LIGHT AND MOLT IN WEAVER FINCHES

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INTRODUCTION

THE problem of cyclic behavior of animals has long been an intriguing one. Some well-known cycles are the annual migration of birds, the periodic development and regression of their reproductive glands, and their seasonal plumage changes. In the past much speculation has been advanced as to the control of these activities. They have been variously considered as inherent rhythms or as environmentally induced ones and many factors of the environment have been called upon to account for them.

After Garner's clear demonstration of the importance of daylight lengths, or photoperiodism, in determining seasonal activities in plants, it seemed logical that perhaps animals, as well, were responsive to such a stimulus. Eifrig (1924) was the first to state clearly that photoperiodism might control the migrations of palaearctic birds. To Eifrig the gradual change in daylight periods appeared to be the only environmental factor varying regularly enough to account for the predictable arrivals and departures of migrant birds. More recently, due particularly to the excellent researches of Rowan (1925, 1926, 1927, 1928, 1929, 1930, and 1932), Bissonnette (1930a, 1930b, 1931a, 1931b, 1931c, 1932a, 1932b, and 1933), Bissonnette and Chapnick (1930), and Bissonnette and Wadlund (1931, 1932, and 1933), we know the daylight period to be an important factor in determining sexual and migrational activities in temperate-zone birds. Rowan's work was performed principally on the Junco and the Crow. He demonstrated that increasing lengths of light periods stimulated enlargement of the gonads and northward migration. Conversely, decreasing light periods induced reduction in gonad size and permitted southward migration. In the absence of gonads the birds proceeded south in spite of stimulation by increased light periods. Rowan concluded that it was the increased exercise of the birds permitted by the longer light period that was the effective agent rather than the light stimulation itself.

Bissonnette, working with the European Starling, repeated and extended the work of Rowan. Bissonnette confirmed the testis-stimulatory action of increased light periods. He found white light of an intensity between 29 and 186 foot-candles to be the most effective for supplementing the natural daylight period. Red light had

a definite stimulatory action on the gonad. Green light acted in a reverse manner, inhibiting or retarding gonadal development. Bissonnette was unable to confirm Rowan's conclusion that light was effective only through the extra exercise that it permitted. Instead, he found that extra exercise, by itself, caused slight regression of the testes of Starlings and that in association with supplementary light periods the action of exercise was to render the bird less sharply responsive to increased and decreased periods of illumination. He suggested that this last effect could well account for some of Rowan's data on the apparent effect of exercise.

The simple explanation of northward migration as a result of stimulation by increasing light periods and southward migration as a result of the absence of such stimulation cannot be the whole solution since it has frequently been pointed out that trans-equatorial migrants commence their northward journeys while the days are decreasing in length. It is becoming increasingly apparent that although light is a major factor in determining a number of seasonal activities of birds, yet other factors must be involved. Bissonnette (1932a, 1933) finds reason to suspect that types of food may be influential. There is also reason to assume some inherent rhythm. For instance, even when all conditions are favorable to induce increase of size in the testis the birds show a rise to a peak of testis activity and then testis regression. In a constant and favorable environment, this might result in a rhythmic behavior of an inherently determined frequency. In the normal changing environment the inherent rhythm might be present but its frequency determined by external factors. In this case the frequency would be lower than the maximum possible.

Since it is quite definitely established that photoperiodism can modify periodic sexual and breeding activities in temperate-zone birds which experience considerable variation in lengths of days and nights, it becomes interesting to learn to just what extent, if any, tropical and equatorial birds are similarly affected. Only on the equator itself are the days and nights of nearly equal lengths throughout the year. Six degrees north or south of the equator the difference in lengths of the day and night is about forty minutes, and ten degrees north or south of the equator it is about seventy minutes. Moreau (1931) has already suggested that it would be well worth while to repeat on equatorial birds the type of experiment performed by Rowan and Bissonnette.

The experiments reported herein were performed to determine to what extent tropical and equatorial birds may have their normal

plumage changes and regenerated feather types modified by changing photoperiods and in what ways they are similar to and differ from temperate-zone birds in such responses. The birds selected for the experiments were whydahs and weavers of the species, *Steganura paradisea, Pyromelana franciscana,* and *Vidua principalis.* Their normal geographic range is in Africa from about twenty degrees north to about twenty degrees south of the equator. These particular genera were chosen upon the advice of Mr. Rudyerd Boulton of the Field Museum of Natural History. The experimental observations were made by the junior author.

