

CASTRATION AND SPRING MIGRATION IN THE WHITE-THROATED SPARROW

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According to the gonadal hypothesis of the stimulus for migration in birds, developed chiefly by Rowan (1926, 1929, 1932), spring migration is induced by the increasing production of gonadal hormones as the gonads recrudescence in response to lengthening days. This idea of a direct gonadal stimulus has not been widely accepted by critical ornithologists for a variety of inferential reasons which have been reviewed thoroughly by Farner (1950:107). Among these are the following. (1) Spring migration occurs in some species before there has been much, if any, gonadal development. (2) The premigratory physiological changes are similar in males and females, requiring the unlikely assumption that the male and female sex hormones have similar actions, or alternatively that at least one sex produces both androgens and estrogens in effective quantities. (3) The profundity and diversity of the physiological changes associated with migration appear to be too great to be attributed solely to gonadal hormones. (4) Closely related migratory and nonmigratory forms exhibit similar cellular and histological development during their gonadal cycles. (5) The physiological and behavioral changes associated with migration are similar in spring and fall, despite drastic differences in gonadal activity and hormonal balances.

While the first three of these arguments have been weakened by subsequent discoveries, nevertheless altogether they have been so convincing that there have been relatively few attempts to obtain direct evidence on this question by means of hormone-injection experiments or castration experiments. Some early investigators (see Discussion) claimed actual migration by birds which had been castrated and released into the wild. However, nearly all their results are open to question on the basis of: (1) weak criteria, *e.g.*, the assumption that mere disappearance from the release point constitutes migration; (2) failure to perform a final autopsy to check for incomplete castration or regeneration of gonadal tissue; or (3) the use of species in which the likelihood of social regulation of migratory behavior is extremely high.

More recently the increased understanding of migration physiology and behavior has made it possible to detect the migratory condition with considerable confidence in caged nocturnal migrants. The chief criteria for the spring migratory condition are rapid fat deposition with concomitant body-weight increase, and the development of nocturnal restlessness, or *Zugunruhe*. Castration experiments using these techniques have been performed by Lofts and Marshall (1961), on the Brambling, *Fringilla montifringilla*; by Morton and Mewaldt (1962) on the Golden-crowned Sparrow, *Zonotrichia atricapilla*; and by Millar (1960) on the White-throated Sparrow, *Z. albicollis*. In these experiments the birds were castrated in late winter or early spring and held in cages under outdoor conditions of temperature and photoperiod until late spring or early summer. In all three experiments the castrates developed the migratory condition, although they differed in some respects from control birds in the timing and magnitude of the physiological events. Morton and Mewaldt (1962:246) concluded that the gonads are not essential for migration, although "gonadal recrudescence and the concomitant release of gonadal hormone has a modifying role in the total physiological preparation for and manifestation of migration."

Prior to the above studies, in 1953 I had conducted a castration experiment on

the White-throated Sparrow using the same criteria but different experimental conditions and had obtained apparently contrary results (Weise, 1956a). This experiment was repeated and extended in 1959 and again in 1961. It is the purpose of this report to present the combined results of these castration experiments and to reconcile them with the results of other investigators mentioned above.

METHODS

Male White-throated Sparrows were used in these experiments. Vernal pre-migratory fat deposition and *Zugunruhe* have been well documented in this species (Odum, 1949; Odum and Perkinson, 1951; Weise, 1956b, 1963). All birds were autumn migrants captured in 1952 in Champaign, Illinois, and in 1958 and 1960 in Milwaukee, Wisconsin. They were placed in indoor cages holding four to six birds each, at room temperatures and at photoperiods which were regulated weekly to approximate natural conditions. When natural daylengths reached the minimum of about 9.5 hours in December, the photoperiods were further reduced to LD 9:15 and then held constantly at that level. In both the holding rooms and the experimental chambers light intensity at cage level was 300 to 400 lux during the light period. Light intensity during the dark period was not measured but was very low, just sufficient for the expression of *Zugunruhe*. Lights were turned on and off abruptly, roughly in phase with natural cycles, *i.e.*, at 0800 and 1700, respectively for the LD 9:15 regime and at 0500 and 2000 for the LD 15:9 regime.

Birds from the LD 9:15 holding rooms were castrated or sham-operated (laparotomized) during three fairly distinct periods: (A) from late December to early February, with photostimulation and experimental observations beginning in February or early March, 3 to 5 weeks after castration; (B) in March or April, with photostimulation and observations beginning in late March, April, or early May; (C) in June or July with photostimulation and observations beginning in July. The majority of birds were in Period A. Thus at the time of photostimulation most of the birds had been on the short daylength regime for only a month or two and were in normal winter condition. Some, however, had been on this regime for up to seven months with suppression and disturbance of the natural cycle, as described by Weise (1962). The effects of this were largely on the condition of the birds at the beginning of the experiment; however, control birds of Period C responded somewhat more rapidly to photostimulation than did those of A and B, presumably due to increased photosensitivity as described by Laws (1961). The total effect of these complications was nevertheless minor, and the results from all three experimental periods have been combined for analysis in this paper.

Castrations were usually done one testis at a time in two separate operations. Testes were removed by simple excision with forceps. This unfortunately was an inefficient method, and many of the birds regenerated testicular tissue. All the birds were killed and autopsied at the end of the experiment, and those initially presumed to be completely castrated were reclassified definitively as "castrates," birds having no testicular tissue discernible with the aid of a dissecting microscope, or as "regenerates," birds having small, usually misshapen, sometimes displaced, bits of testicular material. All control birds were subjected to bilateral laparotomy and the testes were manipulated with forceps. During the experiments the control, castrate, and regenerate birds were in the same chambers and could see and hear each other. I do not believe the migratory responses to be significantly influenced by social stimuli in this species.

During the experimental periods of observation the following data were collected for each bird.

Locomotor activity. This was recorded continuously by methods described elsewhere (Weise, 1956b, 1962, 1963). The basic activity unit was a 3-minute interval, during which at least one movement of the bird was registered. Thus the *activity index* ran from 0 to 20 units per hour, and in an eight- or nine-hour dark period such as used in these experiments, from 0 to 160 or 180 units. In this study nocturnal activity is usually expressed as the total number of activity units per dark period, regardless of the length of the period. Normal White-throated Sparrows in an outdoor aviary exhibited 50 to 150 units of activity per night during nights of similar length in the spring (Weise, 1963).

Body weight. Weekly examinations were made of weight, fat, molt, and cloacal protuberance. At these times the birds were removed from the activity cages shortly after the middle of the light period and held without food or water for about two hours before examination. This insured a virtually empty digestive tract at the time of weighing and minimized error due to freshly ingested food or retained feces. Body weight was measured to the nearest 0.1 g.

Fat deposits. Subcutaneous and abdominal fat was estimated by a system of classes (Weise, 1956b) running from none (0) to very heavy (4). Despite the recent criticisms of Hailman (1965), these classes have been treated by parametric statistics in the belief that the method as used here at least approaches true interval estimation and is not simply a ranking system.

