might be available with the feral, wintering population of juncos, periodic samples were taken in the nets. These birds, most of which were taken in 1960, are henceforth designated as "net" birds. It is important to note that the local juncos began to diminish in numbers by the end of March, with only an occasional individual or small group being found until mid-April. Furthermore, only two males, as compared with 11 females, were caught after 1 April. The assumption is that the bulk of the population (especially the males) migrates northward from the Winston-Salem area by the end of March. A comparable migratory pattern is known for other parts of North Carolina and for Winston-Salem in other years except for one interesting exception. A single, lingering female was watched for two weeks after all the other juncos had migrated by mid-April of 1961. This female was finally trapped on 30 April and will be considered later in this discussion.

At approximately two-week intervals after mid-March two to four birds from each of the four groups (net, control, 16L–8D, 6L–18D) were killed with ether, weighed, and frozen. From each bird three weights were obtained: water, nonlipid dry (principally protein and carbohydrate), and lipid. The birds were first desiccated in a vacuum oven for at least 24 hours, thus providing by subtraction from the original total weight the data on water content. The dried carcass was then ground in a blender and extracted with two boilings of 95 per cent ethanol and ethanol : diethyl ether (2: 1). This mass was filtered, and the dried residue provided the nonlipid dry weight. The filtrate was finally extracted with petroleum ether from which the total lipids were obtained (by evaporation of the solvent) and weighed. This technique is a refinement of that employed by Odum (1958).

Prior to freezing, the gonads of each bird were examined and measured. The testicular volume was computed by employing the formula for the volume of an ellipsoid ($V = 4/3\ \pi a b^2$).

Subspecific Determination

Because Wolfson (1942) clearly demonstrated that the nonmigratory subspecies of *Junco oreganus* in California do not have heavy lipid deposits, it was deemed necessary to identify critically the subspecies of *Junco hyemalis* wintering in the Winston-Salem, North Carolina, area. Accordingly, a series of junco study specimens was prepared from random birds caught in the nets between 12 November and 21 January. Nine birds, representing both adult and first-year males and females, were examined carefully, and showed none of the distinctive subspecific characteristics of either *J. h. carolinensis* or *J. h. cismontanus*. Alden H. Miller subsequently identified all of these specimens as *J. h. hyemalis*. Although *carolinensis* is known to breed in the mountains 120 km (75 miles) to the west, apparently it is sedentary and does not come to the Winston-Salem area in winter.

Results

Gonadal recrudescence. The gonads of all birds were examined for evidence of increased development, with gonad size being used as the criterion. No histologic sections were prepared, but some large testes were macerated to show spermatozoa. The results of these examinations are summarized in Table 1. Noteworthy is the absence of a significant increase in gonad size of all wild, premigratory birds. On the other hand, the control males, especially, showed an increase in testis size under a natural

TABLE 1
SIZE OF GONADS IN WILD AND EXPERIMENTAL JUNCOS

	Beginning of experiments	*Termination of experiments*		
	January–February	*Early April*	*Late April*	*Early May*
Net				
males	*1.09 mm^3 (6**)	1.57 (2)		
females	follicles < 1 mm (4)	fol. < 1 (11)		
Control				
males		2.65 (2)	7.32 (3)	18.8 (2)
females	fol. < 1 (2)	fol. < 1 (1)	fol. < 1–1 (2)	
16L–8D				
males	2.35 (1)	178.7 (2)	131.7 (1)	91.4 (1)
females		fol. 2 (1)	fol. 1 (1)	fol. 1 (1)
6L–18D				
males		0.70 (3)	0.61 (2)	1.96 (3)
females	fol. < 1 (1)	fol. < 1 (1)		

* Average volume of left testes.
** Figures in parentheses are number of birds examined.

12- or 13-hour daily photoperiod by late April. Microscopically, however, no mature spermatozoa could be found in the slightly enlarged testes of these control males, but mature sperm were present in all the greatly enlarged testes of the 16L–8D males after 1 April. Males on 6L–18D all had small testes.