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THE EXPERIMENTAL ANIMALS AND THEIR GENERAL CARE

All the birds used in these experiments were trapped near Senangambi and shipped here by an agent. It was impossible to ascertain their exact age upon arrival but, judging from their small size and their juvenile plumage, they could not have been more than two or three months old. Their exact weight was not checked, inasmuch as it seemed inadvisable to handle them in their wild condition.

No difficulty was encountered in feeding the birds. Fountains kept clean drinking water always available and hoppers were filled with canary seed and different varieties of millet. The seed was always before them in excess of the quantity consumed. Trays of gravel, charcoal, and oyster shell were provided and pieces of cuttle bone were fastened to the wire in the cages. *Tenebrio* larvae were cultured and fed to the birds twice a week, about four or five larvae per bird. The birds were given green food or fruit on alternate days.

There is a very marked sexual dimorphism of plumage type during the breeding season in all three species investigated. The males wear the nuptial plumage during the breeding season and the eclipse or hen plumage during the remainder of the year. The females remain drab throughout the year.

In nuptial plumage the male *Steganura paradisea* (Paradise Whydah) has a black head, back and shoulders. This black ends at a point on the chest. The nuchal collar and chest are chestnut brown, gradually fading into white at the vent. The tail-feathers are black and greatly elongated. The bill is black. The male *Vidua principalis* (Pintail Whydah) in nuptial plumage is black and white with elongated tail-feathers narrow and irregular in length. The bill is

red. The male *Pyromelana franciscana* (Orange Weaver) when in color has a black head and abdomen and a large ruff and tail of orange. The bill is black.

NORMAL PLUMAGE CHANGES OF *Pyromelana* AND *Steganura* AT THE LATITUDE OF CHICAGO

In order to determine the normal plumage changes of these equatorial birds when they are held captive in the region of Chicago, a pair of juvenile *Steganura* and two juvenile male *Pyromelana* were carefully observed over a period of three years. The records commenced in November 1934, when the birds were at most only a few months old.

In July 1936, the two male *Pyromelana* started to molt into nuptial plumage and their bills turned black. At about the same time the bill of the female *Steganura* became black. The male *Steganura* died during the molt from unknown causes. The remaining birds stayed in nuptial plumage for about two months and then assumed the eclipse plumage. In July 1937, the males assumed nuptial plumage again and remained in color up to the conclusion of the observations in December 1937. At this time the birds used in this experiment were included along with a new lot of juveniles in the following experiment.

LIGHT AS A FACTOR IN MODIFYING PLUMAGE CHANGES IN EQUATORIAL WEAVER FINCHES

The Experiment

The experiment was conducted in a basement. The two birdcages faced three west windows with shades. Heat was supplied by two steam radiators and the temperature was kept at about 80 degrees Fahrenheit. Moisture was maintained constant at 40 per cent by means of a Walton electric humidifier. This temperature and humidity were chosen because it was found to be the easiest to maintain constant in summer.

The two cages were constructed of wood and wire with wire floors which allowed droppings and the spray from the baths to fall through on to paper. Each cage was of the dimensions 36 x 18 x 18 inches. One of the cages (the light cage) was given light supplementing the natural daylight to extents to be described, by means of two 25-watt incandescent lamps with reflectors. After the experiment had been under way for two months an additional 40-watt lamp with reflector was added thereby raising the illumination at the level of the perches from 50 to 110 foot-candles. The second cage (the

control cage) was separated from the light cage by black oilcloth which hung between them.

The experiment began on December 5, 1937. At this time four male and one female *Steganura,* one male and two female *Vidua,* and four male and three female *Pyromelana* were put into the light cage. Into the control cage were put one pair of *Vidua,* one pair of *Steganura,* and four male and three female *Pyromelana.* These were all freshly received juvenile birds except for one male *Pyromelana* in each cage and the female *Steganura* of the control cage. These latter were the three-year-old birds whose history had been followed as described in the preceding section of this report. The three-year-old *Pyromelana* were at this time in nuptial plumage.

The first five days of the experiment the lights on the light cage were turned on from 4.00 to about 4.30 p.m. irregularly. After this, the light period was extended fifteen minutes each night until January 5, when the lights were on until 11.00 p.m. and thereafter the lengths of daily illumination remained constant.

