EFFECT OF PHOTOPERIOD ON MOLTING OF FEATHERS [1]

BY S. W. LESHER AND S. CHARLES KENDEIGH

THE regulation of seasonal activities of birds is of great interest and requires correlation of physiological processes with changes in environmental conditions. Considerable attention has been given to the effect of increasing daily photoperiods on the maturing of gonads and the reverse effect of decreasing photoperiods. The present study is an investigation as to the possible effect of changing photoperiods on regulating the time and rate of molting and renewal of feathers.

As early as 1908 Beebe made an experimental attempt to find the cause of molt. He gradually reduced the amount of light per day and increased the food given captive male Scarlet Tanagers, *Piranga erythromelas,* in full breeding plumage. The birds skipped their normal autumn molt. During the winter sudden controlled changes of temperature either to a higher or a lower degree caused all of the birds to lose weight, and a few molted. Among other early workers, Seligmann and Shattock (1914) failed to find a relationship between seasonal assumption of eclipse plumage in the Mallard, *Anas platyrhynchos,* and the spermatogenic function of the testis.

Miyazaki (1934, 1935) was able, by manipulating the photoperiod, to induce three sexual maturations within a year in *Zosterops palpebrosa japonica.* Each time that the photoperiods were reduced from fifteen hours to nine hours per day not only did the gonads regress in size but molting also ensued. Van Oordt and Damste (1935) obtained similar results for the Greenfinch, *Chloris chloris,* in Holland. Cages containing these birds were placed in a cabinet with the door partially open. Each day the door was closed a fraction until at the end of ten days (May 22) it was completely closed. The birds began molting in June and completed the process in July. Since the size of the testes also decreased with the reduction of the photoperiod, Van Oordt and Damste believed that molting may be due to an interacting influence of the gonads and the thyroid.

Very little is known as to the effect of increased photoperiod on the spermatogenic development of birds living in tropical regions where the days are of nearly the same length throughout the year. However, Brown and Rollo (1940), working with whydahs and weaver finches of the species, *Steganura paradisea, Pyromelana franciscana,* and *Vidua principalis,* found that the normal breeding plumage in these equatorial birds could be obtained in one year, instead of the normal two years, by artificially subjecting them to increased periods of daily light. *Steganura* underwent a complete molt before assuming nuptial

[1] Contribution from the Zoological Laboratory of the University of Illinois, No. 589.

plumage whereas the other two genera renewed only the feathers that changed color. Of direct concern in this connection are the observations of Witschi (1935) that the season of year when plumage changes occurred in the African weaver finch, *Pyromelana franciscana,* one of the species used by Brown and Rollo, was the same for birds caged in his laboratory in Iowa City as it was for birds in Africa, although the seasonal changes in the photoperiod are just reversed in these two localities.

In a recent paper Burger (1941) states that the European Starling, *Sturnus vulgaris,* came into molt under a constant light ration of fifteen to sixteen hours per day. However, Starlings, whose light rations were reduced to nine hours, molted earlier and the new feathers grew more rapidly than in the birds which remained on a constant long photoperiod. On a basis only of observations made in the field, Salomonsen (1939) predicts that the season of molt is controlled by time and rate of changes in temperature rather than length of day. Although the literature is thus suggestive of various controlling influences over molt, it is confusing and often contradictory.

Materials and Methods

We have carried out two experiments (1939–40 and 1940–41) of like nature and observed the reactions of four species. All the birds were trapped on or near the University of Illinois Campus, Urbana, Illinois.

The White-throated Sparrow, *Zonotrichia albicollis,* is a migratory species in this locality. According to Dwight (1900: 196), it goes through two molts each year. The pre-nuptial molt occurs during April and May and involves only body feathers. The post-nuptial molt is complete. It starts in July and extends into late September or early October. The English Sparrow, *Passer domesticus,* a non-migratory species, has no pre-nuptial molt but does have a complete post-nuptial molt beginning in early July and extending into October. The Slate-colored Junco, *Junco hyemalis,* a migratory species, has only the complete post-nuptial molt, starting in July and continuing into September. The Bob-white, *Colinus virginanus,* a non-migratory species, has a very limited head molt in the spring and a complete post-nuptial molt from August to October (Bent, 1932: 17).

