EFFECT OF LIGHT ON THE MOULTS AND SEQUENCES OF PLUMAGE IN THE WILLOW PTARMIGAN

BY PER HÖST

Plates 12, 13

INTRODUCTION

PTARMIGAN, like many other Arctic and high Boreal birds and mammals, show a pronounced seasonal dimorphism, and have, as do many of them, a white winter and a pigmented summer garb. But Ptarmigan are not limited to one summer and one winter garb. The spring plumage following the white winter one is subject to a series of changes during the summer, giving three to four distinct seasonal attires depending on sex and species. The striking manner in which the different plumages blend with the environment has caused ptarmigan to become a classical example of 'seasonal dimorphism' and 'protective coloration.'

Johnsen (1929) and Salomonsen (1939) have given broad surveys of the extensive older literature dealing with the change of plumage in ptarmigan. Detailed descriptions of the plumage changes in these birds have long been available, but until recently little has been done in investigating the mechanism behind the phenomenon, the joint actions of impulses from the environment and from the organism itself, which may be assumed to control the different changes. The first one to take up these questions in a really broadly planned investigation was Finn Salomonsen (1939). With a very large number of skins of Rock Ptarmigan and Willow Ptarmigan he tried to analyze the relation between the moults, the seasonal feather patterns, and the factors controlling them. First by comparison of the moults in various populations of birds living under different climatic conditions; secondly by a very detailed analysis of the feather pattern in the various stages of feather growth during the year, he arrived at the conclusion that *temperature* is the external factor controlling the rhythm of plumage changes. He also touched upon the idea that *light* might be a regulator for the changes in plumage. But without having any experimental work as a basis for his conclusions, he found no support for this idea in his material. I quote from his paper (1939: 337–338): "Although the matter is not quite settled we may conclude that: *The increasing amount of light is able to influence the development to maturity. It is, however, very unlikely that the annual light-cycle controls the moult. If the increase (or decrease)*

in illumination induced and encouraged the moults it would be very difficult to explain the moulting-rules and would presuppose that the ptarmigan formed very different physiological races."

In the experiments to be described in this paper, the same problems that were the objects of Salomonsen's investigation were approached by entirely different methods. Experiments were conducted to determine to what extent the rhythm of change in plumage was genotypically or phenotypically controlled, to determine whether an external stimulator was necessary for promoting the different phases of the changing rhythm, to determine the nature of this stimulator, and to answer a series of questions which arose in connection with it. This involved keeping the birds in captivity over a considerable length of time, and developing a technique for this.

During the summer of 1936 I conducted an experiment with keeping young Willow Ptarmigan (*Lagopus lagopus*) in captivity. The young were gathered in the wild a few days after being hatched and were placed in an artificial brooder. I succeeded in raising to maturity five out of twelve young. In the autumn of the same year I was requested by the Norges Jeger & Fiskerforbund (The Hunters' and Sport Fishermen's Association of Norway) to organize a project for raising ptarmigan on a large scale. The association pledged itself to furnish the money needed for carrying out the experiments. To Norwegian hunting, the Willow Ptarmigan is of greater importance than any other kind of small game. If the birds could be raised in captivity on a large scale, this might become of great importance in game management. During the winter an experimental station for the breeding of ptarmigan was completed and a number of birds necessary for breeding were secured. On this station, located near Oslo, Norway, were also performed the experimental studies on the change of plumage and the reproductive cycle of the Willow Ptarmigan which form the basis of the present publication. The main experiments were made in 1937–38, with some supplementary studies made later, until the work was interrupted early in 1940. Due to the war conditions and other unfavorable circumstances, the publication of the results has been delayed.

I am indebted to the Norges Jeger & Fiskerforbund and to the Fridjof Nansen Foundation (Nansenfondet, Oslo, Norway) for granting the funds that made the work possible. My acknowledgments are also made to Dr. T. H. Bissonnette for valuable suggestions, and to Dr. A. L. Rand, who has kindly read this manuscript and has been helpful in the final editing of it.

MATERIAL, TECHNIQUE AND GENERAL OBSERVATIONS

At the experimental station was kept, in the different seasons, a breeding stock varying between thirty and sixty birds. The breeding experiments were continued over several years and are—as far as the author knows—still going on. We succeeded in raising artificially a small number of young, and even obtained reproduction from the second generation in captivity but we did not succeed in raising them on a larger scale, as most of the young died in early stages. Any further reference to this point is, however, outside the scope of this publication (for a detailed account, see Höst, 1938); the experiments to be described here deal with adult birds only. It is of interest to mention the experimental arrangements applied to the adult ptarmigan and how their behavior and different functions adapted themselves to the experimental conditions.