Cloacal protuberance. This was measured by a scoring system as follows: minimum protuberance = 0; slight = 1; moderate or prominent = 2; and moderate or prominent protuberance with the seminal vesicle tubules enlarged, whitish and visible through the skin = 3. The extent to which the cloaca developed was assumed to be a rough index of androgen production.

Molt intensity. Semiquantitative records ("few," "some," "many") were kept of the number of regenerating feathers in each of the major feather tracts. On the basis of these each bird was assigned a body-molt score of 0 (none), 1 (light), 2 (moderate), or 3 (heavy).

This is comparable to the system used by Morton and Mewaldt (1962).

Two types of experiments were conducted simultaneously, using the same stocks of birds and the same chambers. In the first type (the *prestimulus* castration experiments) the castrations and sham operations were performed while the birds were still in the holding cages at LD 9:15. Several weeks later the birds were transferred to activity cages and the photoperiod was increased to LD 15:9 or 16:8. The observation period in most cases extended from 1 to 3 weeks before photostimulation to 3 to 13 weeks after. In some cases the observation period before photostimulation was omitted.

In the second type of experiment (the *poststimulus* castration experiments) the first step of the castration was performed while the birds were at LD 9:15; then they were transferred to activity cages and were photostimulated. After three, four, or five weeks at the long photoperiod, when the birds had begun to exhibit migratory responses, *i.e.*, body weight and fat increase and *Zugunruhe*, the castrations were completed and observations were continued.

RESULTS

PRESTIMULUS CASTRATION EXPERIMENTS

The results of the prestimulus castration experiments are shown in figures 1 and 2, representing the weekly means for the three experimental groups. These curves are somewhat damped because of individual differences in timing of the events. Therefore the data have been organized in a different way in tables 1 and 2 to show more accurately the magnitude of the individual responses and variations. In organiz-

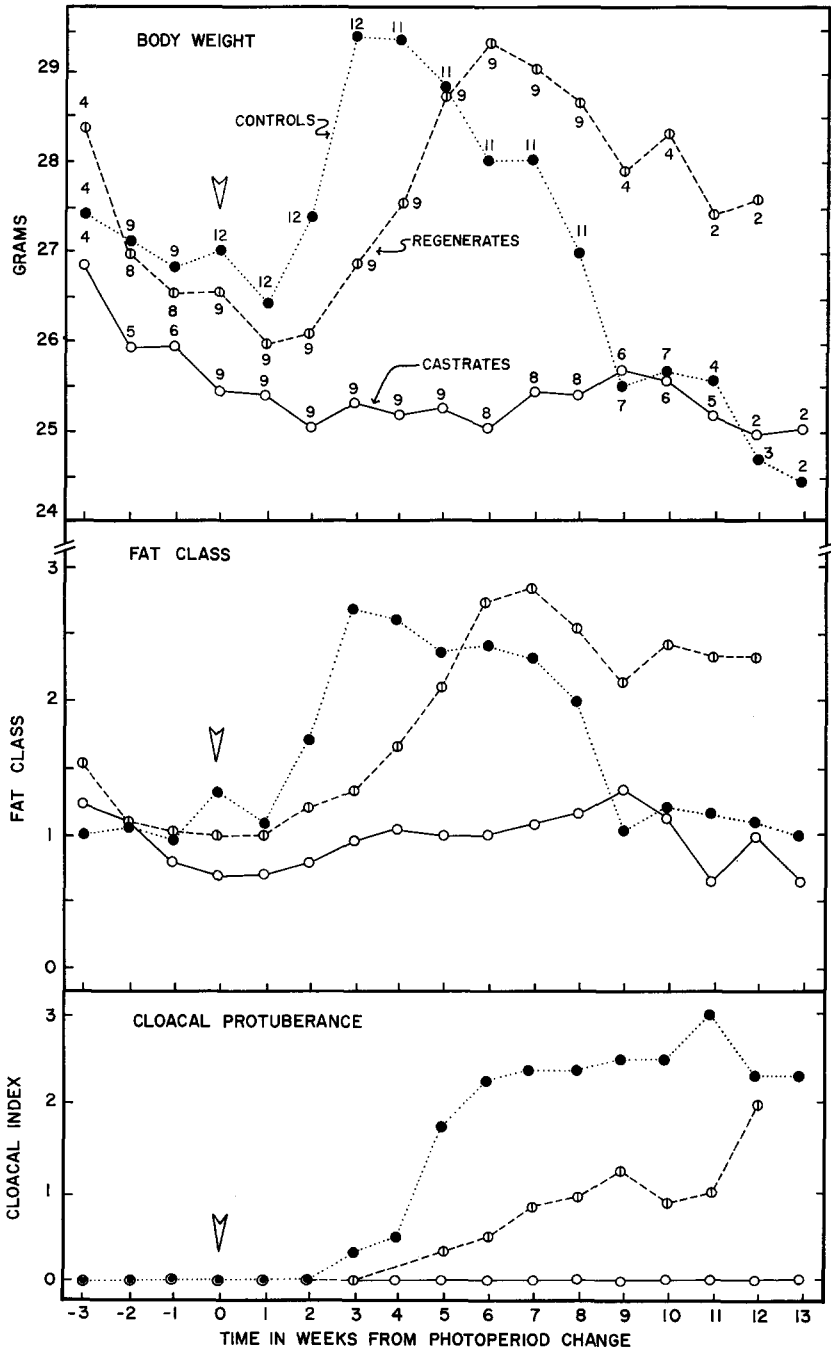


Figure 1. Weekly means of body weight, fat class, and cloacal protuberance in prestimulus castration experiments. Number of birds for each point shown in body weight graph; these apply to all curves in figures 1 and 2 except cloacal protuberance curve, which is based only on 1959 and 1961 experiments. Arrows indicate date of change from short to long photoperiod.