The experiments here to be reported were performed in a glass house exposed on four sides to normal daylight, from the north, south, west, and ceiling. The room was sufficiently isolated to eliminate any but minor reflections at night from the street lights and sky. The room was divided into two parts by an opaque partition by which the light over the experimental cages was completely shut off from those containing the control birds.

The cages used for retaining the birds in the first experiment were entirely metal, cylindrical in shape, and covered with fine screen wire. They were one and a half feet in diameter and five feet long. All waste food and excrement were removed from the cages at least twice weekly. New cages were built for the second experiment. The frame work was constructed of wood, then enclosed on the top, bottom, and front with hardware cloth and on the other three sides with pressed wood. The open mesh bottom permitted elimination of waste food and excrement, thereby reducing opportunities for spread of pathogenic bacteria and coccidiosis. Each cage was individually lighted with 150 watt, incandescent, frosted bulbs; two being required for each cage in the first set of experiments but only one in the second. In the second experiment the average light intensity at the level of the roosting perches was 39 foot candles; at the bottom of the cage, 14 foot candles. Two additional metallic cages of the type used in the first experiment were set up to house the unlighted controls for the second experiment.

Fresh water and feed were kept constantly before the birds. At the beginning of the first experiment the food consisted of cracked grain, mostly corn, and fresh lettuce leaves. The birds were weighed at the beginning of the experiment and at irregular intervals thereafter. A noticeable drop in body weight together with a tendency towards droopiness of the birds made it necessary to make changes in the diet. The grain portion was changed to hemp, which is high in fat content, and canary seed. The birds rapidly gained weight and were soon normal. In the second experiment a commercial preparation, which included irradiated yeast and cod-liver oil added to a base of ground sweet meal, was fed daily in addition to the grain mixture to all except the English Sparrows. Fine gravel and cuttle bone were placed in each cage. Every effort was made to eliminate any vitamin deficiency which might influence the results of the experiment. On the later diet the birds remained constant in weight and slightly higher than birds being trapped in the wild at the same time.

At the beginning of both experiments (Table 1) the lights were turned on at two o'clock in the afternoon and continued fifteen minutes beyond sunset. Each day the light period was increased fifteen minutes except in the controls. As the length of normal day light at this time of the year was decreasing at the rate of two minutes a day, actually the artificial lights were left on for an additional seventeen minutes daily. After the artificial day reached its full length of fifteen hours, which is comparable to the maximum length of a summer day, the lights were turned on and off manually at the same time each day. The time the birds were held at the full fifteen-hour day was 45 days in the first experiment and 139 days in the second. After all molt due to increased photoperiod had ceased and the birds had reached an apparently constant physiological state, the length of day was shortened.

TABLE 1

DATA ON TIME RELATIONS OF EXPERIMENTS

(Molt is here used to include the period of feather loss only)

	First Experiment	Second Experiment
Date experiment begun	December 4, 1939	October 14, 1940
Date photoperiod of 15 hours attained	December 23, 1939	November 4, 1940
Date partial molt started	December 25, 28, 1939	November 10, 1940
Date partial molt ended	January 8, 1940	November 24, 1940
Date shortening of photoperiod started	February 6, 1940	March 23, 1941
Date photoperiod of 9 hours attained:		
Cage A	February 6, 1940	June 2, 1941
Cage B	February 29, 1940	April 15, 1941
Cage C	February 29, 1940	March 23, 1941
Cage D	April 17, 1940	Held at 15 hours
Cage E	Controls	Held at 15 hours
Cage F	Controls	March 23, 1941
Cage G		March 23, 1941
Cage H		April 15, 1941
Date complete molt started:		
Cage A	February 16, 1940	April 15, 1941
Cage B	February 21, 1940	April 5, 1941
Cage C	February 24, 1940	March 30, 1941
Cage D	March 4, 1940	Held at 15 hours
Cage E	Controls	Held at 15 hours
Cage F	Controls	March 30, 1941
Cage G		March 30, 1941
Cage H		April 8, 1941
Date complete molt ended:		
Cage A	February 25, 1940	June 8, 1941
Cage B	March 19, 1940	April 29, 1941
Cage C	March 19, 1940	April 11, 1941
Cage D	May 11, 1940	Held at 15 hours
Cage E	Controls	Held at 15 hours
Cage F	Controls	April 11, 1941
Cage G		April 11, 1941
Cage H		May 2, 1941