Body weight. On the basis of previous work on premigratory conditions of birds a decisive weight increase would be expected in at least the feral juncos, but Figure 1 shows no such weight increase except in the 16L–8D birds. In Illinois Wolfson (pers. comm.) has noted a gain in male juncos from 18–20 to 23–26 g in the spring, and a comparable gain in females from 16–18 to 21–23 g.

Of 60 birds examined in the present study between January and mid-April, wild males showed a loss in weight of 4.5 per cent, and the 6L–18D males had a loss of 2.5 per cent. On the other hand, the control males showed a gain of 7.1 per cent, and the 16L–8D males, a gain of 12.3 per cent. Weights of 10 females followed a similar pattern. In no instance, however, were there weight increases comparable to those reported by Wolfson for juncos in Illinois or for the White-throated Sparrow in Georgia (Odum, 1949).

Attention should be called to some additional features of Figure 1. The noticeable weight loss of all birds in mid-February was probably the result of extreme ambient temperature of –8 to –10° C (10–15° F) and a heavy blanket of snow that persisted for more than two weeks. It appears likely that all juncos, both caged and feral, necessarily burned up most or all of their lipid deposits at this time. In fact, a few juncos expired in the cages, and others were found dead in the snow near the nets, their carcasses

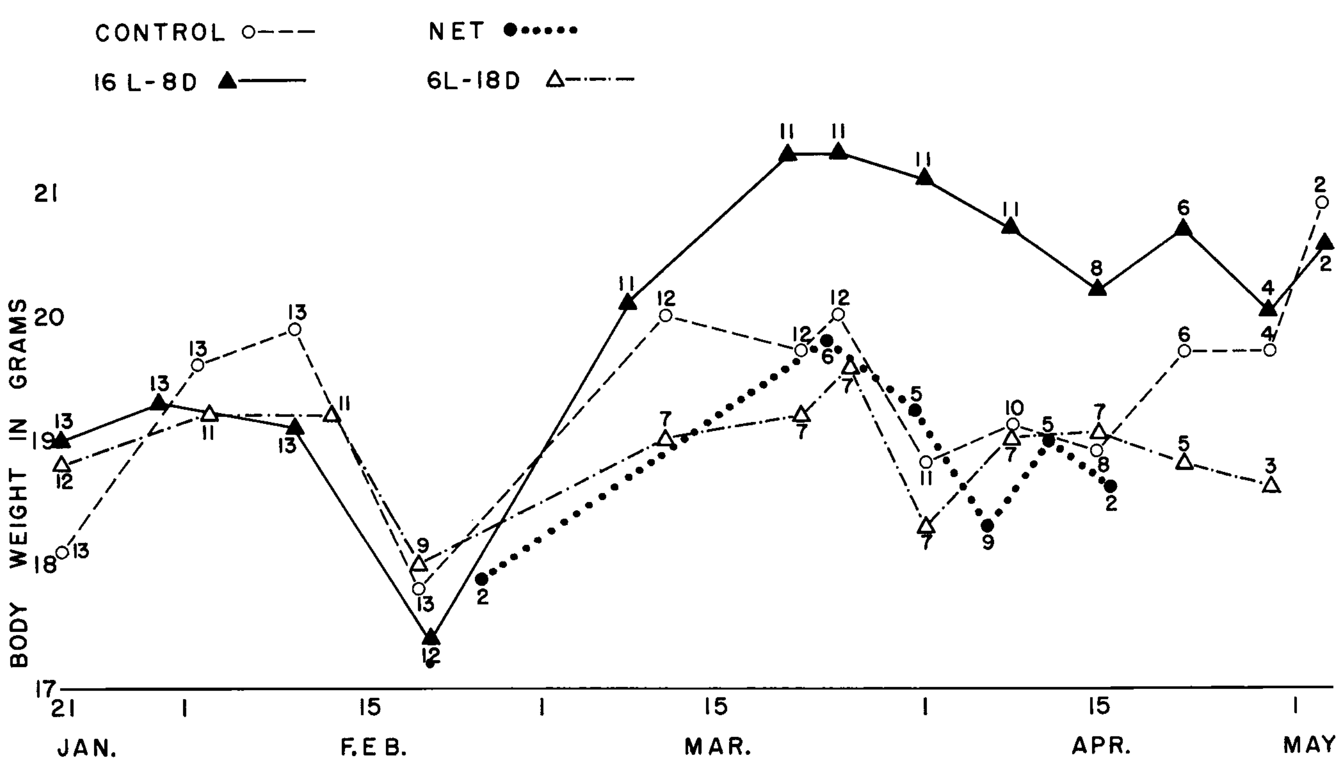

Figure 1. Mean weights of Slate-colored Juncos under different light conditions. Numeral at each point is the number of birds examined.

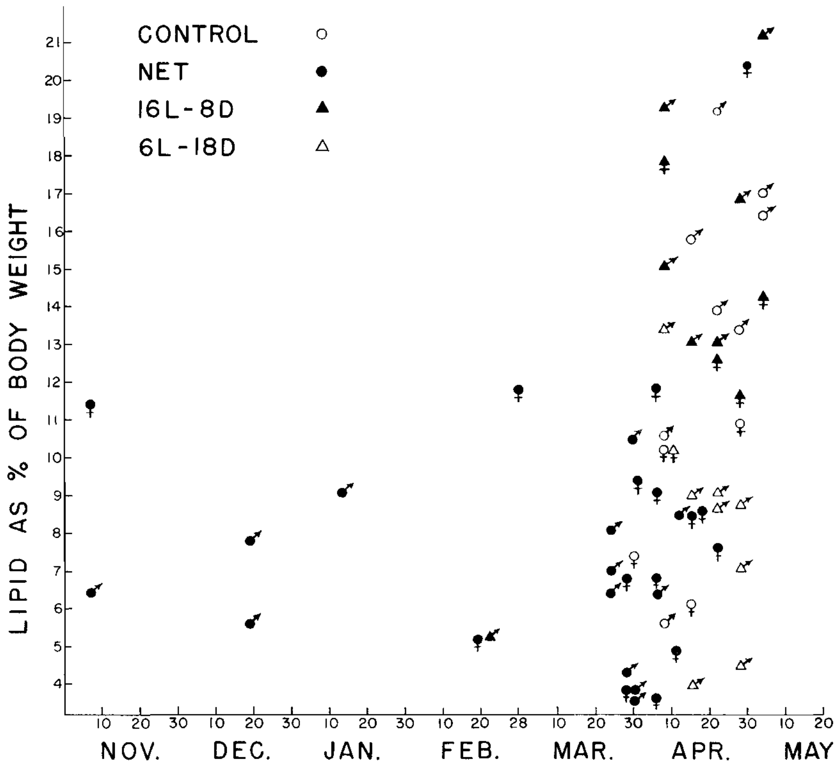

Figure 2. Lipid contents of Slate-colored Juncos under different light conditions.

being extremely emaciated. This observation is consonant with the report of Helms and Drury (1960: 27) that the winter weight of juncos is temperature-dependent. It is also interesting to note that the juncos in the present study regained their normal weights in at least two weeks (perhaps sooner) but that the experimental White-crowned Sparrows of King (1961) regained normal weight in three to five days.

An increase in weight of the control birds after mid-April occurred at a time when all juncos had migrated northward from the area. One might postulate that if juncos had remained here until early or mid-May as they do at other latitudes (for example, Illinois), they would have gained weight appreciably. This suggestion is further strengthened by one female in 1961 that lingered two weeks after all the other juncos had migrated. This bird weighed 21.3 g and contained 4.36 g of lipid (20.4 per cent of wet weight), a value higher than that of most birds exposed to the increased photoperiod (see Figure 2). These changes in body weights will be discussed further as they relate to lipid deposition.

