

EFFECTS OF EXTENDED TROPICAL PHOTOPERIOD AND TEMPERATURE ON THE DICKCISSEL

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The interplay between exogenous and endogenous factors in the regulation of the annual cycle of birds has received considerable discussion and experimental attention since the work of Rowan (see Marshall, 1961; Wolfson, 1960a). It has been argued that the annual cycle of tropical residents must be under predominantly endogenous control because of the constancy of their environment; but there are few instances reported for which such influence has been suggested to be primary (Chapin, 1954; Marshall and Roberts, 1959; Miller, 1959). With most tropical residents, environmental factors still operate to adjust the annual cycle so that the species breeds at the time most propitious for the survival of the young (Keast, 1959; Marshall and Disney, 1957; Skutch, 1950; Voous, 1950).

It has also been suggested that temperate-zone breeders wintering in the tropics likewise must be under a high level of internal control, and that exogenous factors must operate primarily during the period of the year at higher latitudes, annually setting the cycles of internal physiological events (Curry-Lindahl, 1958; Marshall and Williams, 1959). Merkel (1963) compared the long-term effects of constant photoperiods on two species of passerines having different migratory ranges. He concluded that the gonadal and weight cycles are more internally established in the Whitethroat, *Sylvia communis*, which is an equatorial migrant, than in the Robin, *Erithacus rubecula*, which remains within the North Temperate Zone during its migration. These results again suggest that tropical-wintering species depend to a great extent on endogenous control of physiological events.

The success of the Dickcissel, *Spiza americana*, which breeds in temperate North America and winters in the neotropics, is related to the photoperiod to which it is exposed during the breeding season. The longer photoperiods of the temperate summer result in the attainment of a positive energy balance of sufficient magnitude to facilitate successful breeding, even though the mean temperatures at these latitudes are a few degrees lower than those of its winter range during the same months (Zimmerman, 1965b). While still on the contranuptial area, Dickcissels initiate gonad recrudescence, accumulate depot fat, and captive birds show *Zugunruhe*. Although the photoperiodic control of these events has not been experimentally verified, it is probable that the developments of the reproductive and migratory states are partially dependent on light stimulation, as they are in temperate-zone (Dorst, 1955; Farner, 1964; Wolfson, 1963) and transequatorial migrants (Engels, 1959; Wolfson, 1963). To suggest that in the tropics these birds are unresponsive to the relatively constant daylengths is to disregard the conclusions of Wolfson (1952, 1960b) and Farner *et al.* (1953) on the nature of the effects of light. Through natural selection a species could adapt to the light periods that are experienced in its annual distributional pattern either by changes in the rate of response to stimulation (Wolfson, 1959a) or the inclusion of a refractory period of appropriate length (Marshall, 1960), or both.

In order to ascertain the dependency of Dickcissels upon their natural photoperiod regime, birds were held for as long as 21 months under conditions of temperature and photoperiod that approximated those of their wintering grounds. This

paper reports the effects of this treatment on body weight, molt, and locomotor activity.

METHODS

Four groups of birds were utilized: winter-range control, summer-range control, experimental I, and experimental II.

The function of the two control groups in the experimental design was to allow monitoring of weight changes, molt, and nightly unrest of captives exposed to naturally occurring temperature and photoperiod of the summer and winter ranges. These data could then be compared with weight change, molt, and migration in the wild population as well as providing reference for these kinds of data collected from birds similarly held captive in the experimental groups. The winter-range controls were 14 males and 9 females captured from wintering flocks near Tocumen and Pacora, Republic of Panamá, during January and early February 1961. These birds were kept outdoors on Barro Colorado Island in the Canal Zone until 6 May, which is after the peak of Dickcissel migration at this latitude. At this time they were sacrificed so that the amounts of water, lipid, and protein in their bodies could be determined (Zimmerman, 1965a).