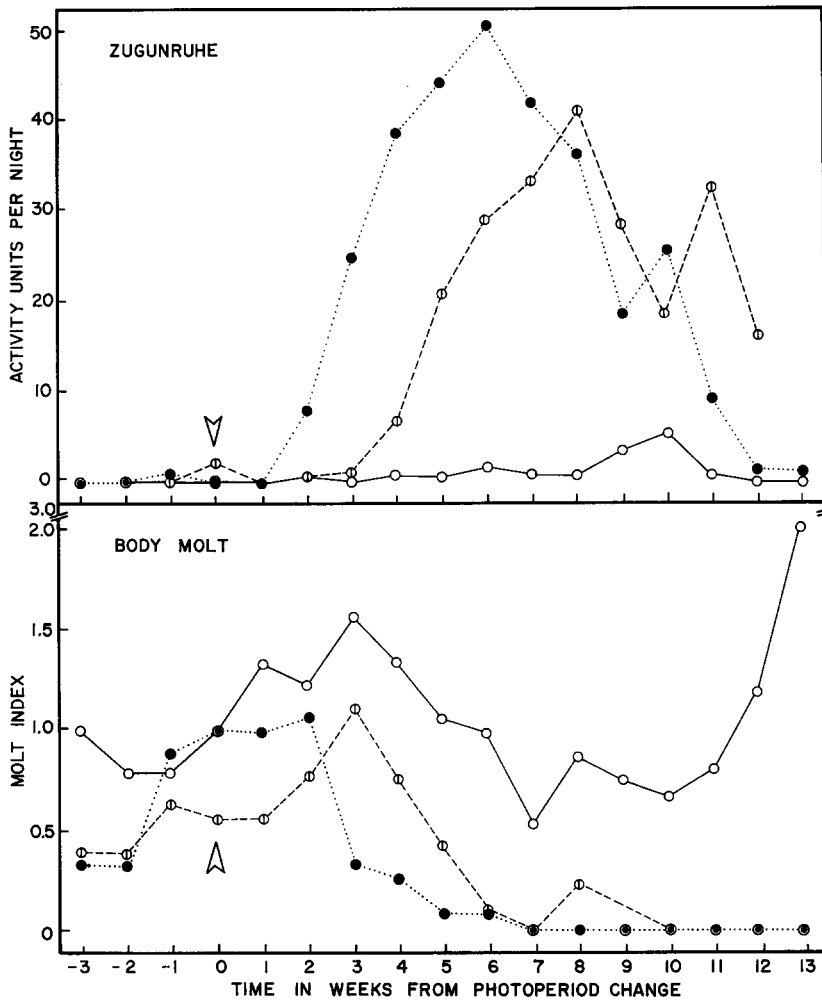


Figure 2. Weekly means of *Zugunruhe* and body molt in prestimulus castration experiments. Legend as in figure 1.

ing the data the week preceding the date of the photoperiod increase was designated Week 0, and the data are summarized by weeks before or after that time. In the figures and tables the weight, fat, molt, and cloacal protuberance values are those determined on the examination at the end of the week; the *Zugunruhe* values are the averages for the six nights preceding the examination.

Body weight and fat class. Since the fat-class curves essentially paralleled the body-weight curves, it is assumed in the following discussion that the observed weight changes were primarily due to the deposition or utilization of fat, and that such terms as weight increase and fat deposition can be used interchangeably.

At the time the birds were transferred from the holding cages to the activity cages there was great variability in weight, fat, and molt condition, depending

TABLE 1
BODY WEIGHT, FAT CLASS, CLOACAL, AND GONADAL RESPONSES IN PRESTIMULUS
CASTRATION EXPERIMENTS

	Groups ^a		
	Controls	Regenerates	Castrates
Body Weight			
Preresponse minimum (g)	25.59 ± 0.47 (12)	25.18 ± 0.52 (9)	24.46 ± 0.45 (9)
Week of minimum	+ 0.25 ± 0.45 (12)	+ 1.00 ± 0.53 (9)	+ 1.11 ± 0.59 (9)
Response maximum (g)	30.40 ± 0.59 (12)	30.24 ± 0.74 (9)	26.72 ± 0.37** (9)
Week of maximum	+ 3.67 ± 0.26 (12)	+ 5.78 ± 0.52* (9)	+ 5.89 ± 0.92 (9)
Per cent increase	18.89 ± 1.89 (12)	20.67 ± 2.51 (9)	9.50 ± 2.36** (9)
Fat Class			
Preresponse minimum	0.7 ± 0.19 (12)	0.7 ± 0.24 (9)	0.3 ± 0.17 (9)
Response maximum	3.2 ± 0.18 (12)	3.2 ± 0.22 (9)	1.8 ± 0.32** (9)
Classes gained	2.6 ± 0.29 (12)	2.6 ± 0.24 (9)	1.4 ± 0.34 (9)
Cloacal Score			
Response maximum	2.8 ± 0.52 (8)	1.4 ± 0.51 (5)	0* (6)
Gonadal Condition at Autopsy			
Combined testis weight (mg)	343.6 ± 48.0 (8)	8.8 ± 3.3* (5)	0** (9)
Combined seminal vesicle weight (mg)	66.3 ± 14.8 (8)	4.8 ± 1.0* (5)	2.3 ± 0.2* (6)

^a Data given as mean ± SE. Sample size is given in parentheses. Statistical significance (*t*-test) is noted as follows: * differs from controls at $P < 0.01$; ** differs from both other groups at $P < 0.01$.

largely on the length of time that they had been at LD 9:15. Birds of experimental Period A were in normal winter condition—moderately fat and heavy, and exhibiting little or no body molt. Birds of Period B were less fat, and most of them had begun the prenuptial molt. Birds of Period C were still less fat and were still molting irregularly (cf. Weise, 1962).

Regardless of the experimental period, individual birds typically lost weight because of reduced feeding and stress when transferred to the activity cages. Most individuals showed a further slight loss during the week after the photoperiod change. Thereafter the responses of the control, regenerate, and castrate groups diverged greatly. The controls deposited fat rapidly, reaching peak body weights about 19 per cent above the minimum three or four weeks after the photoperiod increase. There was then a sharp decline, coinciding with the rapid development of the cloacal protuberance; this continued until very low weights were reached in Weeks 9 to 13. These were similar to the levels attained in normal male White-throated Sparrows in outdoor aviaries just before the postnuptial molt. In other photoperiod experiments in this laboratory (unpublished), normal males have exhibited similar weight-fat responses and have begun the postnuptial molt 12 to 16 weeks after the photoperiod increase.

Regenerates attained weight and fat peaks nearly identical with those of the controls. However, there were two notable differences: the onset of fat deposition was delayed, and the rate of deposition was more gradual so that the peaks were reached in Weeks 5 or 6 or even later in some cases.

The weekly means of the castrates indicate virtually no change in weight after the photoperiod increase. However, study of the individual curves shows that nearly all of the birds gained slightly in weight and fat, although with much variation

TABLE 2
Zugunruhe AND MOLT RESPONSES IN PRESTIMULUS CASTRATION EXPERIMENTS

	Groups ^a		
	Controls	Regenerates	Castrates
<i>Zugunruhe</i>			
(10 or more activity units per night)			
Onset: days after photoperiod change	24.6 ± 18.1 (12)	29.4 ± 2.4 (9)	41.0 ± 7.6 (4) ^b
Frequency: per cent of nights after			
Week 2	57.8 ± 9.1 (12)	52.7 ± 7.7 (9)	6.0 ± 2.9** (9)
Intensity: maximum for a single			
night (units)	76.4 ± 14.6 (12)	73.8 ± 12.9 (9)	10.6 ± 3.6** (9)
Greatest weekly mean (units)	56.3 ± 13.2 (12)	53.6 ± 10.0 (9)	5.6 ± 2.4** (9)
Week of greatest mean	+ 6.2 ± 0.7 (12)	+ 7.1 ± 0.5 (9)	+ 7.8 ± 1.3 (4) ^b
Body Molt			
Max. score in Weeks 0-3	1.5 ± 0.3 (12)	1.1 ± 0.3 (9)	1.9 ± 0.4 (9)
Min. score in Weeks 3-9	0 (11)	0 (9)	0.1 ± 0.04 (9)
Max. score in Weeks 6-13	0 (11)	0.2 ± 0.2 (9)	1.3 ± 0.4* (8)
Flight Feather Molt			
No. of birds observed beyond Week 5	11	9	8
No. of birds in which molt of			
primaries was observed	0	1	6
Week of onset	14.0 ± 0 ^c (11)	13.1 ± 0.9 ^c (9)	11.0 ± 1.0* (8)

^a Data given as mean ± SE. Sample size is given in parenthesis. Statistical significance (*t*-test) is noted as follows: * differs from controls at $P < 0.01$; ** differs from both other groups at $P < 0.01$.