TABLE 2

WEIGHTS IN GRAMS OF CARCASS FRACTIONS OF MALE SLATE-COLORED JUNCOS

		Water			*Nonlipid, dry*			*Lipid*		
	N	*Mean*	*S.D.*	*V.*	*Mean*	*S.D.*	*V.*	*Mean*	*S.D.*	*V.*
Net	12	12.4 (62.1)*	0.82	6.6	6.2 (31.1)	0.63	5.2	1.4 (6.8)	0.37	26.4
Control	8	11.6 (57.3)	0.54	4.7	5.8 (28.7)	0.45	7.8	2.9 (14.0)	0.75	25.8
16L–8D	7	11.4 (56.4)	0.89	7.8	5.8 (28.8)	0.96	16.5	3.1 (14.8)	1.19	38.4
6L–18D	8	11.9 (62.9)	1.40	12.1	5.5 (29.0)	0.72	13.1	1.6 (8.1)	0.56	35.0

* Figures in parentheses are mean percentages of total body weight.

Lipid deposits. In Figure 2 lipids are plotted as percentage of total weight against time for the four groups of juncos. It can be seen that lipid weights tend to vary as total body weight (cf. Figure 1). Thus a heavy bird, whether control or 16L–8D after mid-March, had a noticeably high lipid content (10–20 per cent). Conversely, the premigratory, wild juncos, which averaged only about 19 g in body weight, contained only from 3 to 9 per cent lipids. Birds on the decreased light schedule had similarly low lipid values.

As in the case of body weights, the lipid percentage increased sharply in control birds after all the wild birds had migrated. Here, again, the gain in weight attributable to increased lipid deposition would be noticeable only if the juncos were to remain beyond mid-April.

The other carcass fractions (water and nonlipid, dry weights; see Table 2) obtained during lipid extractions were much less variable. Variance within a given experimental group is considerably greater for the lipids than for the other fractions. The average water content of juncos in all four groups was about 60 per cent, and the average lipid-free, dry weight was about 30 per cent. Of course these values varied somewhat as the lipid per cent varied, but the water content and lipid-free, dry contents were more nearly constant. This is substantiated by the earlier report of McGreal and Farner (1956) to the effect that White-crowned Sparrows have a premigratory weight increase in spring due to increased lipids, not water content.

DISCUSSION

In general, previous investigations on the reproductive condition of premigratory birds have shown an increase in gonad size and activity prior to migration, and, under photoperiodic stimulation, migratory subspecies of juncos and *Zonotrichia* sparrows respond with gonadal recrudescence. Wolfson and Winchester (1960), for example, reported that Slate-colored Juncos in Illinois had greatly enlarged testes containing spermatozoa after about 30 days of a 16L–32D light schedule. Wolfson, working with Oregon Juncos (*Junco oreganus*), noted a premigratory testicular enlargement to only 4 mm^3, but these testes contained a maximum of interstitial cells. The experiments reported there differed from these patterns, however, for none of the premigratory, wild juncos showed any significant gonadal recrudescence (up to 1.57 mm^3 volume), and the 16L–8D juncos required about two months for the appearance of complete spermatogenesis. These differences, as elaborated upon below, are believed to be associated in part with genetic population differences.

Marshall (1961) discusses in some detail matters relating to "inactive" gonads and asserts (p. 328) that "there is as yet no valid evidence that any prenuptial migrant has left its contranuptial locality with truly inactive gonads." Although there is no evidence to show that the small testes of the premigratory juncos in this study were "truly inactive," *i.e.*, displaying no increase in number or activity of the interstitial cells, it is nonetheless true that their gonads were extremely small as compared with the size attained by birds on the 16L–8D schedule.