This shortening of the photoperiod was at various intervals to determine any possible effect on the rapidity of the produced molt (Table 2).

EFFECT OF INCREASED PHOTOPERIODS

First Experiment—Two days after the added light had increased the photoperiod to fifteen hours in the first experiment, the White-throated Sparrows in cages A and B (Table 2) began dropping feathers from the anterior region of the ventral tract. Three days later the birds in cage D began losing feathers from the same tract. The molt progressed from anterior to posterior in both the ventral and spinal tracts with the molt beginning in the spinal tract soon after the first signs of molt in the ventral tract. Feathers also were dropped from the posterior region of the capital or head tract. No remiges or rectrices were

TABLE 2

DISTRIBUTION OF BIRDS IN DIFFERENT CAGES

CAGES	White-throated Sparrow	English Sparrow		Slate-colored Junco	Bob-white Female	Rate photoperiod reduced from 15 to 9 hours
		Male	Female			
	First experiment					
A	8					Immediately
B	8					15 min. daily
C		1	8			15 min. daily
D	8					5 min. daily
E		4	4			Control
F	5					Control
	Second experiment					
A	8					5 min. daily
B	8					15 min. daily
C	8					Immediately
D	3			3		Held at 15 hours
E		8				Held at 15 hours
F		4	4			Immediately
G					1	Immediately
H			8			15 min. daily
I		4	4			Control
J		4	4			Control

molted. The White-throated Sparrows of the unlighted control cage (F) showed no signs of molting. The testes of six birds, sectioned and examined microscopically during this partial molting period, were in complete spermatogenic development. The molt was short in duration and by the end of the second week was completely over (Figure 1). None of the English Sparrows showed any sign of molt although the blackening of the bill in the males showed that the gonads were increasing in size in the expected manner.

Second Experiment—In the second experiment, six days after the photoperiod had reached its full length of fifteen hours, the White-throated Sparrows began molting. The molt in this experiment was more extensive than in the first experiment. This time it included the rectrices and a few scattered secondaries in all except the birds in cage D, which were birds that were carried over from the first experiment, and five birds in cage A. The molt progressed rapidly to its peak in eleven days, then ceased entirely after another three days. The gonads of those birds examined at the start and during the molt were in complete spermatogenic development. During this period of extended day length and up to the time that the light was reduced, the White-throated Sparrows showed many signs of mating behavior and often attempted copulation. Early in the morning and again at night before the lights were turned off, their singing was loud and natural.

The Bob-white (cage G) molted only a few feathers around the head and throat. One hundred twelve days after the photoperiod reached fifteen hours, this solitary female laid an egg and followed this with one every six days for four successive weeks, until the photo-period was