^b Based only on birds that exhibited *Zugunruhe*.

^c Assuming that molt would have started in Week 14 if not begun earlier.

both in the timing and in magnitude. The increases averaged 9.5 per cent of the initial weight, or 1.4 fat classes, these changes being statistically significant ($P < 0.01$). As seen in table 1 these gains were significantly less than those of the control and regenerate groups. The castrate that achieved the greatest percentage gain was a small bird with a very low minimum weight. Its pattern of weight gain was more like that of the regenerate than of the control group. Only one castrate, 3161, exhibited fat and weight increases approaching those of the controls in timing and magnitude.

The castrates as a group were initially lower in weight and fat than the regenerates or controls, although the differences were not statistically significant. These differences also obtained at the time of the castrations and sham operations. To determine if the castrates were actually smaller birds than the others, a comparison was made of the wing chords as measured at the time of capture. The means for control, regenerate, and castrate groups, respectively, were 72.4, 72.7, and 72.2 mm, the differences being insignificant. Thus the three groups were homogeneous in size, but it is probable that my castration technique had a higher chance of success in the leaner birds.

Molt. As explained previously, birds in experimental periods B and C were exhibiting irregular body molt even before the photoperiod was increased. After photostimulation this intensified somewhat in these birds, and slight or moderate molt appeared in some, but not all, of the Period A birds. In the control and regenerate birds molting then declined and disappeared during Weeks 3 to 6, and no further molt was observed except in one regenerate bird. This was a bird that

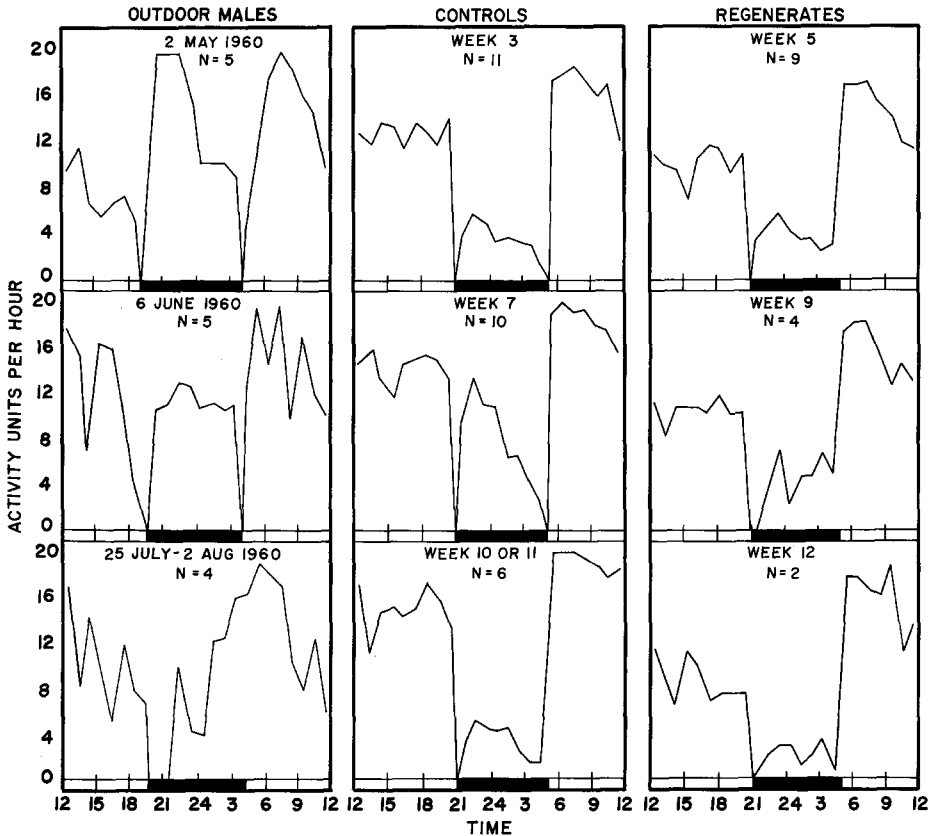


Figure 3. Diurnal activity patterns in male White-throated Sparrows in an outdoor aviary and in control and regenerate groups of prestimulus castration experiments. Outdoor birds: each graph based on a single 24-hour period beginning on date shown. Others: each graph based on one-week period. N = number of individual birds.

had regenerated only a minute amount of testicular tissue. Although it had exhibited fairly strong migratory responses, a molt of the postnuptial type (with primaries renewing in normal order) had begun by Week 6.

The castrates as a group exhibited more intense molting throughout the experiment than did the other groups. Individually there was much variation. Most of the birds exhibited intensification of the molt for several weeks after the photoperiod increase; then some time between Weeks 4 and 10, molting declined and disappeared entirely, the single exception being a bird that was observed only through Week 5. Unlike the controls and regenerates, however, most of the castrates (six of eight that were retained long enough) again began to molt in the later weeks of the experiment; this molt included the primaries as well as body feathers. The onset of this "postnuptial" molt varied from Week 6 to 13; some individuals were beginning the postnuptial molt before others had finished the prenuptial. Therefore, castration not only caused an intensification and prolongation of the prenuptial molt (as found also by Morton and Mewaldt, 1962, and Millar, 1960) but also induced the postnuptial molt to begin significantly earlier than in normal birds.

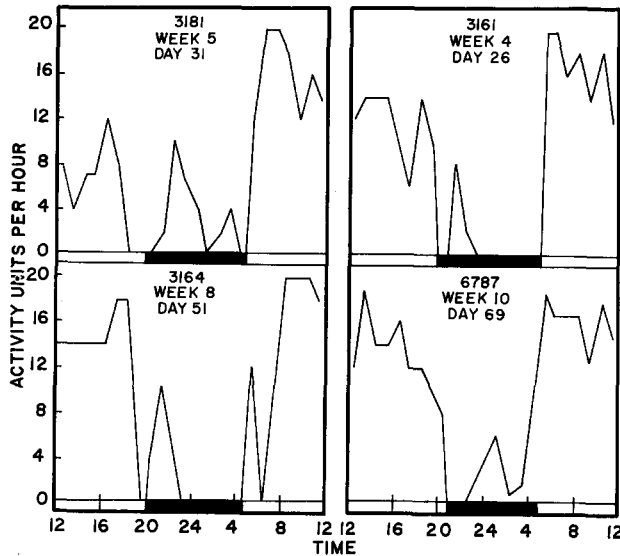


Figure 4. Diurnal activity patterns of individual castrates in prestimulus castration experiments. Each graph based on a single 24-hour period including the night of most intense *Zugunruhe*.