The summer-range control group of 10 birds was started at Champaign, Illinois, during late May and June 1961, and held outdoors past the period of the species' normal fall departure. Some of these birds (3 males and 3 females) had been captured during the spring migration in the Canal Zone and sent by air express to Illinois. The remaining birds (3 males and 1 female) were obtained in Piatt County, Illinois, in June. Since the Dickcissel cannot survive the climatic conditions of winter at the latitude of Illinois, this second control group was terminated by the deaths of the birds. This prevented the maintenance of the controls under outdoor conditions through the second year of the experiments. It had to be assumed that the repetition of fat deposition, molt, and nightly unrest would be similarly related to the occurrence of these events in the wild population during 1962. There is some basis for this assumption since Whitethroats and Robins held in captivity for as long as five years failed to show any alteration in their annual weight cycles (Merkel, 1958). The weight and molt data of the control groups have been previously published in detail (Zimmerman, 1965b), so only the periods of occurrence for these events are indicated in figures 1 to 4, with the data being simply repeated for 1962.

The experimental I group consisted of four males and five females, which were captured from the same flocks and at the same time as the winter-range controls and placed in a thermostatically controlled, walk-in temperature cabinet at 29°C and a 12-hour daily photoperiod. On 11 May 1961 these birds were shipped by air express to Champaign, Illinois, and on 13 May were returned to a 12-hour photoperiod, but the temperature was not controlled at the previous level until 23 May. This group remained under these light and temperature conditions until 17 and 18 October 1962.

The experimental II group was composed of six males and two females obtained in Piatt County, Illinois, during the breeding season of 1961 and held outdoors until 20 August 1961. At this time they were subjected to a photoperiod regime that simulated a migration to the Panamanian wintering area, "leaving" Illinois on 20 August at 13 hours and 30 minutes of daylight, "reaching" southern México on 31 August at 12 hours and 30 minutes of light, and "arriving" in Panamá on 21

September at a daylength of 12 hours. These birds were then randomly placed with the experimental I group and held under the same constant environment until 17 and 18 October 1962. Since the two experimental groups differed in the amount of time they had been in captivity, any effect related to the duration of captivity was ascertained by a comparison of events between these groups.

The birds in all groups were housed individually in identical cages that were equipped for the continual recording of each bird's activity by a channel of an Esterline-Angus operations recorder. *Zugunruhe* is evidenced by a rapid increase over several weeks in nocturnal activity above 10 to 20 per cent of the total daily activity. Although in the temperate-wintering White-crowned Sparrow, *Zonotrichia leucophrys gambelii*, high ambient temperatures result in greater nocturnal activity in the absence of a long daily period of photostimulation (Farner and Mewaldt, 1953), similar results do not occur in the Dickcissel until air temperatures reach at least 42°C (Zimmerman, 1965b), well above the 29°C used in this investigation.

RESULTS

The partial prenuptial molt of the wild population was already in progress while birds were being captured in Panamá during late January. This molting decreased by the end of February and was finished by mid-March. In Illinois, Dickcissels begin the complete postnuptial molt immediately after nesting is completed. Although some wild males were in molt by the third week of July, the population as a whole did not reach a peak until the first week of August, and by mid-August the molt had tapered off markedly. Vernal fat deposition in Panamá is greatest in April, although the amount of lipids in the wild population at this time is still less than that of the winter-range controls killed about a month later (Zimmerman, 1965a). Dickcissels arriving in Illinois in May are not fat. There is no evidence of autumnal fattening in Illinois birds in early August; birds killed during migration in early October are fat (Tordoff and Mengel, 1956). Spring migration in Panamá is first apparent in late February, reaches a maximum from the middle of March to early April, and then is almost over by the end of April. Dickcissels could still be found on Barro Colorado Island, however, as late as 12 May. In Illinois fall migration begins in late August, and by mid-September they are gone.

In comparison with the wild population, the prenuptial molt of the winter-range controls was somewhat protracted, not ending in some individuals until the middle of April. Similarly the postnuptial molt of the summer-range controls was also drawn out, beginning during the first half of July and extending to the middle of September. The start of weight increase due to fat deposition in the winter-range controls is concurrent with this change in the wild population; but since the Canal Zone migrants that composed part of the summer-range controls did not undertake a migratory flight, these birds remained fat into June. Autumnal fattening of the summer-range controls was also coincident with the period of fat deposition in wild birds. Rapid increases to high levels of nocturnal activity occurred in the control groups during the spring and fall migratory periods and can properly be considered as expressions of *Zugunruhe* (Merkel, 1956).