Most of the stock birds were caught during the winter months, from the middle of December to the middle of March. It is in this period that most of the commercial hunting takes place in the larger and sparsely populated mountain areas in Norway. An announcement in the newspapers to the effect that live, uninjured ptarmigan would be bought at a price several times above the market value for dead ones resulted in a large number of ptarmigan being sent in by trappers. The collection of stock birds that we gathered in this manner consisted of ptarmigan from practically all the bird's range in Norway.

At the experimental farm the ptarmigan were placed in wire cages of different sizes. The largest cages we used had a floor area of eight square meters, as the ptarmigan showed a very quiet temper and did not seem to require so much space in order to thrive as had been generally believed. During the mating season we divided the ptarmigan so that there was, on the average, about one square meter of floor area to each individual, while at other seasons we had them considerably closer together. In the course of a few weeks the birds became rather tame, learned to know the cages and the person who fed them, and discontinued the habit of flying against the netting when somebody approached the cages. From the very beginning they appeared less nervous than some pheasants and Hungarian Partridges we had in captivity at the same time.

Those ptarmigan that got through the first difficult period of adjustment gradually reached very good condition and appeared normal in every respect. Weighings taken from time to time showed that the average weight of ptarmigan that had been in captivity for

some time was equal to or greater than the weight of ptarmigan in the field in the corresponding seasons. The health of the captive birds was very good, except during a period in the autumn of 1938, when an infection with high mortality spread among the birds, causing the experiments to be disrupted, so that they could only be taken up again later with a new stock of birds. The process of reproduction and moult in the captive birds was normal, and occurred at normal times compared with those of wild ptarmigan.

During the two seasons 1937 and 1938, the larger number of ptarmigan on the experimental farm began laying in the latter half of May and the first days of June; this entirely covers the period for the start of egg-laying in most of the ptarmigan grounds in southern Norway. The average number of eggs in ptarmigan nests in the wild is, in most years, eight or nine. In the 1938 egg-laying season, an experimental group of eleven ptarmigan hens, having their eggs removed daily, averaged 16.8 eggs per hen, with individual yields up to 27 eggs. Also in the male birds, the reproductive functions seemed to be normal; the high fertility of the eggs gave evidence of that. The percentage of fertile eggs for the seasons 1937 and 1938, all eggs and all experimental groups taken together, was more than 80%, and in some experimental groups it was considerably higher.

The time of completing the different phases of the spring and summer plumages varied greatly in the different individuals, and followed very closely the variation in the periods of reproduction. Females that laid their eggs early in the season also got their breeding or summer plumage early, while individuals that were late in their laying assumed their summer plumage correspondingly late. A similar close relation between plumage stages and reproductive activities was observed also in the males. In fact, the changes in plumage followed the reproductive development so closely that, from the experience we got throughout the first breeding season, we could predict from looking at the plumage—with a chance of error limited to only a few days—when the different hens would be laying their first eggs or when the male birds would be in their active mating stages. This was of great use in our breeding experiments and made it possible to pair the birds so that the males and females that were put together in the same pen were individuals that would come into their mating stages at the same time.

The close synchronization of plumage changes with reproductive activities suggested that the plumage changes were controlled by hormones from the reproductive system, or that both processes were

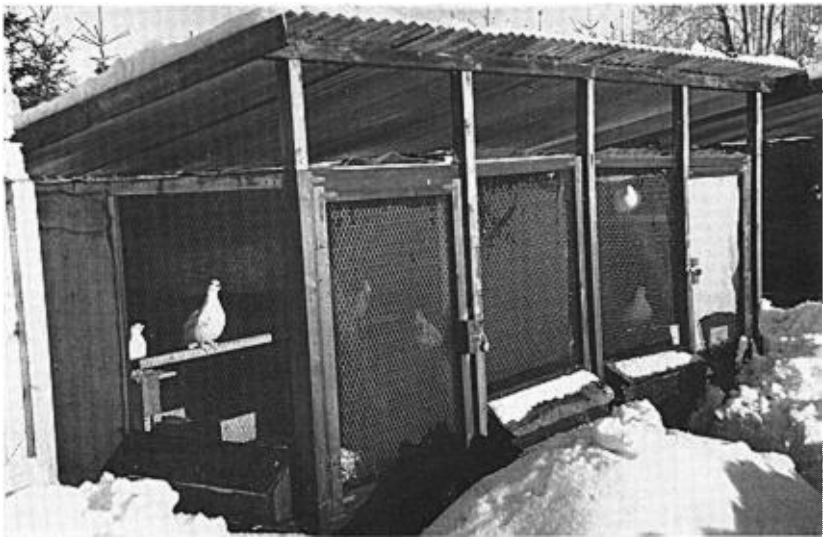
affected simultaneously by some factor in the environment. Experiments by Rowan, Bissonnette and others had already shown that in several species of birds light seems to be the most important factor controlling the reproductive cycle, and if given in quantities large enough it can produce activities of the gonads even during periods when they normally are resting. We decided to test this also on our ptarmigan, and in view of the relation we had observed between the plumage cycle and the reproductive cycle, we hoped that such an experiment might also give some clues to the mechanism behind the plumage changes.