Zugunruhe. Figure 2 illustrates the differences in weekly mean *Zugunruhe* among the control, regenerate, and castrate groups. A few controls (those of Period C) became active at night as early as the second week after the photoperiod increase; thereafter nightly activity became very intense, reaching a peak in Week 6. *Zugunruhe* then declined, becoming much more irregular in the later weeks of the experiment. By Weeks 12 and 13 there was almost no activity at night. This pattern is very similar to the seasonal pattern seen in captive White-throated Sparrows under outdoor conditions.

The regenerates differed from the controls only in timing, as was the case in regard to fat deposition and body weight. *Zugunruhe* first appeared in this group in the third and fourth weeks and reached its peak in Week 8, then declined until the end of the experiment.

Castrated birds exhibited very little *Zugunruhe*, and this was so variable in timing among individuals that the weekly means for the group remained low throughout the experiment. The slight upsurge in Weeks 9 and 10 was entirely due to two birds, 3164 and 6787 (see fig. 4).

Table 2 indicates more precisely the *Zugunruhe* responses in the castrate birds, as compared with regenerates and controls. Judging from the criteria shown in the table, four of the nine castrates exhibited *Zugunruhe* at some time during the experiment, but it is obvious that compared with the other groups this was much delayed in onset, was much more sporadic and irregular in occurrence from night to night, and was much less intense.

Hourly activity patterns. Lofts and Marshall (1961), Morton and Mewaldt (1962), and Millar (1960) reported an effect of castration on the hourly pattern of nocturnal activity. In particular the peak of the activity curve of the castrates was several hours later than that of the controls. This sort of a shift has been

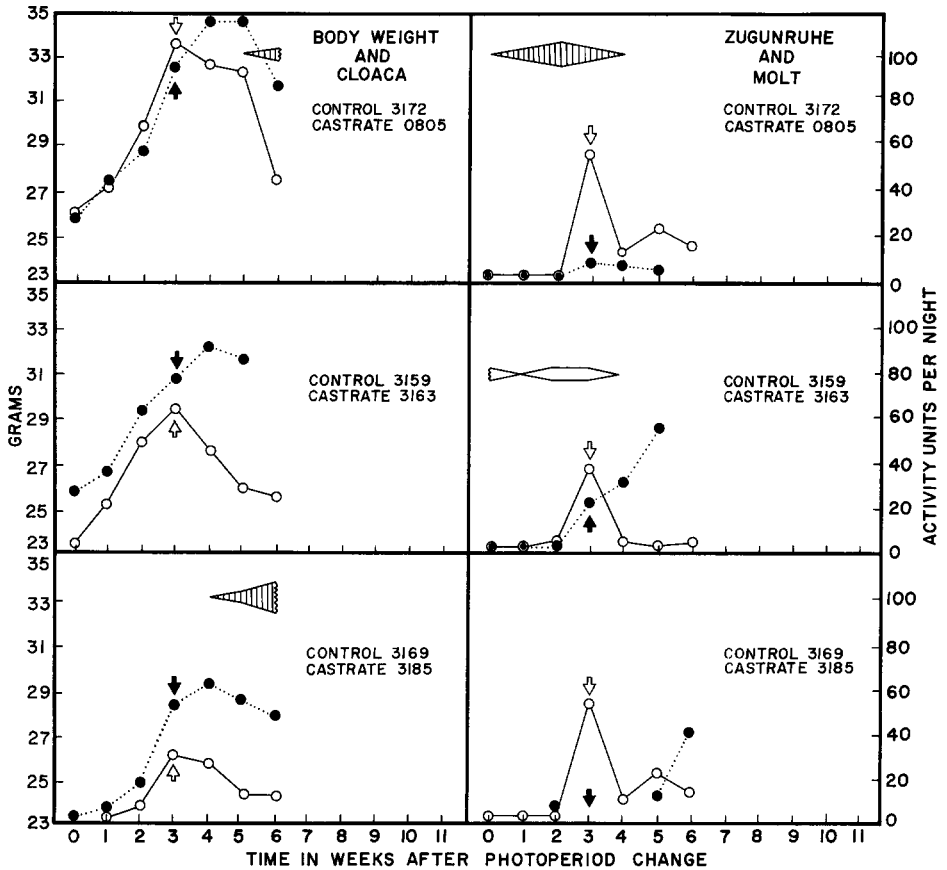


Figure 5. Responses of individual birds in the 1953 poststimulus castration experiments. Graphs on left indicate body weight (curves) and cloacal protuberance score (polygon); those on right show *Zugunruhe* (curves) and body molt score (polygon). Open symbols = castrates; closed or hatched symbols = controls. Photoperiod increased from LD 9:15 to LD 15:9 in Week 0; arrows indicate date of castration and sham operation.

observed by me in normal outdoor caged birds of several species, during the week or two preceding the onset of the postnuptial molt, when the gonads are regressing. Figure 3 illustrates this change in pattern in one group of outdoor White-throated Sparrows and in the control and regenerate groups of the present experiment. For each group the top graph represents the period when *Zugunruhe* was just developing, the second graph represents the probable period of maximum gonadal activity, and the bottom graph represents the period shortly before the postnuptial molt. The curves for these outdoor males, as well as for others observed by me, suggest that there are two components of nightly activity, an early-night component which is strongest during the spring migration period, and a late-night component which develops later and becomes prominent just before the postnuptial molt (when *Zugunruhe* ceases altogether). In the control birds of this experiment the late-night component developed only weakly, probably because the gonads had not begun to regress. In the regenerates the late-night component was fairly conspicuous.