The weight and molt data for the experimental I group are illustrated in figures 1 and 2, and similar data are presented in figures 3 and 4 for the experimental II's. Nocturnal locomotor activity as a percentage of total daily activity is presented in figure 5 for all groups. The points indicate weekly averages for each group. The periods of *Zugunruhe* in the controls are indicated on this figure. The vernal period

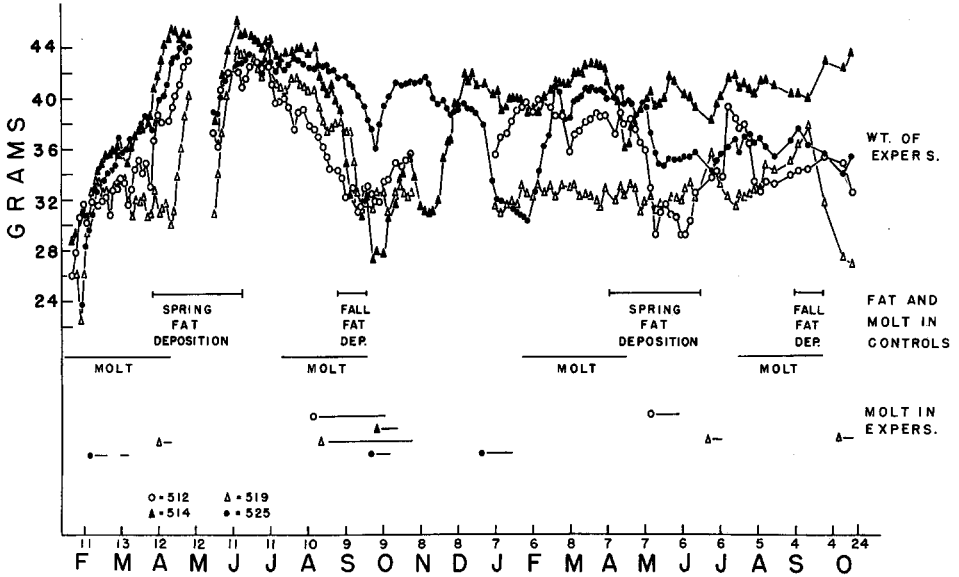


Figure 1. Time course of weight and molt in experimental I males.

has estimated limits, since the late molt of many of the winter-range controls appeared to interrupt the development of *Zugunruhe* and the birds were removed from the activity recorders before nightly unrest had begun to dissipate. Periods of missing data resulted from the nonavailability of activity recorders. Again, data for the controls are repeated for 1962.

A scoring system was devised to relate the temporal occurrence of premigratory

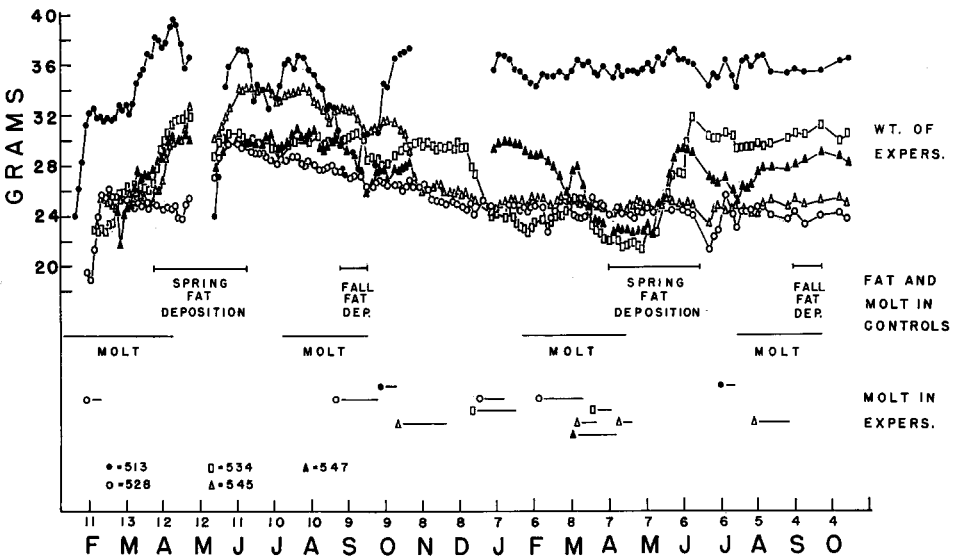


Figure 2. Time course of weight and molt in experimental I females.