We started the first of these experiments in November, 1937. At this time the number of healthy and normal ptarmigan at the experimental station was 42. As most of these birds were needed as breeding stock in our experiments in raising ptarmigan, only a small number could be used in our studies on the influence of light. The rest of the birds, however, served as controls for these experiments, and were kept in open pens and exposed to the natural temperature and light conditions of the seasons (Plate 12, upper fig.).

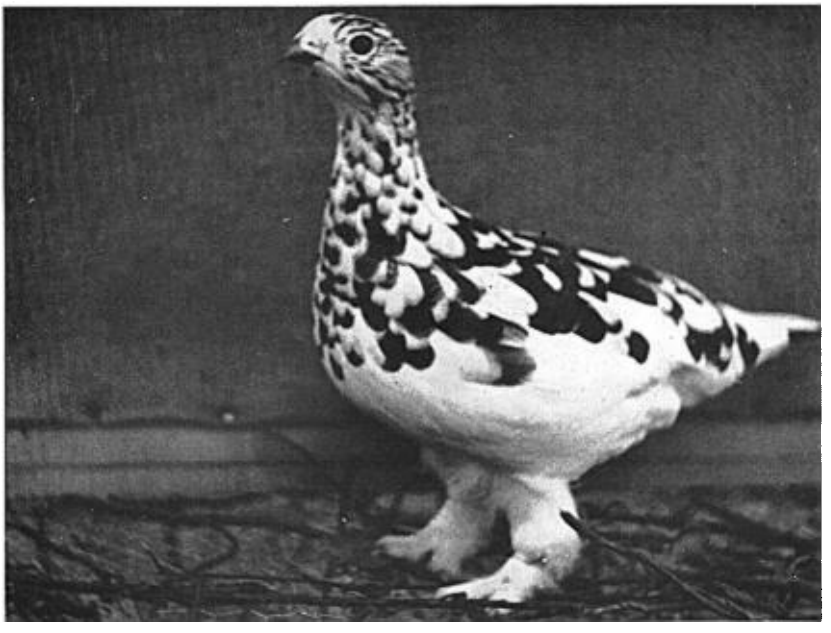
The birds actually used in the experiments, as well as the control birds, were examined frequently as to general condition and changes of plumage. Every second week kodachrome pictures were taken of the different individuals, giving a visual record of the gradual plumage changes throughout the experiment and making it easier to compare the different stages. All birds at the experimental station were numbered, and carried their numbers on conspicuous badges fastened to the wing. In the description of the experiments, I shall use these numbers when certain individuals are referred to.

In order to facilitate understanding the account, I shall first give a short description of the annual plumage cycle as it is normally found in the Willow Ptarmigan of the Norwegian mountains, and as we could also observe it in our breeding stock. For a more detailed description, see Johnsen (1929).

First of all it should be noted that the changes are produced by moults and the appearance of new feathers, and not by bleaching and other changes of feathers already grown out. Some of the moults are only partial, while others are complete. The males have one incomplete moult more than the females, resulting in a 'courtship plumage' between the winter plumage and the summer plumage, and giving that sex four different plumages in the course of a year. The plumages have very different durations; the winter plumage lasts for more than five months, while the other plumages are of such a short



CONTROL BIRDS IN CAGES. JANUARY, 1938.



PTARMIGAN IN TRANSITION TO WINTER PLUMAGE, INDUCED BY SHORTENING LENGTH OF DAY. SEPTEMBER 20, 1939.

duration that they often overlap. From the end of March to late in October the ptarmigan are subject to continuous moulting and changes of dress, so that the different attires run from one into another, making it difficult to decide exactly where one plumage ends and the other begins. Great individual variation, both in moulting time and in feather patterns, also makes it difficult to give a description that is at the same time brief and accurate.

Winter plumage (male and female): Pure white with the exception of the rectrices, which are black with a white edging. Normally lasts from the end of October to the end of March, and is the same for both sexes.

Spring or courtship plumage of male: Develops from late in March to the beginning of June. Characterized by moult and the formation of new feathers on head, neck, upper breast, and back, while on most of the under side the white winter feathers remain. The new feathers are pigmented in different colors and patterns, mostly brownish red (mahogany red to brick red) and black. The feathers on the back are affected last, and this part of the body only gets full coloring at the time when actual mating takes place. The naked wattle over the eye is enlarged and assumes a shining red color.