The shades were drawn every night and not raised until 7.00 a.m. The birds, therefore, did not get the benefit of the increasing morning light in the spring. At night the time-switch which controlled the artificial lights of the light cage was set ahead as the day lengthened in order that the birds receive all the natural daylight with a gradually decreasing amount of artificial light after January 5. Thus the ratio of natural daylight over artificial light in the constant sixteen-hour light period gradually increased.

Results

Both the 'light' birds and the 'control' birds started to molt from their juvenal plumage into their first-winter plumage soon after the experiment began. Only the small feathers were dropped. There were many more of these in the light cage than in the control cage. The light birds were bare around the neck by December 20, showing that they were molting very rapidly. The controls appeared to be molting less rapidly. By the middle of January the light birds were in their first-winter plumage, as were the control birds soon after. The buffy-white parts on the *Pyromelana* in the light cage had turned yellowish, while they remained buffy white on the *Pyromelana* in the control cage.

A noticeable effect of the light upon the birds was the relatively great increase in weight of the birds in the light cage. The accompanying table shows the gain in weight of the birds in the light cage over the birds in the control cage by February 26.

Birds	*Light Cage*	*Control Cage*
	Average Weight, Grams	Average Weight, Grams
Steganura (male).....	18.6	16.7
Steganura (female).....	17.7	14.6
Vidua (male).....	12.3	10.0
Vidua (female).....	12.2	10.5
Pyromelana (male).....	20.7	15.8
Pyromelana (female)...	14.0	12.3
Pyromelana (mature)...	20.5	15.6

In February, remiges and rectrices were found in both cages, many more in the light cage than in the control cage.

Males in the Light Cage

Steganura.—By February 26, *Steganura* had a few chestnut feathers on the neck and a few black wing-coverts. Two males had regenerated new fifth primaries. By March 10, each had regenerated several primaries, and one had started to molt the secondaries. On April 1, they all had two to four new tail-feathers. The bills were black by April 4 and it was now evident without handling the birds that they were coming into color. On April 20, the black outline of the head and throat ending in a point on the chest was very definite. Chestnut spots on the chest and nuchal collar had appeared. All of the remiges and rectrices had been renewed and the lower back and rump were black. By May 1, their molt was completed except for the elongated tail-feathers, but the heavy quills which were to carry the latter had appeared above the other tail-feathers. By May 15, these were four or five inches long and the birds were transferred to an aviary. By May 25, the tail-feathers were nearly ten inches in length.

Vidua.—The male *Vidua* showed signs of coming into nuptial plumage by March 10. It did not molt the remiges but these darkened and the inner margins seemed to become much whiter. The crown molted first and assumed a solid black instead of stripes as in the eclipse plumage. The sides of the breast became black to form gorgets. The brown edges of the back feathers all dropped off in one week. The nuchal collar, scapulars and coverts became white. By April 1, three tail-feathers started to become elongated; on April 20 they were four inches, and on May 1, from eight to ten inches long.

Pyromelana.—The male *Pyromelana* were the slowest of the males to respond to the light treatment. By April 20, there were many orange feathers less than a centimeter long. By May 15, these had increased in number and could be seen on the flying or resting bird.

Some of the orange ruff had appeared. The bills were beginning to darken but did not become black for several weeks. By July 1, the *Pyromelana* were in full color. The remiges and rectrices had not been molted.

The adult male *Pyromelana* in the light cage, which was in color when the experiment began, retained its nuptial plumage and black bill throughout the experiment. The remiges and rectrices were not molted. In February, a few part-orange and part-black feathers appeared on the abdomen which is ordinarily black.

Females in the Light Cage

None of the females in the light cage showed any change from the first-winter plumage. The *Pyromelana* retained their yellow bills but the bill of the *Vidua* had changed from red to brown by May 1 and that of the *Steganura* had darkened by about July 1.

Males and Females in the Control Cage

None of the juvenile birds in this cage showed any change in plumage or bill color after assuming the first-winter plumage. The adult *Steganura* (female) molted and its bill which was black when the experiment began, turned yellow by January 5.

The adult male *Pyromelana* in the control cage, and in color when the experiment began, started to lose the black color of its bill about December 30. On January 5 its bill was yellow. Some orange feathers were found in the cage. From then on the molt proceeded rapidly until March 1, when the bird was in eclipse plumage.