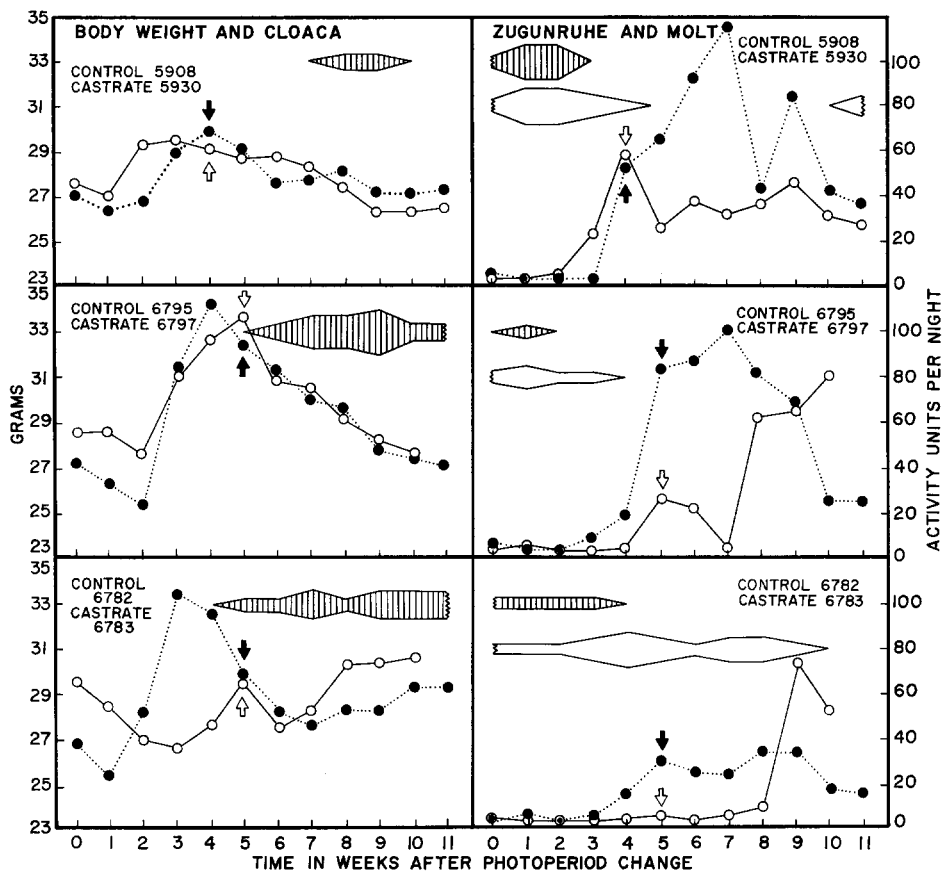


FIGURE 6. Responses of individual birds in the 1961 poststimulus castration experiments. Legend as in figure 5.

Because the castrates in this experiment exhibited such weak and sporadic *Zugunruhe*, it is not possible to include this in figure 3. Figure 4 illustrates the hourly patterns for the 24 hours embracing the night of most intense nocturnal activity for each of the four castrates that developed *Zugunruhe*. In three of the birds the early-night component of activity was most conspicuous. In the other bird, 6787, the late-night component was prominent; this bird had already begun its postnuptial molt at this time.

Cloacal protuberance and gonadal condition. The cloacal protuberance developed rapidly in the controls during Weeks 5 and 6 and remained in the fully developed condition (score 3) in most birds until the end of the experiment. The period of rapid development coincided with the onset of body weight and fat decline after the "migratory" peak. Presumably this is a period of increasing production of gonadotropic hormones and androgens. Whether there is a cause-effect relationship here is not known. At autopsy all of the controls had greatly enlarged testes and seminal vesicles. Gonadal regression was not evident even in birds held until Week 13.

As might be expected, cloacal and gonadal conditions in the regenerate group were

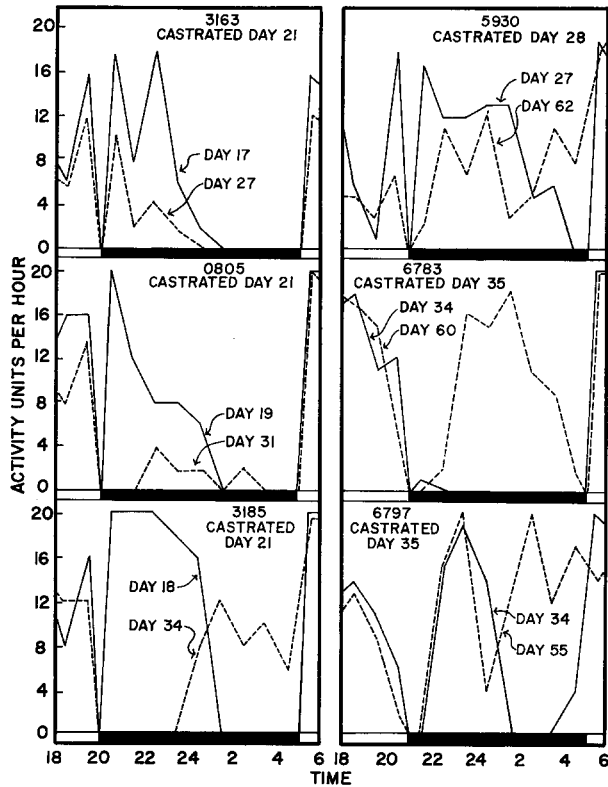


Figure 7. Nocturnal activity before and after castration in the poststimulus castration experiments. For each bird the nights represented are those of most intense *Zugunruhe*. Solid line = before castration; dashed line = after castration.

highly variable. Only one bird was known to have achieved cloacal score 3, but the regenerates with the largest testes were in the 1953 experiments when degree of cloacal protuberance was not estimated. In any case the cloacal responses were significantly lower in this group than in the controls, and it can be assumed that the production of androgens was correspondingly lower. Nevertheless, as indicated previously, these birds after an initial delay exhibited fully developed migratory responses. There was no consistent relationship between the size of the testes at autopsy and the intensity of the migratory responses of fat deposition or *Zugunruhe*. However, it should be noted that regression was well underway in some of the regenerates at the time of autopsy, so that it is not known what maximum size these testes had reached.

POSTSTIMULUS CASTRATION EXPERIMENTS

Experiments of this type were performed during the 1953 C and the 1961 A periods. Birds were unilaterally castrated before photostimulation, then placed in activity cages and exposed to the long photoperiod. For each experimental bird a bird of similar weight was laparotomized to serve as a control. After three weeks in 1953, or four or five weeks in 1961, the castrations were completed and the controls

were again laparotomized. Testes at this time were beginning to enlarge (2 to 4 mm long). Observations were then continued until Week 6 in 1953, or until Week 10 or 11 in 1961. Castrations were especially inefficient in these experiments, owing to large fat deposits, and at the time of autopsy only six birds could be classified as castrates. The results for these and their designated controls are shown in figures 5 and 6. Body weight and cloacal responses are shown on the left and *Zugunruhe* and molt responses on the right for each pair of birds.

The three birds castrated in Week 3 (fig. 5) began to lose weight immediately after the operation while the controls continued to gain to normal peaks in Weeks 4 or 5. Those castrated in Weeks 4 or 5 (*i.e.*, at about the time of the normal peak) lost weight no more rapidly than did their controls (fig. 6).

In nearly all birds, controls as well as castrates, nocturnal activity ceased for a few nights after the operation. In the controls *Zugunruhe* then reappeared and continued to increase essentially normally. In the castrates the depression of *Zugunruhe* appeared to last longer. In the three birds of the 1961 experiment, however, a resurgence of more intense activity occurred several weeks after the operation. The important point is that all of the castrates exhibited *Zugunruhe* after the castration. While the weekly means for 3163 were very low following the castration, this bird did exhibit an occasional night of low-level activity (see fig. 7).

In light of the previous discussions regarding the hourly pattern of nocturnal activity, it is of interest to compare these patterns before and after the completion of the gonadectomy in these birds. Figure 7 depicts, for each of the castrated birds, the night of maximum activity before, and the night of maximum activity after the castration. In five of the birds there was evidence of development of a late-night component of activity, and in three of these it was quite strong. The only bird that failed to develop the late-night component was 3163 which, as mentioned above, exhibited *Zugunruhe* only sporadically during the three weeks after the castration.

Thus poststimulus castrations had little effect on the normal body weight and fat trends, and although *Zugunruhe* was temporarily depressed, in no case was it permanently extinguished. These results are in sharp contrast with those of the prestimulus castration experiment.