It has long been assumed that premigratory lipid deposition is a prerequisite for spring migration (for a summary and review see Farner, 1955). This belief stemmed from observations on juncos by Wolfson (1942, 1945) and on the *Zonotrichia* sparrows by Odum and Perkinson (1951) and McGreal and Farner (1956). In fact Odum and Perkinson stated (1951: 230) that "lipid deposition is a necessary prerequisite for migration and that an individual bird will begin migration only when this is completed." It seems, however, that there are notable exceptions to this condition, for observational and experimental data on juncos presented here clearly do not show a premigratory increase in lipid deposits or an increase in weight. Furthermore, Nice (1946) indicated that there is no significant premigratory increase in weight of migratory Song Sparrows (*Melospiza melodia*) when compared with the resident birds in Ohio.

In the southeastern United States (especially North Carolina and Georgia) at least four passerine species show differences in vernal migratory patterns and lipid deposition. White-throated Sparrows and Myrtle Warblers (*Dendroica coronata*) remain quite late in the spring (mid-May) before migrating northward, and, in the few days or weeks just prior to migrating, deposit significant quantities of lipids. We assume that these two species then migrate, perhaps nonstop, to their northerly breeding grounds. (Wolfson (1954) believes that the White-throated Sparrows migrating through Illinois move in hops of about 480 km (300 miles) at a time, but this is not necessarily true for the populations wintering in the southeastern United States.) On the other hand, Purple Finches (*Carpodacus purpureus*) and Slate-colored Juncos migrate earlier (by the end of March), do not have increased lipid deposits, and, we assume, carry out their migratory journeys in short hops. In the latter instance a bird would not need as much energy supply afforded by lipid deposits.

Odum, Connell, and Stoddard (1961) have clearly shown a correlation between premigratory lipid deposition and migratory patterns. The Slate-colored Junco, wintering in North Carolina, evidently belongs to their first class of migrants, *i.e.*, short-range migrants, which become moderately obese, but begin migration before a peak lipid deposition. The closest possible breeding grounds for typical *J. h. hyemalis* is midcentral New York, about 720 km (450 miles) northeast of Winston-Salem (Miller, 1941: 323). Perhaps the juncos wintering in North Carolina are from this New York population, but banding records from the files of the U.S. Fish and Wildlife Service indicate otherwise. At least two birds, both banded near Toronto, Ontario (one in July), have been recovered at Wilson and Merry Hill, North Carolina, more than 160 km (100 miles) east of Winston-Salem. The distance from the Ontario breeding grounds to mid-North Carolina is somewhat greater than 800 km (500 miles). Several birds banded in Massachusetts were taken in the Carolinas about 800 km away and some in Quebec 650 km (400 miles) to the north. It would seem, then, that we are dealing with flight ranges of some 600–800 km overland. If the assumptions made by Odum *et al.* (1961: 520 ff.) are correct, we can then estimate the flight ranges for these juncos. The premigratory males, containing an average of 1.4 g lipid, could fly only about 210 km (130 miles); the heaviest control male, having 3.6 g lipid in early May, could fly 560 km (350 miles); and the 16L–8D males, containing an average of 3.1 g lipid, could fly about 517 km (320 miles). From these data it would be impossible for these juncos to migrate nonstop from North Carolina to the breeding ground. These estimated flight distances further assume that all the lipid deposits can be or are used for flight energy, but there is much evidence to indicate that a migrant at the terminus of its flight has not always depleted its lipid stores.

The fact that some subspecies might be short-distance migrants with small, vernal lipid deposits has also been reported by Farner *et al.* (1961). In this study, lipid and glycogen deposits are compared for a long-distance migrant (*Zonotrichia leucophrys gambelii*) and a short-distance migrant (*Junco oreganus montanus*) in Washington. The conclusion of the study (p. 137) was that in the junco ". . . in which the distance between wintering and breeding areas is relatively small, the photoperiodically induced fat storage, as indicated by change in body weight . . ., is much less extensive . . ." than in the White-crowned Sparrow. The data, however, are not for total body lipids but were taken from analyses of samples of liver and muscle, and from body weights that are an index of the amount of fat deposited.