Later Treatment of Control Birds

A pair of *Pyromelana* about six months old, from the control cage, were put into the light cage on May 15. The birds showed no signs of molting to nuptial plumage. The male started regenerating orange feathers on the forty-sixth day thereafter.

The male *Pyromelana* about three and one-half years old, of the control cage, was put into the light cage on May 15. It showed orange feathers on the fifty-second day thereafter.

A pair of *Pyromelana* about six months old were taken from the control cage and given twenty-four hours of light daily (twelve daylight and twelve artificial measuring about 110 foot-candles at the perches) from May 15 to June 5. On June 5 they developed tremors and were put into the light cage where they received sixteen hours of light as previously described. The male started coming into color by the forty-sixth day after the beginning of the twenty-four-hour light period stimulation.

A pair of *Pyromelana* about eight months old which had started to molt and regenerate hen feathers in the control cage were put into the light cage on July 1. The male started showing nuptial plumage on July 10. It gained five grams in weight from July 1 to July 10.

The results of the foregoing experiments are diagrammatically shown in Text-figure 1.

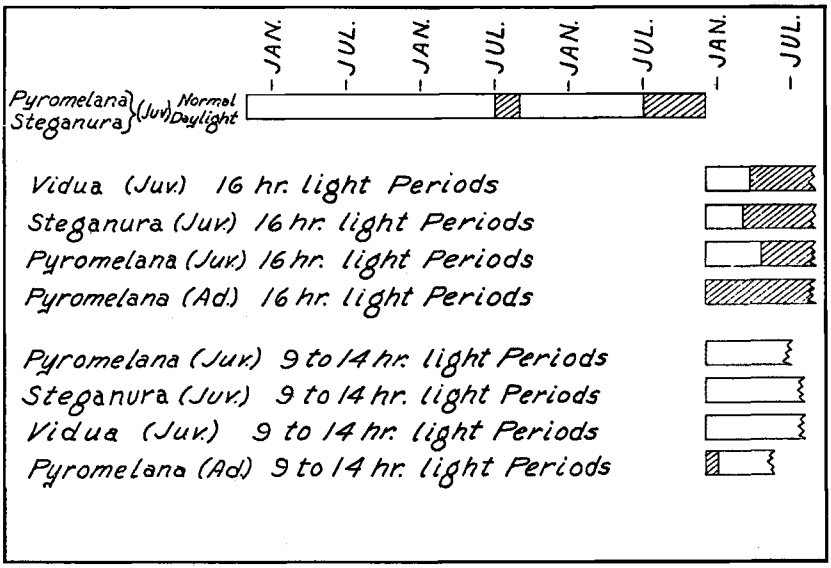


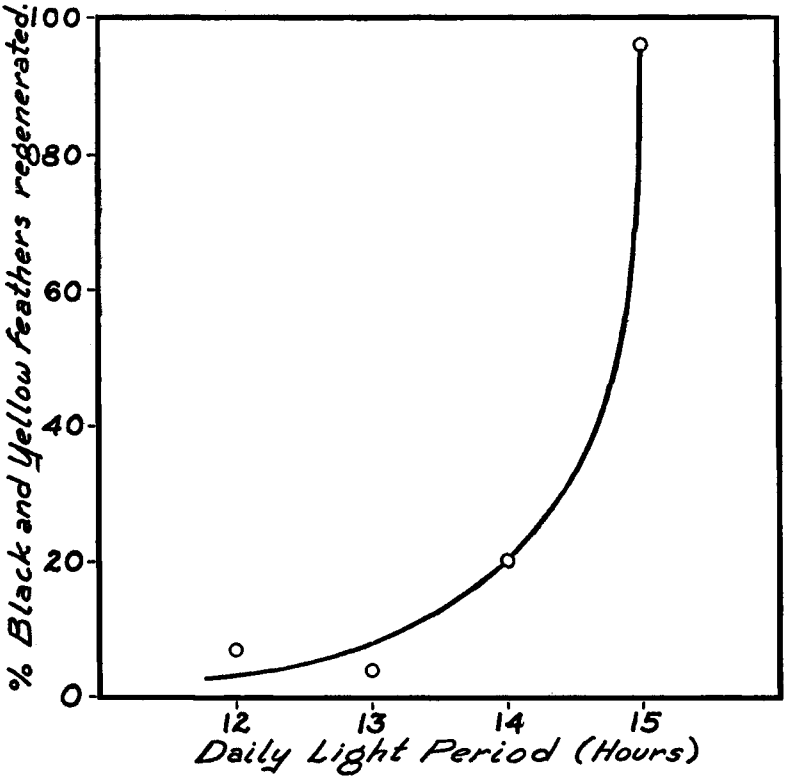
FIG. 1 Effects of Daily light upon Plumage type
▨ = Nuptial and □ = Eclipse Plumage