Summer plumage of male: Starts developing from the beginning of June, sometimes before the spring plumage is fully completed. Characterized by moult of the remaining winter feathers as well as the spring feathers. The new feathers are pigmented in black, gray, brown and yellow, in a different pattern from that of the spring plumage, and the reddish colors of the spring are lacking. Shows great individual variation, partly caused by remaining spring feathers.

Breeding or summer plumage of female: Starts developing by the end of March, at the same time as the spring plumage of the male; is usually completed in the last days of May and the beginning of June, at the time when laying starts, and is maintained during the incubation season and the first weeks of raising the young, when no moulting takes place. It resembles greatly the summer plumage of the male, but shows differences in details.

Fall plumage (male and female): Develops from the beginning of August. Summer feathers on head, neck, throat, breast, and flanks are replaced by feathers pigmented in color patterns of cinnamon-rufous or hazel to chestnut brown, more or less marked with black. On the back, new feathers in brown and black are mixed with summer feathers; abdomen more or less white from partly colored feathers.

EFFECTS OF EXPOSING PTARMIGAN TO ARTIFICIAL LIGHT IN ADDITION TO NORMAL DAYLIGHT

For the first of the experiments four normal and healthy birds were selected, two males and two females. As I found it desirable to have a larger number of birds in this experiment, but did not have the opportunity to take too many birds away from the breeding stock, I also included four birds from an isolated pen where I kept certain defective individuals. These birds were suffering from injuries caused by flying against the wire of the pens or by fighting. As this might have influenced their reactions to the experimental conditions, they will be treated separately from the normal birds.

At the beginning of November the eight birds mentioned were moved from their pens and placed in roomy cages in a one-room house, located a few yards from the nearest of the ordinary ptarmigan pens. The room had a floor space of about 24 square meters, and received normal daylight through large windows on two sides. These windows were kept constantly open, to make the temperature in the room as nearly as possible the same as that outside. There were no heating units in the room. Daily temperature readings in the room and outside showed, when compared, so little difference from each other through the period of the experiment that this can be regarded as insignificant.

In addition to the daylight coming in through the windows, the room was artificially illuminated by two ordinary electric bulbs, each of 25-watt size. The experiment was started November 15. During the first week the light was put out in the evenings, so that the 'day-length' in the room was twelve to fourteen hours. From November 21, the light was kept on constantly, day and night.

Already, after two weeks of this added illumination, the birds were in actual moult, and December 4, after nineteen days of exposure to artificial light, the two normal males (Nos. 47 and 14) showed the first new, pigmented feathers on the neck. No. 14 had them more pronounced than the other. The first signs of new pigmented feathers in the normal females (Nos. 46 and 7) were noticed on December 8. While in the males the new sprouting feathers were located on the neck, in the females they were scattered irregularly over the neck and the back.

December 22, after 37 days of exposing the birds to artificial light, my notes on the four normal birds are as follows:

The females, Nos. 46 and 7, have 'summer feathers' on head, neck, back and the sides. The stage of plumage is about the same as it is normally at the start of the

egg-laying. The plumage of No. 46 is slightly more completed than that of No. 7. The normal males, Nos. 47 and 14, are in partial spring plumage, as when courtship is at its peak. The wattles over the eyes are shining red and enlarged; in No. 47 they are protruding with the upper edge at the same level as the top of the head; in No. 14 they are somewhat smaller and less conspicuous. The change of plumage is more pronounced in No. 47 than in No. 14, and No. 47 is showing a more ardent courting behavior. Both birds are frequently uttering the calls typical of the mating season, and are showing the typical pugnacious attitude, threatening each other from their different cages. No. 47 is also chasing and pecking at the female with which it is paired. Both have changed plumage totally on head, neck and the upper breast, while on the back there are still many white feathers among the new pigmented ones. From our experience with the birds in the breeding season, the plumage is not developed quite as far as it normally is when the males are in the actual mating stage.

January 3, we found five eggs in the cage of female No. 46. The first egg was laid about December 29, or approximately 45 days from the beginning of the increased exposure of the birds to light. The eggs were frozen, as the temperature in the cage, being about the same as that outside, had been far below freezing most of the time. The lowest temperature so far recorded in the room during the experiment had been — 20° Centigrade, and during the period of egg-laying the temperature varied between — 7° C. and + 1° C. This female laid nine eggs, the last one on January 11; then the bird started incubating them on a nest she had made from heather twigs and sawdust in a corner of the cage. An examination on January 13 showed that the female had developed brood spots on the under side. The eggs were later placed in an incubator, but having been frozen, showed no development, and it was not determined whether they had been fertile or not.