DISCUSSION AND CONCLUSIONS

The results of these experiments indicate that in the White-throated Sparrow the removal of the testes in photosensitive birds prior to artificial photostimulation effectively suppresses the migratory responses of fat deposition, body-weight increase, and *Zugunruhe*. The prenuptial molt is intensified and prolonged and the postnuptial molt is premature. Birds that regenerate testicular tissue have the migratory responses delayed but not suppressed. Apparently the amount of testicular tissue necessary for a full response is quite small. Castration performed after the birds have been photostimulated for several weeks does not, however, extinguish the migratory responses: fat deposition and body weight are little affected, and *Zugunruhe* is only temporarily depressed. In either type of experiment there is a tendency for castrates and some regenerates to reduce the early-night component of *Zugunruhe* and to strengthen the late-night component, which is generally absent or weak in normal birds except at the time of gonadal regression.

While at first glance these results may appear contrary to those in the literature, they are in fact quite consistent. All of the experimental evidence so far adduced for the spring migration of castrated birds is either equivocal for reasons already

mentioned, or is based on birds castrated after photostimulation has begun, and therefore comparable to the poststimulus castrations of this study, rather than the prestimulus castrations.

Actual migration by birds that have been castrated and released has been reported by Putzig (1938, 1939) for Hooded Crows, *Corvus cornix*, by Hann (1939) for White-throated Sparrows and for Rufous-sided Towhees, *Pipilo erythrophthalmus*, by Drost (1941) for a European Blackbird, *Turdus merula*, and by Emlen (Wolfson, 1942:260) for White-crowned Sparrows, *Zonotrichia leucophrys gambelii*. Emlen's birds were recovered at the release point on the wintering grounds in a subsequent winter, but there is no assurance that they migrated to and from the breeding grounds in the interim. Hann's criterion for migration was simply the disappearance of the birds from the release point. Again there is no assurance of continued migration, and in fact some of the presumed castrates remained in the area as long as 49 days, indicating that migration was retarded or possibly prevented until regeneration had occurred. The single bird of Drost was castrated and released at Helgoland and was recaptured three years later in Sweden, but the bird was not examined for gonadal regeneration. Putzig gonadectomized large numbers of Hooded Crows during spring migration and released them from Berlin and Rossitten. Some of these were subsequently recovered from points to the north or northeast, but in my opinion only two of the recoveries were sufficiently far away to indicate sustained migration; one Berlin release was recovered in Sweden about 300 miles away, and one Rossitten release was recovered in Estonia, 350 miles away. Neither bird could be examined for regeneration (although some of the birds recovered from shorter distances were). Aside from the small distances involved and the possibility of regeneration, it seems probable in this species that social inducement of migration is particularly likely, since the birds migrate in short daylight flights requiring little physiological or behavioral adaptation, and the species, like other corvids, has a complex, highly developed social organization.

Thus it is evident that these experiments are not conclusive, and, in any event, all of the castrations were performed in the late winter or spring when the birds had been exposed to increasing photoperiods for several months.

The more recent experiments involving the observation of fat deposition and *Zugunruhe* in caged birds overcome the objections relating to criteria, gonadal regeneration, and, in some cases, social stimulation; but in all of them the castrations were performed in late winter or spring. Lofts and Marshall (1961) castrated Bramblings in March just a few weeks before migration. Controls began to exhibit *Zugunruhe* in the first week of April, while the castrates (isolated in a separate room) began about a week later. Thereafter, however, the curves for the two groups were identical. A peculiar feature of this experiment is that in both groups the *Zugunruhe* declined to minimum levels by the first of May. In all other studies of *Zugunruhe* with which I am familiar, including one of the Brambling (Wagner and Thomas, 1957), nocturnal activity has persisted through what would normally be the breeding period of the birds.

Morton and Mewaldt (1962) castrated 33 Golden-crowned Sparrows in California in the early spring of 1960, and six in the spring of 1961. These, along with control birds, were then held in outdoor aviaries until late June. In each year the castrates began to deposit fat and to gain weight concurrently with the controls, but attained peak weights about three grams lower. The difference was statistically significant, and the investigators concluded that the mechanism controlling vernal fat deposition

includes at least two components, one of them dependent on increased production of testosterone.

The castrated Golden-crowned Sparrows began to exhibit *Zugunruhe* a week or two later than the controls, but eventually reached the same levels of intensity. King and Farner (1963) reported similar results in two castrated White-crowned Sparrows (*Z. l. gambelii*).

The experiment of Millar (1960) is particularly pertinent to the present study since it employed the same species, the White-throated Sparrow, but in an experimental situation similar to that of the studies mentioned above. The castrations were performed in late February, and the birds were observed in outdoor cages until July. The data provided by Millar do not reveal the amount of variation among the castrates in respect to the migratory responses, nor is it possible to determine the ontogeny of *Zugunruhe* since the activity of each bird was monitored for only a short period. Under these outdoor conditions, at least some of the castrates deposited fat and gained weight to a level near that of the controls. However, this did not occur until early June, more than a month after the intact birds had exhibited these responses. Four of the nine castrates exhibited *Zugunruhe* when tested in June or later, commensurate with that observed in controls; the remaining birds exhibited weaker *Zugunruhe*. Although Millar (personal communication) interprets these results as consistent with those of Lofts and Marshall and Morton and Mewaldt, the timing of the responses and the apparent variation in *Zugunruhe* seem to me to indicate that the castrations had a far more drastic effect in this case.

Thus despite the indirect evidence summarized by Farner (1950, 1955), all these experiments with captive birds reveal some effect of castration on the timing and magnitude of fat deposition and on migratory behavior. However, there are important differences in the extent of this effect, and an exploration of this is necessary. This needs to be done in the light of the known effects of castration on hormonal levels. Two such effects can safely be assumed: first, a direct effect, the elimination of gonadal hormones, and second, an indirect effect, the intensification of the gonadotropic activity of the hypothalamo-hypophysial system due to the lack of feedback control by the gonadal hormones (Engle, 1929; Phillips, 1942; Payne, 1947; Kobayashi and Farner, 1966). The question then is why these hormonal conditions had different degrees of effect in the experiments described above. The answer may lie in any or all of three sorts of differences involved in the experimental procedures.

First, there were differences in the time of the gonadectomy relative to the period of photostimulation and to the period of spring migration. In these respects the experiments can be placed in the following order. (1) Poststimulus castration experiments of the present study. The castrations were performed after intensive photostimulation and indeed after migratory responses had appeared. The effect on fat deposition was slight, and the effects on *Zugunruhe* temporary and minimal. (2) Experiment of Lofts and Marshall. The castrations were performed in March, just a few weeks before the appearance of *Zugunruhe* in the controls in the first week of April. The effects on *Zugunruhe* were slight. No fat or body weight data were presented. (3) Experiments of Morton and Mewaldt (and possibly that of King and Farner). The castrations were performed in February or March about four to six weeks before the onset of *Zugunruhe* in controls in late March or early April. The effects on both fat deposition and *Zugunruhe* were intermediate. (4) Experiment of Millar. The castrations were performed in late February, about two months before the first *Zugunruhe* in controls in late April. The effects of castration on fat deposition, and

probably also on *Zugunruhe*, were quite severe. (5) Prestimulus castration experiments of present study. The castrations were performed before any photostimulation at all (comparable to December). The effects of castration on both fat deposition and *Zugunruhe* were maximal.