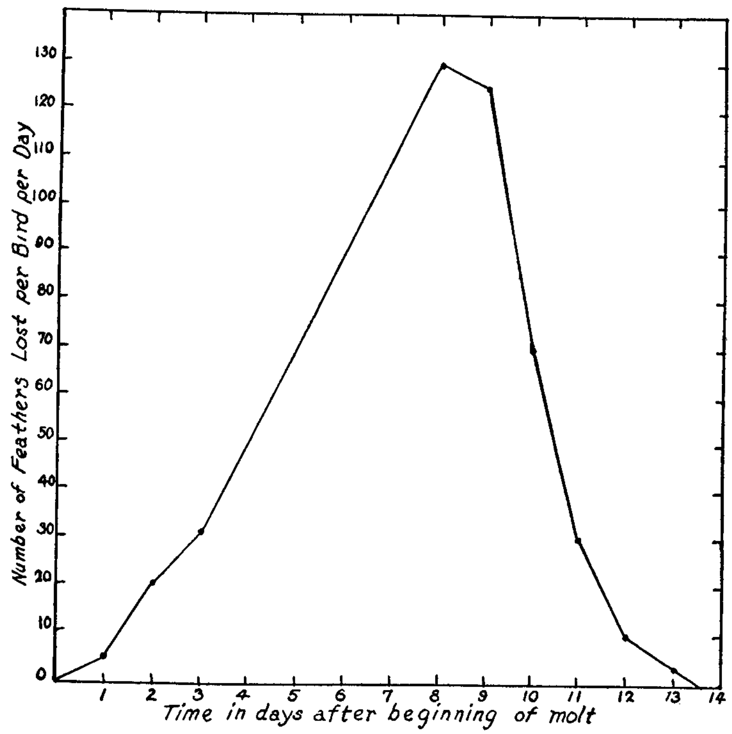

Figure 1. Average rate of feather loss in White-throated Sparrows during a partial molt induced in two experiments by increasing the daily photoperiod to fifteen hours.

reduced. None of the control White-throated Sparrows, nor any of the English Sparrows, nor the Slate-colored Juncos showed any sign of molt.

Effect of Decreasing Photoperiods

First Experiment—All of the birds in the first experiment, both White-throated Sparrows and English Sparrows, molted as the day length was decreased. The beginning of complete molt and the rate of progress appeared to depend upon the rate of the reduction in daily light. Birds reduced suddenly on February 6 from fifteen to nine hours light (Table 2, cage A) began molting ten days later. The molt began with the loss of primaries but thereafter the feathers fell so rapidly and in such great numbers that it was impossible to trace any definite sequence. The molt was completely over nine days after it began (Figure 2). All birds lost weight rapidly and by February 29 all were dead. The shortened feeding hours together with the sudden molt and the energy requirements for growing new feathers were apparently too great a drain on their body reserve.

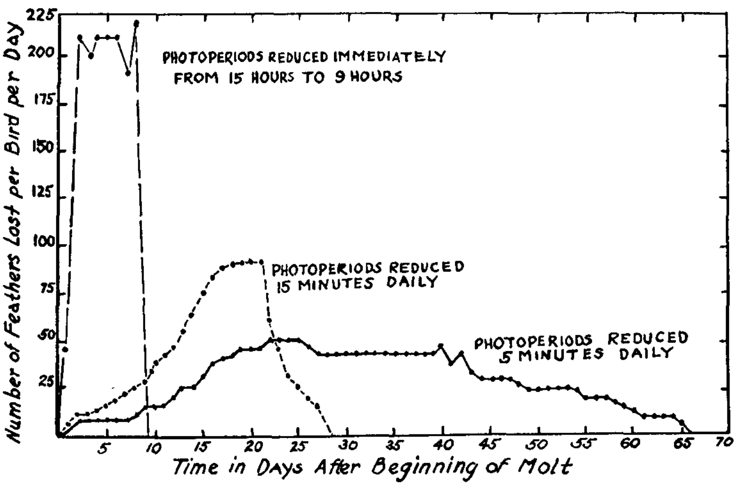

Figure 2. Comparison of rate and duration of feather loss in the complete molt of English and White-throated Sparrows in the first experiment, induced by shortening the daily photoperiod at different rates.

The birds subjected to a light reduction of fifteen minutes daily beginning February 6 (cages B, C), began their molt 15 days later in the White-throated Sparrow and 18 days later in the English Sparrow. The molt in both species was still irregular in sequence but extended over a period of four weeks. In spite of the more gradual molt, the weight of all birds decreased, although they recovered and developed new feathers.