The other female, No. 7, had been somewhat slower than No. 46 in developing the breeding plumage, and laid no eggs. January 19, it was found dead in the cage, and the autopsy revealed a fracture of the skull. This was a result of pecking and rough treatment by the male in the same cage, particularly on January 4, after which the female had appeared sick and miserable. The ovary showed follicles of a diameter up to 3 mm., considerably enlarged as compared with what was found to be normal for the season in the ovaries of wild birds at the same time of year. It was obviously in a phase of regression, however, caused by the poor general condition of the bird. The plumage was a fully developed summer one; all winter feathers on head, neck, breast and sides had been replaced with pigmented feathers.

On February 9, 1938, this experiment was terminated and the

experimental conditions were altered for the remaining birds. Both normal males had, by this time, fully developed spring plumage, and No. 47 had even acquired some feathers of the summer plumage. Female No. 46 had a fully developed summer plumage.

The four defective ptarmigan used in this experiment showed reactions similar to those of the normal birds, but they were slower in starting to moult and develop new feathers, and the females did not lay any eggs. The first pigmented feathers showed themselves in these birds by the middle of December. On December 21 one of these birds, a male, No. 13, died. The testes were considerably enlarged, several times larger than those of wild ptarmigan collected during the same period of the year. It had the winter plumage interspersed with pigmented feathers on head and neck, in about equal proportion to the white ones. On the other parts of the body the white winter plumage still remained unchanged.

When the experiment was terminated, in the beginning of February, the two defective females had almost fully developed breeding plumages. The one remaining defective male had head, neck and upper breast fully covered with pigmented feathers and had a few dark feathers on the back.

Among the control birds not a single individual showed any similar signs during the same period. At the time when the experiment was concluded, all control birds were in their typical white winter plumages.

As a whole it can be stated that in this experiment all eight birds reacted on exposure to increased amounts of light by showing signs of increased activity of the reproductive system and by moulting and developing plumages typical of the spring or the summer season. This happened in spite of the fact that the birds were kept at very low temperatures.

In the fall of 1938, these experiments were repeated under conditions that allowed a more detailed analysis of the plumage changes. Eight birds were used, and each of them was placed in an individual cage, isolated from light from the outside and with its own electric light-source. Unfortunately the experiment had to be discontinued, as the birds became infected with a disease that had high mortality, but some data were secured.

Six of the birds were exposed to electric light day and night from the beginning of November. All the birds reacted more slowly than did those used in the experiments the preceding year. When the experiment started, they were all in normal winter plumage, but two

of the males had some feathers pulled out from the neck, covering an area of about one square inch. November 20, new feathers, pigmented in brown and black, were beginning to cover these spots. By the beginning of December all of the birds were moulting and showing some new pigmented feathers, the males mostly on head and neck, the females more generally over head, neck and back. In the first days of December, two of the birds died. When the experiment was discontinued, by the middle of December, the two birds then remaining, both males, had pigmented feathers covering the head and neck and a few scattered ones on the upper breast and the back.

For two birds that were kept exposed to electric light continuously, day and night, from the beginning of November, hoods were made of black cloth, to cover their heads and eyes. These hoods were removed for six hours every day, but were worn continuously for the remaining hours of the day and the night. With the hoods on, the birds usually kept very quiet and paid little attention to disturbances. One of the birds died 24 days after the start of the experiment, while the other one, a male, was still alive when the experiment was discontinued in the middle of December. By this time, however, it had developed an infection of one of the eyes, possibly caused by irritation from the hood. These birds kept their winter plumages unchanged throughout the experiment, in spite of being exposed day and night to electric light. This indicates the importance of the eye as the main receptor for the light influences that affect the changes of plumage.

Effects on Plumage of Reduced Light

The foregoing experiments clearly indicated that light controls the reproductive activities of ptarmigan and the development of spring and summer plumages. It remained to be determined if the fall and the winter plumages were regulated by light conditions—if these plumages represented reactions on reduced day-lengths in fall and winter.

The first experiment was made on a single individual, male No. 14, and started immediately after the end of the first experiment previously described. On February 9, 1938, after having been exposed to artificial light in addition to normal daylight for almost three months, this bird had a well developed spring plumage. The head and fore part of the body were covered with feathers pigmented in black, brown and red, and the back also was fully covered with pigmented feathers, with the exception of some four or five remaining winter feathers scattered among the spring feathers.

On February 9, this bird was placed in a pen covered with dark

cloth. The cloth was removed every morning, and the pen covered again in the evenings, so that for the first days the bird was exposed to light ten hours a day instead of twenty-four hours as previously. Gradually the time of exposure to light was further reduced until by February 26 the bird had only seven hours of light a day, and this condition was then kept unchanged throughout the experiment. During this experiment a heating unit in the room kept it considerably warmer than the outdoors. Most of the time the room temperature was between + 10° and + 20° C., which is close to summer conditions in the natural domain of the ptarmigan.