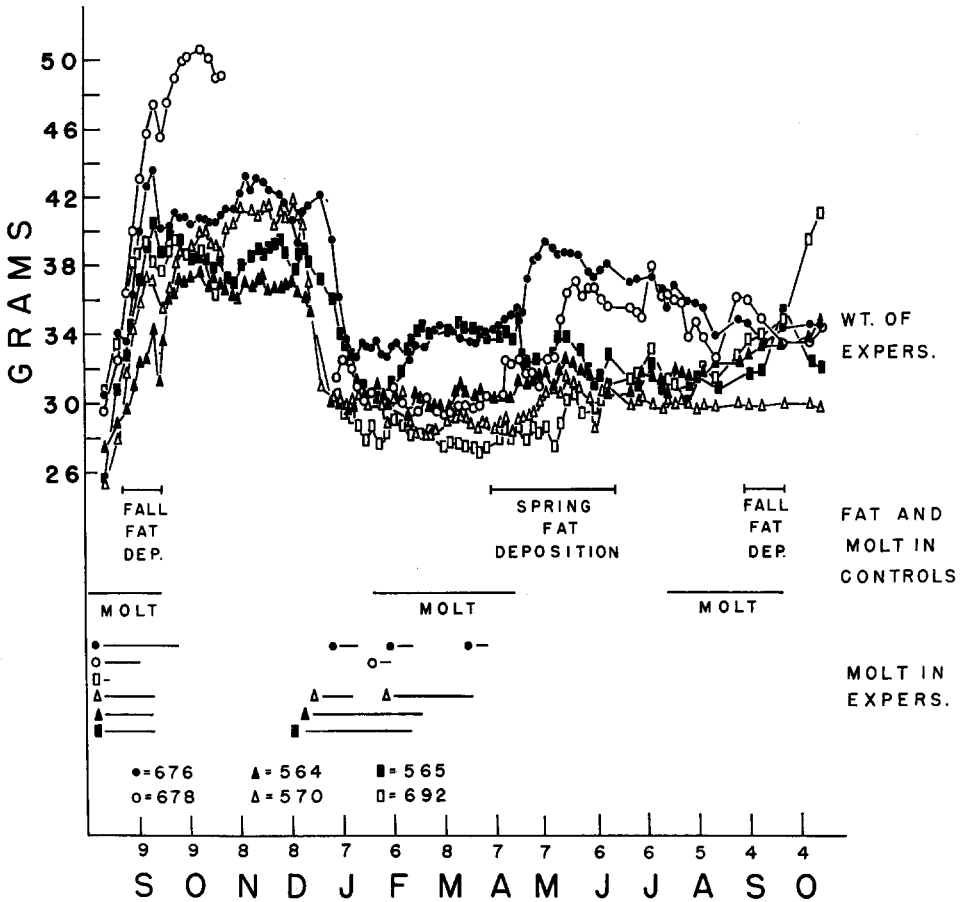


Figure 3. Time course of weight and molt in experimental II males.

fat deposition, as indicated by a rapid increase in weight, and molt in each experimental bird to the time of these events in the control group (table 1). An experimental bird was scored at "0" if fat accumulation began, reached a peak, or was in progress during the period between the beginning and peaking of deposition in the controls. If deposition was later in an experimental, the score is the positive number of days from the end of the control's period to the beginning of the weight increase in the experimental bird. If deposition was earlier in an experimental, the score is the negative number of days from the experimental's peak weight to the start of fat deposition in the controls. The molt of each experimental was scored at "0" if any molt at all occurred at any time coincident with the molt period of the controls. Earlier and later molts were scored in the same manner as for fat deposition. The prenuptial molt of all but one of the experimental I's had been completed before introduction into the controlled environment.