The molt of the birds reduced from fifteen hours to nine hours at the rate of five minutes daily (cage D) began 27 days after the beginning of the light reduction and more nearly approached the normal molt as it occurs in nature. The weight of the birds dropped slightly. The new feathers quickly replaced the ones lost so that the birds never acquired the ragged appearance such as characterized the more rapid molt in the other cages. The count of feathers lost per day (Figure 2) is only an approximate one as some feathers were eaten by the birds and others were lost. The total feather loss was 1500 per bird in those exposed to an immediate decrease in the photoperiod, 1700 per bird in those exposed to a fifteen minute daily decrease, and 1900 per bird in those exposed to the five minute daily decrease. This is to be compared to a total loss about 740 feathers in the partial molt (Figure 1).

Second Experiment—The factors made evident by the first experiment were confirmed by the second. In the birds exposed to a suddenly shortened photoperiod of nine hours (Table 2, cages C, F, G) the molt began almost simultaneously in the White-throated Sparrows, English Sparrows, and Bob-white; but it was more intense with the Bob-white and English Sparrow than with the White-throated Sparrow. The molt began seven days after the photoperiod was shortened. The loss of feathers was not as extensive as in the first experiment and at the end of the twelfth day it ceased. The Bob-white and White-throated Sparrows were given vitamin food with their regular grain rations and suffered no ill effects from their molt. The English Sparrows were fed only their grain rations and though they appeared to be more sturdy, three of the five birds were not able to recover from the effects of the heavy molt (Table 3).

TABLE 3

AVERAGE WEIGHT OF BIRDS IN GRAMS AT DIFFERENT TIMES IN THE SECOND EXPERIMENT

CAGES	A	B	C	D[1]	D[2]	E	F	H
Just trapped, short days	26.2	26.5	24.1	25.1 (1939)	17.3	26.2	25.3	26.1
After one week in captivity	25.9	26.1	23.9	....	17.1	25.4	25.0	25.7
At stage of photoperiod increase represented by 12 hours of daily light	26.3	26.9	24.1	29.0	18.0	25.7	25.2	26.0
After one week in 15-hour photoperiod	27.1	28.0	26.3	29.4	21.0	27.1	26.1	26.0
During period of partial molt	25.7	26.2	24.8	29.5	21.2	27.1	26.3	26.1
After four weeks in 15-hour photoperiod	27.7	28.5	26.6	30.1	21.2	27.2	26.5	26.2
At beginning of complete molt on decreased photoperiod	27.6	28.6	26.6	(29.9)[3]	(20.9)	(27.1)	26.4	26.3
At end of complete molt	25.4	25.7	23.1	(29.3)	(18.9)	(24.0)	23.1	24.2

[1] White-throated Sparrows only.
[2] Slate-colored Juncos only.
[3] Weights in parenthesis are of birds that did not molt but taken at the same time as for birds in other cages that did molt.

The White-throated Sparrows and English Sparrows subjected to reductions in day length by fifteen minute (Table 2, cages B, H) and five minute intervals (Cage A) went through a more gradual and orderly molt, but this was not as complete a molt as in the first experiment. The birds were in excellent condition but suffered some decrease in weight (Table 3). The birds subjected to photoperiods reducing at fifteen minutes per day began their molt 13 to 16 days after the start of the reduction; those subjected to photoperiods reducing at five minutes per day began 23 days after the start of the experiment.

In addition to the cages subjected to a reduction in photoperiod, two cages (D, E) were kept at a constant fifteen-hour day. As the days were rapidly increasing in length, the amount of added artificial light was reduced each day at a corresponding rate. Neither group of birds molted. The White-throated Sparrows skipped the normal partial molt which occurs in spring.

The three White-throated Sparrows retained from the first experiment (Cage D) were more uniform and natural in their molt than those freshly secured for the second experiment. Since these three White-throated Sparrows were trapped in October, 1939, they had experienced three partial and two complete molts, namely: an induced partial molt beginning December 25, 1939; an induced complete molt beginning February 16, 1940; a partial molt in May, 1940; a normal complete molt in August, 1940; and an induced partial molt beginning November 10, 1940.

Many remiges and rectrices of the White-throated Sparrows, which replaced feathers molted during the complete molts, came in as albino feathers. All the feathers in the other tracts were normal in color. This occurred in forty per cent of the birds of this species, but did not occur in the English Sparrow, Slate-colored Junco, or Bob-white, although these birds were under comparable conditions. No explanation can be advanced for this phenomenon at the present time.