By February 15, only six days after the light had been reduced, moulting began and a number of feathers were found on the bottom of the pen. Most of them were pigmented feathers from the new spring plumage, but there were also white feathers from the remaining parts of the old winter plumage. February 19, a number of feathers were pulled out from the bird's neck, to make it possible to see promptly when pigmentless feather growth appeared. On February 26, seventeen days from the start of the experiment, it was noticed that new white feathers were developing on this bare spot. A few days later, new white feathers were beginning to show themselves also on other parts of the neck and on the head. Photographs taken March 8 show the spring feathers on head and neck interspersed with a number of new feathers. Moulting was now proceeding very rapidly, and new white feathers soon started to show themselves also on the back. The plumage change which now took place had no parallel in the normal plumage cycle in nature. This bird did not go through the normal stages of a summer plumage and a fall plumage, but went from spring plumage directly into a new winter plumage. Photographs taken on March 23 show the dark plumage on head, neck, breast and back abundantly interspersed with new white feathers. Also, parts of the body that were covered with white feathers of the old winter plumage were moulting and regenerating new feathers. So by this time the plumage was composed of: (1) old winter feathers; (2) spring feathers; (3) new winter feathers.

March 29, the plumage change was already almost completed; only on the hinder part of the back a few dark feathers remained. When the bird was photographed on April 9, only four dark feathers were left on the back. A few days later these feathers also were moulted. The winter plumage was complete slightly more than two months from the beginning of the experiment, and it had developed in spite of temperatures that approached summer conditions.

Another interesting fact in connection with this experiment is the high number of plumage changes this individual had gone through in one year. In April and May, 1937, it had changed from winter plumage to spring plumage, and during summer and fall, had passed through the natural stages of summer plumage, fall plumage and a new winter plumage. Then, under experimental conditions, it had developed a spring plumage, complete by February 9 when, again under experimental conditions, a complete moult was induced, and in two months it developed a new winter plumage. Six different plumages in one year! Shortly after the experiment just described had been completed, the bird was again exposed to light 24 hours a day, starting May 2. On May 16, the first new pigmented feathers on head and neck were observed. Photographs taken June 9, after 37 days of exposure of the bird to continuous light, show an almost complete spring plumage. Photographs taken July 6 show a complete spring plumage in transition to summer plumage. Kept under the same experimental conditions, continuously exposed to light, for four more months, the bird did not develop any typical summer plumage or fall plumage, but developed an atypical mixed plumage that was subject to small changes by incomplete moults at irregular intervals.

Another experiment to test the effect of reduced light on plumage was started in August, 1939. Five ptarmigan, two males and three females, were isolated when the breeding season was over, and placed in pens that could be made dark, at convenience, by means of covers. These pens were kept only a few yards from the row of pens containing the normal breeding stock, and, except for the difference in light, they all had identical conditions.

The reduction of daylight for the five selected birds started on August 4. All the birds were in summer plumage by this time and showed the first signs of developing fall plumage. The exposure to daylight was first reduced to eight hours a day, as the pens were uncovered at 8 A. M. and covered again at 4 P. M. From August 16 the day-length was further reduced to seven hours and kept at this for the rest of the experiment.

During the first month little difference was noted in the plumage stages of the five birds in the experimental pens as compared with the control birds in the open pens. When examined on September 5 they were all, with some individual variation in both the experimental and control groups, in stages that can be termed 'fall plumage.' After this time, however, a marked difference in moulting intensity was noted in the experimental group as compared with the rest of the birds.

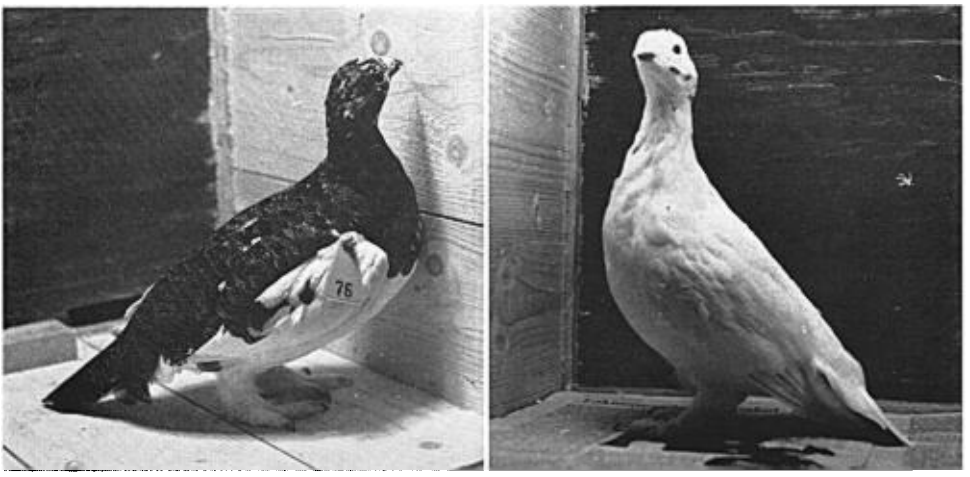
September 20, the birds were photographed and showed one bird, a female, No. 103, with an already fully developed winter plumage, except for about half a dozen dark feathers still scattered on the back. The rest of the birds were all in transition to winter plumage, but had more dark feathers remaining on neck and back than No. 103 (Plate 12 lower fig.). At the same time the control birds in the open pens were in typical fall plumage, with no winter feathers yet showing on head, neck, breast or back.