The effects of the different photoperiods upon gonadal recrudescence and lipid deposition in *Junco hyemalis* have been reviewed by Wolfson (1958, 1959a, 1959b). For example, in juncos kept on a 4L–8D–4L-8D schedule (1959a) there was no gonad or lipid response, but with a longer light period (Wolfson, 1959b; 12L–16D) there was both gonadal and lipid response. At least, there was a gain in weight of males from 18 to 23.5 g. Also, birds on a 16L–32D schedule (Wolfson and Winchester, 1960) and those given 15.5 hours of daylight (Wolfson and Winn, 1948) both showed a marked increase in weight, attributed to increased lipid deposits.

Since the photoperiodic experiments reported here failed to produce results exactly similar to those reported by Wolfson and by Helms and Drury, we must attempt to rationalize the differences. At first, it seemed that there might be some error in the photoperiodic experiments, but this possibility was ruled out when all juncos, both caged and wild, showed similar responses. Another possibility of error was the marked weight loss by all birds in February, but this situation has been discussed earlier. Furthermore, Engels and Jenner (1956) have reported that low temperatures merely retard the rate of testicular recrudescence in juncos, and are not prohibitive. In other words, the low temperature would have only a temporary modifying effect.

It seems, however, that there is a different physiologic response based upon differences in local populations and their migratory patterns. The wintering juncos in North Carolina occur at a different latitude (35° N) than the birds in Illinois (42° N) and, as indicated above, migrate earlier. If these populations were rather constant year after year, we could postulate that the North Carolina birds simply migrate before natural photoperiodic stimulation affects either the size of the reproductive organs or lipid deposition, but that these birds are physiologically capable of amassing considerable lipid deposits and gonadal recrudescence.

Finally, attention should be drawn again to the assertion of Wolfson (1947) that preliminary to spring migration there is a ". . . deposition of large amounts of . . . fat, with a concomitant increase in body weight to a maximum." Of course, Wolfson was not writing about resident species or subspecies. In any case, though, one must consider the migratory status of the local population. As demonstrated clearly here, those forms that migrate early and evidently more slowly do not necessarily have a marked, premigratory lipid deposition. Thus, the changes in physiologic state usually associated with the premigratory bird may or may not include lipid deposition.

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SUMMARY

In January 1960 Slate-colored Juncos were trapped at Winston-Salem, North Carolina, and were kept in outdoor cages until April or May. Three groups of the birds were subjected to the following photoperiods: (1) control, 10–13 hours of natural light, (2) increased light, 16 hours of light per day, and (3) decreased light, six hours of light per day. Periodically, wild juncos were obtained to provide data from nonconfined controls. Most wild juncos migrated northward by the end of March, and all were gone by mid-April (with only one known exception).

Samples were taken from each group through the spring to determine the extent, if any, of gonadal recrudescence, weight increase, and lipid deposition. None of the wild juncos showed any increase in gonad size or significant gain in weight or lipid content. Caged controls had enlarged gonads, increased weight, and lipid content only after mid-April when all the wild birds had migrated. Birds on the increased light schedule had enlarged gonads by 1 April, and by mid-March showed an increase in weight and lipid content. Birds kept on the short, six-hour photoperiod had undeveloped gonads and tended to lose weight and lipid deposits during the experiment period.

It is concluded that this population of wintering juncos does not increase its vernal, premigratory lipid deposits because it migrates relatively early in the spring and presumably covers short distances per unit time in the northward movement. The lean condition of these juncos amends previous contentions that migratory populations of birds must have additional lipid deposits prior to migrating, and suggests that the time and distance of migration are factors affecting lipid deposition.

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Department of Biology, Wake Forest College, Winston-Salem, North Carolina.