Discussion

These experiments demonstrate definitely that, at least under certain experimental conditions, changes in the length of the daily light period will induce molt and renewal of feathers at other than the normal time of year. Not only that, but the rate at which the photoperiod is reduced will affect the time the molt is initiated and the rapidity at which the feathers are lost. The inference is not justified at the present stage of the investigation, however, that the season and regulation of molt is determined only by changes in the photoperiod. As yet we have only started the investigation of the influence of changes in temperature, which Salomonsen (1939) claims to be the primary factor, and other factors may also be important.

The molt brought about by the reduction in the photoperiod occurred in three species and was more or less complete (less so in the second than in the first experiment), as is true for natural conditions when birds undergo their post-nuptial molt in the autumn. The molt produced by increasing the photoperiod occurred only in those species where a pre-nuptial spring molt is known to occur under natural conditions and not in the others. This molt in nature is a partial one, and this was true for the artificially produced molt, except in the second experiment with many of the White-throated Sparrows when it was abnormally heavy.

The total time required for birds to lose their feathers and then completely replace them was nearly the same (65 to 73 days) regardless of the rapidity at which the feathers were lost (Figure 3). This

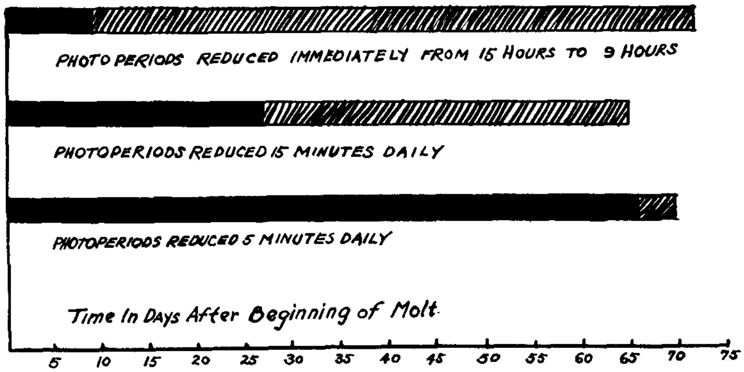

Figure 3. Comparison of time required to lose old feathers and to grow new ones in English and White-throated Sparrows exposed in the two experiments to daily photoperiods decreasing at different rates. The solid portion of the bar represents the period during which the feathers were lost, while the cross-hatched portion is the additional period required for the complete growth of new feathers.

would seem to indicate that the feather papilla begins growth very soon after the photoperiod is reduced and proceeds at nearly the same speed regardless of the rate at which the photoperiod is decreasing. It is possible that loss of feathers and growing of new ones are somewhat independent processes but both related to changing day lengths.

The intermediary mechanism by which length of day produces its effect upon the feather papilla is not known. Length of day supposedly influences the size of the gonads by way of the pituitary gland, and the gonadotropic hormones of the pituitary have received considerable study. Perhaps the pituitary gland is also involved in producing molt, but there is very little evidence for such a direct relationship. There is as much reason to believe that the thyroid glands may be involved as the gonads, but it is realized that the activity of both of these glands is affected in turn by the pituitary. In these experiments the testes varied in size and development with increasing and decreasing lengths of light period in the manner to be expected. It might be reasoned that they regulated the loss and renewal of feathers. Molt occurred in females similarly as in males, although very likely their ovaries did not reach as complete development as did the testes of the males, except in the Bob-white. It is very possible that the influence of the photoperiod over gonad development and feather molt is entirely independent. We have made plans to test this point with castrated birds. Contrary to what Burger (1941) found, molt did not occur in our birds maintained continuously at the fifteen-hour day.