When examined on October 4, all the birds in the experimental pens were either in fully developed winter plumage or in white plumage with only a small number of dark feathers remaining on the back (Plate 13, upper right fig.). The control birds by this time had just started to show the first signs of winter plumage, with a few white feathers appearing on head and back, while some individuals were still in their typical fall plumage (Plate 13, upper left fig.).

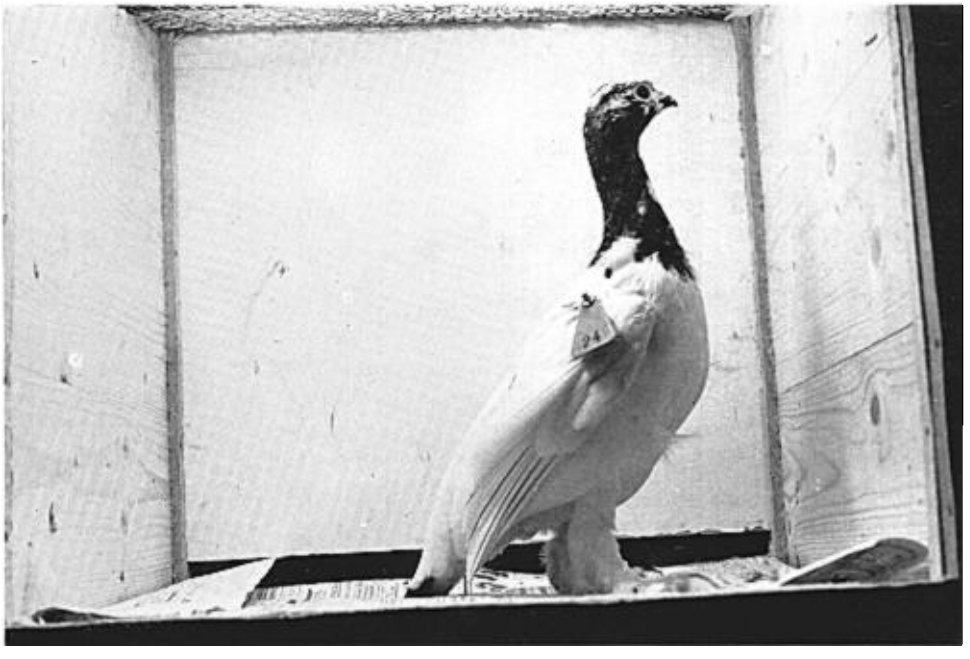
The results of the experiments on the effect of reduced light on the plumage cycle seem to justify the conclusion that the development of fall and winter plumages likewise is controlled by light conditions, while temperature conditions seem to be of little or no importance. The remarkable plumage change in male No. 14 during February and March, which went from spring plumage directly into a new winter one without showing signs of the intervening plumages, is correlated with the violent and abrupt changes in light conditions used in this experiment. Within two weeks the daily amount of light was changed from twenty-four to seven hours a day. In nature a similar change in light conditions would take many months and thus make more gradual the endocrine changes controlled by light. In the experiment, the summer plumage and the fall plumage, which can be considered as responses to gradual internal changes, were not given sufficient time to develop before a hormonal balance corresponding to winter conditions was already established. In the second experiment, however, the changes in light conditions were much less pronounced. Furthermore, they came at a moment when the birds were about to change from summer plumage to fall plumage, and gave the latter time to develop. The difference from normal development in this case was mainly that the plumage changes were speeded up, giving the fall plumage a shorter duration than normal.

Effects on Plumage of Small Changes in Light

The experiments already described have shown that all the different plumages of the Willow Ptarmigan respond to light conditions. With the large number of different plumages that the ptarmigan



(Right) PTARMIGAN IN WINTER PLUMAGE INDUCED BY REDUCING LENGTH OF DAY.
(Left) CONTROL BIRD. OCTOBER 4, 1939.