Nocturnal activity of the two experimental groups was scored against the periods of *Zugunruhe* in the controls (table 2). A score of "0" was given if the experimental group's average was beginning to increase, peaking, or progressing upward

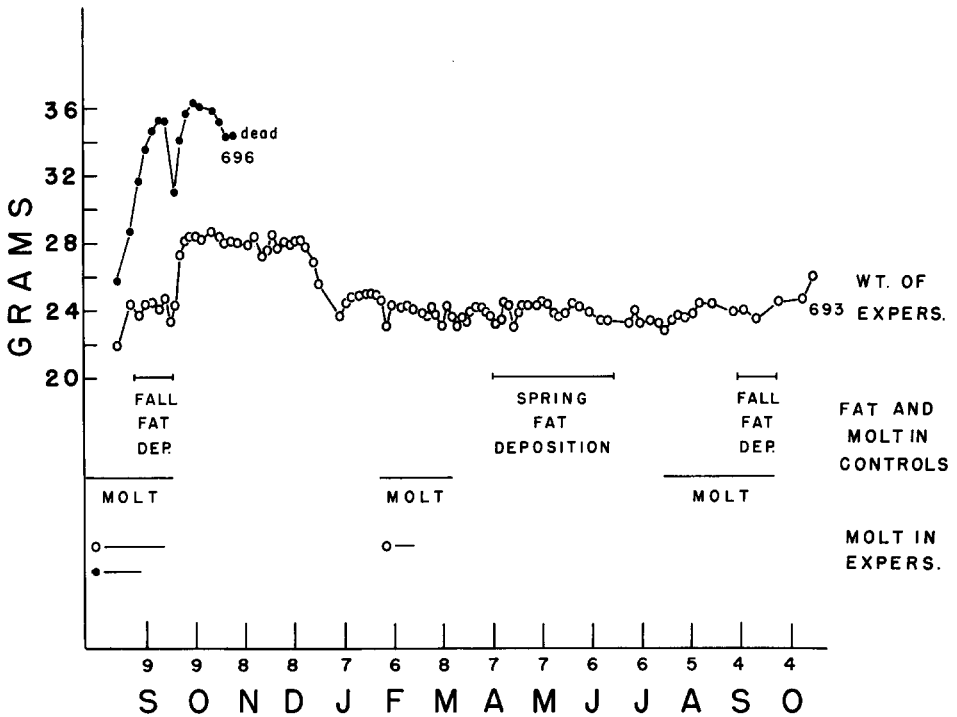


Figure 4. Time course of weight and molt in experimental II females.

during the occurrence of *Zugunruhe* in the controls. Early or late expressions of high nightly unrest were scored the same as the scoring of fat deposition in individual experimental birds.

In all cases if an event did not occur, it was scored as "not expressed (N.E.)." The scoring for all events in both experimental groups is summarized in table 3, and the percentage of each group that was in phase with the controls, out of phase, or not expressing the event is indicated.

DISCUSSION

The accumulation of depot fat and the occurrence of high levels of migratory restlessness are indicative of *Zugdisposition* (Merkel, 1960). This biannual migratory state is not initially suppressed when the Dickcissel is removed from the photoperiod regime it normally experiences in the wild, but it is, in time, essentially eliminated. *Zugunruhe* is either quite out of phase and weakly shown (experimental I's) or not expressed (experimental II's) by the end of one year of captivity under the light and temperature conditions of the contranuptial area. Premigratory fat deposition is still in phase after the end of one year in over 50 per cent of the experimentals, if we allow the 10 days' tardiness for the onset of the autumnal fattening of 1961 in the experimental I group. Beyond this time, however, fat deposition is likewise almost eliminated in, at least, the experimental I group.

These results do not support the notion that some environmental factor or environmentally induced behavioral or physiological event occurring during the nesting