Length of day may affect molt through some other mediation than by direct hormone stimulation. Changes in nutritive balance may be important, as Beebe (1908) hinted. In future experiments we hope to measure rate of energy metabolism at various stages in this molting cycle, but in the present experiments reliance had to be placed solely on changes in weight. With longer days and shorter nights, length of time available for feeding is increased, and the corresponding daily period without food is shortened. The reverse is true with shortening days and lengthening nights. Table 3 shows a strong tendency for birds to increase in weight when subjected to a fifteen-hour photoperiod. The White-throated Sparrows that underwent a partial molt on the long photoperiods decreased in weight at this time, but not as much as did all birds that underwent a complete molt on the shortened photoperiods. The results are not entirely consistent as the Slate-colored Juncos in cage D and the male English sparrows in cage E also decreased in weight, although they were being held at a fifteen-hour light period and were not molting. The average weights of the control birds in cage I, taken eight times during the course of the experiment, varied only between 24.9 and 25.3 grams. Even if a correlation is fully established between loss in weight and molt, this will not demonstrate which is the cause and which is the effect. Perhaps both functions are independently affected, but the growth of feathers must certainly be energy demanding. The death of all birds when thrown into full molt in the first experiment by the sudden decrease of the photoperiod from fifteen to nine hours would seem to demonstrate this requirement.

The present paper is a preliminary report, but the results obtained to date are suggestive, promising, and leading toward future researches.

Summary

1. White-throated Sparrows and a Bob-white, which normally go through a partial pre-nuptial molt in spring as the days are increasing in length, were forced to molt out of season by artificially increasing the length of day, and this was followed by a new growth of feathers.

2. White-throated Sparrows, English Sparrows, and a Bob-white, all of which have a complete post-nuptial molt as days decrease in

length in late summer and autumn, were forced into a similar molt out of season by artificially reducing the length of day to which they were exposed. This was followed by a new growth of feathers.

3. The time for beginning the complete molt and the rate at which the feathers were lost were accelerated by increasing the rate at which the length of day was artificially decreased.

4. The total time (65 to 73 days) required to molt feathers and completely grow new ones was approximately the same at all rates of decrease in the photoperiod and irrespective of the rate at which the feathers were lost.

5. The weight of the birds increased when they were placed on a better balanced diet and when they were subjected to longer photoperiods, but it decreased during the progress of molt and renewal of feathers.

Literature Cited

Beebe, C. W.
1908 Preliminary report on an investigation of the seasonal changes of color in birds. *Am. Nat.*, 42:34–38.

Bent, Arthur Cleveland
1932 Life histories of North American gallinaceous birds. *U.S. Nat. Mus. Bull.*, 162:1–479.

Brown, Frank A., Jr., and Marie Rollo
1940 Light and molt in weaver finches. *Auk*, 57:485–498.

Burger, J. Wendell
1941 Experimental modification of the plumage cycle of the male European starling (*Sturnus vulgaris*). *Bird Banding* 12:27–29.

Dwight, Jonathan, Jr.
1900 The sequence of plumages and moults of the passerine birds of New York. *Annals N. Y. Acad. Sci.*, 13:73–360.

Miyazaki, Hoshimaro
1934 On the relation of the daily period to the sexual maturity and to the moulting of *Zosterops palpebrosa japonica*. *Sci. Rep. Tohoku Imp. Univ.* 4th ser., 9:183–203.
1935 Notes on the relation between the moulting, the sexual maturation and and the light period in *Zosterops palpebrosa japonica*. *Ibid.*, 9:427–429.

Salomonsen, Finn
1939 Moults and sequence of plumages in the Rock Ptarmigan. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 103:1–491.

Seligmann, C. G., and S. G. Shattock
1914 Observations made to ascertain whether any relation subsists between the seasonal assumption of the eclipse plumage in the mallard and the functions of the testicle. *Proc. Zool. Soc. London*, 1914:23–43.

Van Oordt, G. J. and P. H. Damste
1939 Experimental modification of the sexual cycle and molt of the green finch. *Acta Brevia Neerlandica*, 9:140–143.

Witschi, E.
1935 Seasonal sex characters in birds and their hormonal control. *Wilson Bull.*, 47:177–188.

Vivarium Building, University of Illinois, Champaign, Illinois.