This explanation, that the different experimental results are due to differences in the time of castration relative to photostimulation, leads to the implication that the feedback effect of the gonadal hormones is critically important in the initial stages of photostimulation, and that when photostimulation is well underway the response mechanism will irrevocably lead to the migratory condition. Although these implications seem unlikely, they have not been ruled out by the experiments described above. The crucial experiment would be one in which the castrations were performed before the winter solstice, and the birds observed at natural photoperiods through the spring.

A second difference between the experiments lies in the species used. Species differences in the mechanisms that regulate fat deposition are suggested by the relative extent of autumnal fat deposition in the White-throated Sparrow and White-crowned Sparrow. The latter (and apparently also the Golden-crowned Sparrow, judging from the limited information given by King and Farner, 1963, and Mewaldt *et al.*, 1964) deposits fat far more extensively and regularly in the fall than does the former. This could mean that in the White-throated Sparrow fat deposition is more dependent on gonadal factors of some sort.

There are also species differences in the intensity of and proclivity toward *Zugunruhe* (Weise, 1963). White-crowned Sparrows (and again, by inference, Golden-crowned Sparrows) appear to be much more prone to exhibit nocturnal activity in unusual experimental situations, than are White-throated Sparrows (King and Farner, 1963; Eyster, 1954; Weise, 1963 and unpublished). This suggests that the migration-releasing factors are more intimately tied to physiological condition in the White-throated Sparrow.

The third and perhaps crucial difference in the experiments lies in the nature of the photoperiod stimulus and in the rate of response to it. Under natural photoperiods the mechanisms responsible for the migratory condition and for gonadal development proceed slowly, and the events of the cycle are well-spaced with little overlap. Under these circumstances the migratory condition develops when gonadotropic and gonadal secretions are still low or at most moderate (Lofts and Marshall, 1961; King *et al.*, 1966). Therefore the direct and indirect hormonal changes resulting from castration are perhaps only moderate at the time of the migratory response, leading to only moderate impairment of the response (*e.g.*, Morton and Mewaldt's experiment). Under the conditions of forced photostimulation on the other hand the events of the cycle are greatly advanced and telescoped, providing increased opportunity for competition between incompatible mechanisms. Gonadotropic secretion is already high, and the gonads are developing rapidly by the time fat deposition begins and *Zugunruhe* appears (see poststimulus castration experiments). In these early stages migratory and gonadal mechanisms must be assumed to be compatible; however, at about Week 3 or 4 (in the White-throated Sparrow at 15- or 16-hour photoperiods) the upward trend of body weight and fat is suddenly reversed, coinciding with the rapid development of the cloacal protuberance and therefore presumably with maximum output of gonadal and gonadotropic hormones. Apparently, high levels of gonadal or gonadotropic hormone activity are incompatible with the lipogenic mechanisms. The results of the prestimulus castration experiments can then be

explained thus: In the castrates under forced photostimulation the gonadotropic activity reached high levels so rapidly (due to absence of gonadal feedback) that the point of incompatibility was reached before the fat deposition and *Zugunruhe* mechanisms got under way.

The available evidence does not permit a final decision as to which of these explanations accounts for the observed differences in the effects of castration. While the last seems most important, the first two have probably contributed to some extent. Whatever explanation is invoked it seems reasonably certain that the effect of castration is mainly brought about by the hyperactivity of the gonadotropin-secreting mechanism. This implies that such hyperactivity impairs or disturbs the functioning of some other part of the hypothalamo-hypophysial system which is more closely involved with the migratory response. Until now it has not been possible to do more than guess what other part of the system might be involved. Recently, however, prolactin has been implicated as a causative factor in both pre-migratory fattening (Meier and Farner, 1964) and migratory behavior (Meier *et al.*, 1965). Prolactin alone or in synergism with gonadotropins or adrenocortical hormones induced or enhanced fat deposition and nocturnal restlessness in White-crowned Sparrows in a variety of experimental situations. Also, bioassay of pituitaries of wild White-crowned Sparrows collected throughout the year suggested increased levels of prolactin during the migration periods (Meier *et al.*, 1965). There is other evidence that the prolactin-secreting cells and the gonadotropin-secreting cells are stimulated simultaneously by increasing photoperiod in birds (Tixier-Vidal and Assenmacher, 1962). On the other hand, there is considerable evidence of a reciprocal relationship, probably originating in the hypothalamus, between gonadotropin secretion and prolactin secretion. It has been suggested (Haun and Sawyer, 1960) that the same hypothalamic neurohumor(s) that stimulate the discharge of luteinizing hormone (LH) also inhibit the release of prolactin.

Provisionally, then, the differing results of these castration experiments might best be explained by assuming that prolactin is in fact involved in the stimulus for migration and that there is, in some circumstances at least, a reciprocal or antagonistic relationship between the gonadotropin-secreting and prolactin-secreting mechanisms. Impairment of the migratory responses in castrates is then attributed to increased gonadotropic secretion accompanied by decreased prolactin secretion. The changes in hour-to-hour patterns of *Zugunruhe* described above might, however, be due directly to withdrawal of gonadal hormones since similar changes occur in normal birds at the time of gonadal regression when gonadotropic activity is low rather than high as in castrates.

In general, then, the results of the present experiments support the conclusion of Morton and Mewaldt (1962) that gonadal recrudescence and the release of gonadal hormones play a modifying rather than a primary role in spring migration. This role seems to be an indirect one involving the regulation of hypothalamo-hypophysial function by a negative feedback relationship between gonadal hormones and gonadotropic activity. Experiments in which fat deposition has been induced by the injection of androgens, *e.g.*, Schildmacher and Steubing (1952) are consistent with these views, since exogenous sex hormones would reduce gonadotropic activity and permit increased prolactin secretion.

SUMMARY

Castration experiments of two types were performed on White-throated Sparrows.

Poststimulus castrations of six birds performed after they had been exposed to artificial photostimulation had little permanent effect on the development of the spring migratory condition, as determined by fat deposition, body weight increase, and *Zugunruhe*. On the other hand prestimulus castrations of nine birds, performed while the birds were on short winter daylengths, effectively suppressed the development of the migratory condition when the birds were subsequently photostimulated. In both types of experiments castration resulted in the intensification of a late-night component of *Zugunruhe* similar to that also occurring in normal birds at the time of gonadal regression.

The results of these and other castration experiments in the literature exhibit different degrees of effect on the development of the migratory condition, ranging from almost complete suppression to only slight alterations in timing. Possible explanations of these are: (1) differences in the time of castration in relation to the onset of photostimulation, (2) species differences in response mechanisms, and (3) differences in the response rates in forced photostimulation as compared with natural.

The view is supported that gonadal hormones play only a modifying role in spring migration. It is further suggested that the effect of gonadal hormones on vernal fat deposition and migratory behavior is an indirect one involving the regulation of hypothalamo-pituitary function by a feedback mechanism. However, gonadal hormones may have a direct influence on the hourly pattern of *Zugunruhe*.

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