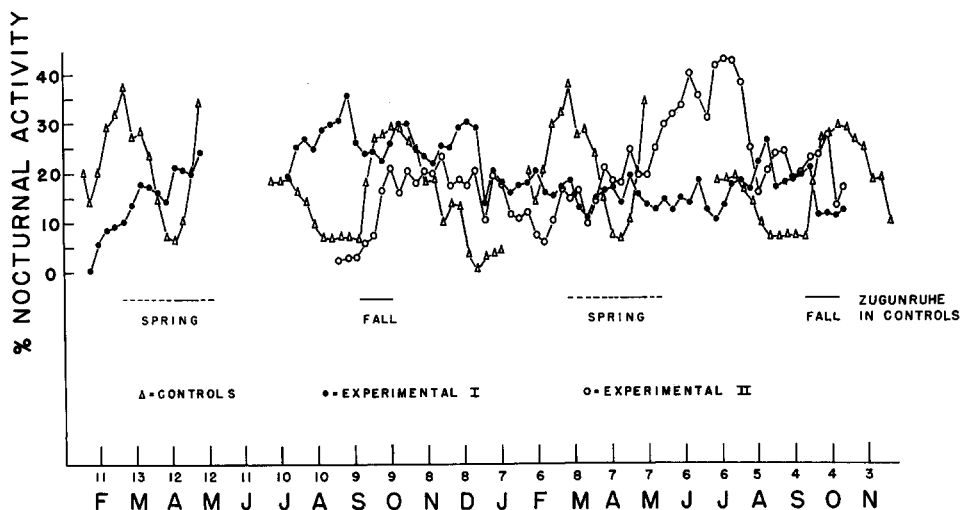


Figure 5. Nocturnal activity of controls, experimental I's, and experimental II's.

season acts as the sole time-giver for the cycling of these events through the entire year. The recency of exposure to the breeding environment between the experimental groups differs by one year; and therefore, the autumnal *Zugunruhe* of the experimental I's should have been eliminated in 1961, as *Zugunruhe* was after a comparable time period, measured from the time on the breeding grounds, in the experimental II group. Using the time of initial captivity as the beginning point, however, the waning of both components of *Zugdisposition* in both experimental groups is similar. The elimination of fat deposition and *Zugunruhe* is temporally dependent, not upon recency of exposure to the breeding environment, but simply upon recency of exposure to the natural environment, either that of the summer or winter range.

These results do show that there is a definite internal component involved in the development of *Zugdisposition*. To say that it is completely endogenous, however, is impossible, since these birds were not isolated from exogenous light and temperature stimuli. The net effect of the light regime was to reduce the total exposure to light, since the birds "missed" the long days of summer. There is no consistent indication in these data to suggest that the cycling of nightly unrest and fat deposition was simply retarded due to the slower rate of summation of light stimulation, as occurred in some of Weise's (1962) temperate migrants and as observed with the gonad response (Wolfson, 1952).

Although Wolfson (1952, 1959b) found that most temperate-wintering passerines kept at a constant 12-hour day did not molt, it was not until one year after being introduced into the experimental environment that molt was not expressed in the majority of these Dickcissels. Molting in this tropical migrant is thus internally regulated to some degree, and its eventual disappearance is related to the time since capture. From the very beginning, however, the expression of molt in the experimental I birds was somewhat disrupted. In over one-half of this group, only body feathers were shed during the postnuptial molt of 1961, and thus the same flight feathers were part of the plumage for the entire 21-month period. Some of these

TABLE 1
MOLT AND FAT DEPOSITION SCORES OF EXPERIMENTAL BIRDS^a

		Vernal fat, 1961	Postnuptial molt, 1961	Autumnal fat, 1961	Prenuptial molt, 1962	Vernal fat, 1962	Postnuptial molt, 1962	Autumnal fat, 1962
Experimental I Group								
Males:	512	0	0	+10	+24	0	N.E.	N.E.
	514	0	+11 ^b	+14	N.E.	0	N.E.	0?
	519	0	0	N.E.?	+69	0 ^c	+16	N.E.
	525	0	+7 ^b	+7	-9	-43	N.E.	N.E.
Females:	513	0	+14 ^b	+7	+82	N.E.	N.E.	N.E.
	528	0	0 ^b	N.E.	0	+9	N.E.	N.E.
	534	0	+88	0	0	0	N.E.	N.E.
	545	0	+28 ^b	N.E.	0	N.E.	0 ^b	N.E.
	547	0	N.E.	N.E.?	0	0	N.E.	N.E.
Experimental II Group								
Males:	676	-	0	0	0	0	N.E.	N.E.
	678	-	0	0	0	0	N.E.	N.E.
	692	-	0	0	N.E.	0 ^c	N.E.	0
	570	-	0	0	0	0 ^c	N.E.	N.E.
	564	-	0	0	0	N.E.	N.E.	0?
	565	-	0	0	0	-64	N.E.	0 ^c
Females:	693	-	0	0	0	N.E.	N.E.	0?
	696	-	0	0	dead	-	-	-

^a See text for explanation of data tabulation.