MALE PTARMIGAN IN TRANSITION TO SPRING PLUMAGE, INDUCED BY PROLONGED ILLUMINATION.
DECEMBER 1, 1939.

develops in the course of a year, one would expect the plumages to be extremely sensitive to small changes in the controlling factor--in other words, that even very small differences in light conditions will have visible effects on plumage development. It would be of interest to determine the lower level of this effect, the minimum change of light needed to produce a visible effect on plumages in the different phases of their cycle. No experiments were directly concerned with this problem, but some incidental observations are pertinent. We have two different types of changes in light conditions to consider here. One is a comparatively small change in light intensity, working over a long period of time; another is a pronounced change in light intensity working through a short interval of time. Observations made during the experiments offer examples of effects from both types.

An example of the first type was given by five ptarmigan which, during the winter of 1937–38, were kept in an open pen very close to the house that was illuminated day and night for the purpose of the experiment described first in this paper. From an open window in the house a beam of electric light was thrown on this pen, the nearest part of which was about five yards from the window. In the beginning no attention was paid to this fact, as we did not expect such a seemingly insignificant exposure to artificial light to have any effect.

However, at the beginning of January, 1938, it was noticed that a male which was kept in the compartment of the pen nearest to this window, showed enlarged wattles as well as a pugnacious behavior, and was uttering calls typical of the spring season. On January 18, it was noticed that this bird had some new, pigmented feathers developed on the neck. Photographs taken on February 16 show this bird with pigmented feathers covering all of the lower part of the neck and the upper part of the breast. Four birds, two males and two females, kept in the other compartment of the pen, showed similar changes in plumage, but at a later date than the male just described. January 29, the first pigmented feathers were noticed on two of these birds. February 3 it was noticed that all of them showed a few new pigmented feathers. This was more than five weeks earlier than any similar signs were noticed among the birds that were kept in pens far away from any influence of artificial light.

A striking example of effect from a very short exposure to artificial light is given by a female that was exposed to artificial light for only four days in January, 1938. On January 26, this bird was placed in

a pen in the illuminated room just mentioned, where it was exposed to artificial light for twenty-four hours a day. On January 30, it was moved back to its original pen. On February 19, examination showed several pigmented feathers coming out on the neck. On February 26, it showed a number of pigmented feathers on the head and upper part of the neck. The middle of the neck was white, but on the lower part of the neck and the upper part of the breast there was a broad ring of dark feathers. On the back there were a few scattered, pigmented feathers. The earliest of the control birds did not show any corresponding stage of plumage development until the beginning of April.

On December 1, 1937, a male, No. 69, was moved from its outside pen because of a broken leg and placed in a small cage in the illuminated experimental room. On December 14, after having been exposed to artificial light twenty-four hours a day for two weeks, it was moved back to its original pen. During the last week of December it was noticed that this bird was moulting, and on January 3, thirty-four days from the start of the fourteen-day exposure to artificial light, it was noticed that it had numerous pigmented feathers developing on the head and on the neck.

SUMMARY

Over several years the author kept between thirty and sixty Willow Ptarmigan, in an attempt to raise them in captivity on a large scale. Observations on these birds, especially during the breeding season, showed a marked synchronization of the plumage cycle with the different phases of reproduction.

Smaller numbers of the birds were used at different times for experiments to test the effects of light and temperature on plumage and reproduction. Birds kept at normal, low temperatures during the winter months, November to February, were exposed to artificial light day and night. They responded to these changes in light conditions by showing different signs of reproductive activity, most marked in a female that laid a normal clutch of eggs in the last days of December and the beginning of January. While all the control birds kept their winter plumage unchanged during this period, all birds that were exposed to light developed different phases of spring plumage and summer plumage, thus indicating that light and not temperature is the main controlling factor for both the reproductive cycle and the development of spring and summer plumages in this species. One of the birds, a male, that showed fully developed spring plumage by the beginning of February, had day-length again reduced to seven

hours a day. It responded to this by moulting and developing new white feathers, and within two months had completely changed from spring plumage directly into a new winter plumage. The winter plumage was developed in spite of the fact that the bird was kept at temperatures considerably higher than normal at the time of year when winter plumage develops in nature. Five ptarmigan, that had the normal day-length reduced at the beginning of August, responded to this by developing winter plumage one month earlier than the control birds which developed this plumage at the normal time. These experiments indicate that the development of fall plumage and winter plumage also are controlled by light conditions, and are caused by the reduced length of day in fall and winter. Several observations from the different experiments are mentioned, showing that even very small changes in light conditions can produce marked effects on plumage development.

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