Light as a Factor determining the Type of Feather regenerated in Pyromelana

Light period.—On September 8, 1938, eight male *Pyromelana* of the preceding experiment were put into four cages, two to a cage. Feathers were plucked from the right breast of each and saved for comparison with the regenerated feathers. From September 20 onward, when the new feathers started to emerge from the sheath, two feathers were plucked each day for study. The experiment was concluded on September 29.

The shades were drawn from 6 p.m. to 6 a.m. central standard time, so that the birds received twelve hours of daylight. Additional light was added in cages 1, 2, and 3 from 60-watt lamps. Cage number 1 received three hours of artificial light from 6 to 9 p.m.; cage number 2, two hours from 6 to 8 p.m.; and cage number 3, one hour from

6 to 7 p.m. Cage number 4 received no artificial light. The light measured about 100 foot-candles the entire length of the perches and about 200 foot-candles at the food on the bottom of the cage. The birds spent about ten times as much time on the perches as at the food. Figuring ten minutes spent upon the perches to one at the food, the light probably averaged about 109 foot-candles, during the artificial-light period.



TEXT-FIG. 2.—Graph showing relation between lighting and type of regenerated feathers in *Pyromelana*.

The feathers that had been originally plucked from the breast were typically black male feathers. Some of the regenerated feathers of all the birds were black and yellow, the black being at the feather tip and base and the yellow in the mid-region. There were more yellow barbs and the depth of color was more pronounced in the feathers of the birds receiving the longer periods of light.

The regenerated feathers which showed this black and yellow marking were then plucked again, counted and compared in number with the black feathers originally plucked. The birds in the fifteen-hour cage regenerated 96 per cent black and yellow, those in the fourteen-hour cage, 20 per cent, those in the thirteen-hour cage, 4 per cent, and those in the twelve-hour cage, 7 per cent. The results are graphically depicted in Text-figure 2.

The feathers on the birds in the cage receiving fourteen hours of light daily, appeared to grow more rapidly than those on the other birds.

Intensity of supplementary light.—On September 29, one male *Pyromelana* was put into each of four cages. Cages 1, 2, and 3 were given eleven and one-half hours of daylight from 6 a.m. to 5.30 p.m. (central standard time) and two and one-half hours of artificial light controlled by a time-switch, making fourteen hours of light in all. The following average intensities were produced:

Cage 1.....	100-watt lamp	250 foot-candles
Cage 2.....	60-watt lamp	109 foot-candles
Cage 3.....	25-watt lamp	30 foot-candles

Cage 4 received no artificial light and was covered from 5.30 p.m. to 8.30 a.m., with a black cloth so that the birds received only nine hours of daylight.

The males were plucked on the left breast and feathers were kept for comparison with regenerated ones. Males in cage 1 regenerated all typically black male feathers. Males in cage 2 regenerated many feathers yellow in the mid-region and black at the tip and base, as in the preceding experiment. Males in cages 3 and 4 regenerated buff feathers with a small amount of black upon the tips.

On October 22, this experiment was repeated with the addition of a cage lighted by a 75-watt lamp and reflector.

Cage 1.....	100-watt lamp	250 foot-candles (bird of 60-watt cage in preceding experiment)
Cage 2.....	75-watt lamp	190 foot-candles (three males)
Cage 3.....	60-watt lamp	109 foot-candles (bird that was in 100-watt cage in preceding experiment)

The male now in cage 1 regenerated all typical black male feathers. This was the same bird that had regenerated feathers part black and part yellow in cage 2 when this type of experiment was first performed.