^b Body feathers only were molted.

^c Weak response.

birds, as well as some in which this molt was quite out of phase with the controls, were in phase for the prenuptial molt the following winter. The molt response among the experimental II's was more uniform, and it is tempting to suggest that it was eliminated only after these birds did not experience the long days of summer. This conclusion, however, is not supported by the response of the experimental I group for the postnuptial molt of 1961.

A comparison between fat deposition and molt in individual birds was made in order to determine whether these two events were equally in or out of phase. In 44 per cent of the 16 experimental birds, fat deposition and molt were about equally in phase when compared with these events in the control group. With 33 per cent, the occurrence of fat deposition was more closely in phase with the controls than was molting; while in 23 per cent, molting appeared to be more in phase with the controls than was fat deposition. It appears then that in any individual experimental, if one of these events is in or out of phase with the controls, it does not follow that the other event will also be equally in or out of phase. *Zugdisposition*, as evidenced by fat accumulation, therefore, cycles independently from the molt under the same environmental conditions, although from an energetic standpoint, molting may impede the development of both fat deposition and nightly unrest (figs. 1, 2, and 5 and Zimmerman, 1965a).

Although it is concluded that the occurrences of premigratory fat deposition, migratory restlessness, and molt are dependent to a large extent on some means of internal regulation, it is also important to emphasize that these events could not be

TABLE 2
ZUGUNRUHE SCORES OF THE EXPERIMENTAL GROUPS^a

	Exper. I	Exper. II
Vernal, 1961	0	-
Autumnal, 1961	-9	0
Vernal, 1962	+46	0
Autumnal, 1962	N.E.	N.E.

^a See text for explanation of data tabulation.

sustained for much more than a year under conditions of the wintering environment. They are not autonomous. Furthermore, the timing of the annual cycles for these events is dependent on the sum total of the bird's environmental experience in the wild rather than just the environment of either extreme of its migratory range.

SUMMARY

The timing of premigratory fat deposition, *Zugunruhe*, and molt in Dickcissels maintained for an extended period at photoperiod and temperature conditions of their contranuptial area was compared with the occurrence of these events in control birds held outdoors on both their tropical wintering and north-temperate breeding

TABLE 3
AVERAGE SCORES FOR MOLT, FAT, AND ZUGUNRUHE OF THE EXPERIMENTAL GROUPS^a

	Exper. I	Exper. II
Vernal <i>Zugunruhe</i> , 1961	0	-
Vernal fat, 1961	0(100) ^b	-
Postnuptial molt, 1961	0 (33)	0(100)
	+30 (56)	
	N.E. (11)	
Autumnal <i>Zugunruhe</i> , 1961	-9	0
Autumnal fat, 1961	0 (11)	0(100)
	+10 (44)	
	N.E. (44)	
Prenuptial molt, 1962	0 (44)	0 (86)
	+42 (44)	N.E. (14)
	N.E. (11)	
Vernal <i>Zugunruhe</i> , 1962	+46	0
Vernal fat, 1962	0 (56)	0 (57)
	-17 (22)	-64 (14)
	N.E. (22)	N.E. (29)
Postnuptial molt, 1962	0 (11)	N.E.(100)
	+16 (11)	
	N.E. (78)	
Autumnal <i>Zugunruhe</i> , 1962	N.E.	N.E.
Autumnal fat, 1962	0 (11)	0 (57)
	N.E. (89)	N.E. (43)

^a See text for explanation of data tabulation.

^b Per cent of each group for each event given in parentheses.

ranges. Under these constant environmental conditions *Zugunruhe* was maintained in phase with the controls for one year, while premigratory fat deposition was still in phase after the end of a year. Molting was not eliminated in the majority of birds until after one year in the experimental environment.

It is concluded that the control of all these events is largely internally regulated and that the eventual elimination of these phenomena is temporally related, not to time since resident on the nesting range, but to the time since introduction into the constant environment, whether from the wintering or breeding area.

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