Of those in cage 2, one male regenerated all black male feathers and the two others, many black and yellow as in the earlier experiments. The male in cage 3 did not regenerate any feathers in the plucked

TABLE I

Daily Light Ration	Feather Regenerated
11.5 hrs. daylight + 250 f.c. for 2.5 hrs.	Exclusively black nuptial
" " " " 190 f.c. " " "	Black nuptial (1 case) Many black and yellow (2 Cases)
" " " " 109 f.c. " " "	Many black and yellow
" " " " 30 f.c. " " "	Buff feathers
9 hrs. daylight only	Buff feathers

parts during this experiment. (It regenerated a full coat of eclipse plumage during the next general molt.) The results are summarized in Table 1.

DISCUSSION

The normal rhythm of plumage changes in these equatorial birds can be modified by light control. Whereas gonad size in temperate-zone birds usually regresses after a certain length of time in spite of light treatments (Bissonnette, 1931a; Bissonnette and Wadlund, 1932), plumage type in these tropical birds apparently does not. They can be kept in nuptial plumage and breeding behavior throughout the year while under other light conditions they have a definite season for breeding behavior and a seasonal dimorphic change of plumage.

These experiments suggest that although the daily light period is of great importance in determining the time of molt and type of plumage in the birds, yet other factors are perhaps influential. The periods of light may be cumulative in their action and therefore a certain total illumination over a period of months may be effective in producing a molt. The type of feather produced appears to be conditioned by at least two factors, daily light period and intensity of illumination. New experiments should be devised to determine the relationships of these three factors (total light, photoperiod, and light intensity) in the process.

Steganura underwent a complete molt including the remiges and rectrices before assuming nuptial plumage while the other genera renewed only the feathers that changed color. The elongated tails

of *Vidua* and *Steganura* grew in last, after their molts were completed in other respects. *Vidua* had feathers on its back that were black in the center and brown on the edges. As in many other species, when the bird changed color these feathers did not molt but the edges dropped off leaving a solid color. This phenomenon is usually attributed to wear, but, from these experiments there would seem to be some kind of control in addition to simple wear or age of the feather. The edges on the feathers of *Vidua* dropped off in one week and out of season. The shabby appearance of remiges at the end of the season may be related in the same way to the molt. The remiges of *Pyromelana* usually become very shabby just before the normal molt, but in one of these experiments *Pyromelana* did not renew its remiges for eighteen months and they were in excellent condition at the end of this long period.

Steganura and *Pyromelana* in the normal daylight periods of this latitude did not assume nuptial plumage for nearly two years. *Vidua,* with supplementary light periods, changed from first-winter plumage to adult nuptial plumage and skipped entirely the first nuptial plumage lacking only the elongated tail, described by Friedmann (1937) for *Vidua macroura* in Ethiopia. However, according to Friedmann's descriptions, except for the tail, the first and the adult nuptial plumage are identical. As light brought this bird into color and as the tail-feathers grow in last, it is not unreasonable to assume that in Ethiopia, the light conditions are such that the bird cannot be brought to the height of its sexual cycle the first year. By the second year the developing bird has physiologically changed to an extent that it is able to respond in full to its natural environmental light conditions.

Friedmann writes that *Pyromelana franciscana pusilla,* at a point north of the equator, is said to be in winter plumage from December to February. In the Sudan the same species is in nuptial plumage from August to January, so not only are the two races geographically distinct, but also they are physiologically isolated, through difference in breeding season. Our experiments suggest that each race might assume the habits of the other if transplanted to the other's latitude.

SUMMARY

1. The equatorial whydahs and weavers, *Steganura* and *Pyromelana,* when kept in captivity at the latitude of Chicago, Illinois, do not come into nuptial plumage until they are about two years old.

2. In suitably controlled experiments *Steganura, Pyromelana,* and

Vidua were caused to come into nuptial plumage during their first year of life by subjecting them to daily light periods of sixteen hours.

3. Assuming the three genera to have been in comparable physiological condition at the beginning of the experiment, the *Pyromelana* were relatively the most resistant to light treatment and the *Steganura* were least so.

4. A *Pyromelana* in nuptial plumage, given sixteen-hour light periods, remained in nuptial plumage during more than a year of observation while a control bird, receiving only the natural daylight, went into eclipse plumage in slightly more than a month after the experiment began in December.

5. A male *Pyromelana,* one year old and in restricted daylight periods, in the process of molting from eclipse to eclipse plumage, almost immediately commenced regenerating nuptial feathers when placed in a sixteen-hour light period cage.

6. The type of feather regenerated in a male *Pyromelana* in nuptial plumage after plucking is affected by daily light periods and by the intensity of the supplementary light given the bird.

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