Article IV.—ON THE SEASONAL CHANGE OF COLOR IN THE VARYING HARE (LEPUS AMERICANUS ERXL.).

By J. A. ALLEN.

Introductory.

Any one at all familiar with the seasonal changes of color in mammals, and also with the periodic shedding and renewal of the pelage, cannot have failed to note the coincidence of the two phenomena. As a rule, particularly among the Rodentia, the change becomes first apparent on the feet and about the nose, extending gradually up the limbs and over the head, and from the base of the tail anteriorly, and from the sides of the body toward the median line. This, perhaps, may be assumed to be the usual method, particularly in the spring molt, but the process is subject to much irregularity, even among individuals of the same species, and it seems to vary somewhat in different groups.¹ Late in spring, usually at the close of the breeding season, the old coat has become worn, faded, and more or less ragged, and the new hair may be seen coming in irregularly in patches, in addition to the more symmetrical method of change already indicated.

The new hair, forming the summer coat, is much shorter and thinner, and usually brighter in color than the coat it replaces. The change from this coat to the winter dress again is generally accomplished more or less insidiously, but apparently in much the same order as in the case of the change from the winter to the summer coat. The summer coat is worn usually for a much shorter period, and fails to show the same amount of wear and fading, so that the transition is generally less marked and abrupt; the new hair comes in gradually, and overtops the short summer coat, which apparently falls out as the new hair becomes more abundant and longer. Only in the case of some more or less radical change in color can the progress of the fall molt be readily traced,

¹ Thus in the Hares, as will be shown later, it is quite different from what it is in the Squirrels.
as in the Varying Hares, forming the subject of the present article. In these a brown summer pelage is replaced by a white winter coat; and the change is thus so radical that it should seemingly be an easy matter to determine how it is produced. Yet just how the change of color is effected is still to some extent a matter of dispute. While supposed to be largely due to a molt, it sometimes appears to take place so suddenly that it is popularly thought to be due, in some degree at least, to the blanching of the summer hair.

**Character of the Pelage.**

In order to understand fully the remarks that follow, it is necessary to briefly describe the summer and the winter pelage.

*Summer Pelage.*—The general color of the upper parts, including the limbs externally, varies in different individuals from pale yellowish gray to deep yellowish brown, and even occasionally to reddish brown, more or less varied with blackish, particularly over the middle and posterior part of the back, due in part to most of the hairs being tipped with black, but often mainly to a strong sprinkling of wholly deep black hairs. There is also a broad pectoral band or 'ruff,' varying from two to three inches in breadth, and in color from yellowish gray to deep rusty fawn. The rest of the lower surface, including the chin and throat, a part of the inner side of the hind limbs, and the whole of the ventral surface posterior to the breast, is white, often washed slightly with fulvous or grayish. The ears are brownish, more or less rusty, the extreme edge whitish, particularly on the posterior border, the apical third externally with a submargin of black, expanding towards the tip into a broad blackish subapical spot. Except basally and along the anterior border, the ears are thinly haired throughout. The soles of the feet are generally more or less dusky.

This pelage, considered in detail, consists of two distinct parts—a thick woolly underfur, and a heavy coat of long overhair. The underfur is plumbeous basally, generally for about two-thirds of its length, with the apical third fulvous or tawny, the exact shade varying in different individuals.

The overhair is of two kinds, as regards both pattern of color and structure. It consists principally of particolored hairs, which are plumbeous basally, generally about as far as the plumbeous zone of the underfur, then blackish for about one-half their total length, then passing abruptly into a broad band of fulvous, and then again abruptly into black at the extreme tip. These hairs
are extremely attenuated at the base, gradually thicken as they become black, attaining their greatest diameter at and throughout the subapical fulvous zone, and then rapidly taper to a fine-pointed tip. Mingled with these particolored hairs is a greater or less profusion of wholly black, rather longer hairs, of coarser and firmer texture. These hairs vary greatly in abundance in different individuals, and over different parts of the body, being most abundant along the middle and posterior part of the back. They taper slightly towards the base and tip, but are of a much more uniform diameter than are the particolored hairs. They overtop the particolored hairs, thus not only greatly increasing the blackish cast of the dorsal surface, but by their rigidity imparting greater firmness to the surface of the pelage.

During the autumnal change the particolored hairs are the first to fall out; the longer, firmer, wholly black hairs persist later, quite a proportion of them often remaining after the particolored hairs have disappeared, giving a more or less leaden or dingy effect to the otherwise white winter coat. This effect gradually passes away, although a few black hairs can be found in most early December specimens, but they generally wholly disappear by the middle or during the last half of the month, excepting at southern localities.

Winter Pelage.—Generally everywhere white at the surface, except the tips and edges of the ears, and the soles of the feet, although the latter are much lighter in color than in summer.

The winter pelage is, of course, also made up of two kinds of hair—a woolly underfur, rather longer and much more abundant than in summer, and the longer, coarser, firmer overhair. The underfur is colored much as in summer, except that the tips of the longer fibres are pure white, like the overhair. The overhair is almost invariably pure white from base to tip, although the extreme basal portions of some of the hairs are grayish and pass into a horn-gray middle zone. This condition is rare, occurring in comparatively few specimens, and then only in a very small percentage of the hairs making up the long white coat of overhair. The hairs composing the white covering of overhair vary greatly in diameter, not only in different individuals, but in
different parts of the body of the same animal, and even from the same region, as from the middle of the back. The coarser hairs have a firm shaft from the tip to the point of insertion into the skin; the finer hairs have only the outer half or two-thirds firm and shaftlike, the lower portion dwindling to a thin filament, and when detached is curly and not unlike one of the coarser fibres of underfur. There is indeed, in some individuals, an almost complete intergradation as regards texture between the coarser over-hair and the longer white-tipped filaments of underfur.

**MATERIAL EXAMINED.**

The following observations are based on a series of about 75 specimens, nearly all of which belong to the Museum Collection. The greater part have been collected for the express purpose of this investigation, and include specimens taken through both the autumnal and vernal changes, as well as at other seasons. About thirty were collected near Andover, New Brunswick, during October, November and December (Oct. 27–Dec. 14), 1894, for the purpose of securing a series showing the transition from the brown summer coat to the white dress of winter. A part of this series was obtained by Mr. J. Rowley, Jr., and his associates, on the recent Museum Expedition to New Brunswick (see antea, pp. 99 and 101), and the rest were secured later from an Indian hunter through Mr. Rowley's agency. The greater part of the rest of the series is from the vicinity of Rutland, Vermont, taken at various intervals from Oct. 17 to April 15, and for which I am mainly indebted to Mr. W. W. Granger, who has also kindly secured a series, collected at intervals during March and April, to illustrate the spring molt. There are also four specimens from Kittson County, Minn. (Nov. 17–22), collected and presented by Dr. E. A. Mearns.

This material shows that there is considerable individual variation in respect to the exact time of change at the same locality. Thus some of the specimens taken as early as Nov. 17, both

---

1 I am indebted to Dr. C. Hart Merriam, of Washington, for the loan of 13 specimens from his own collection, which have proved especially useful in the present connection. Six of them are from the Adirondack region of New York, and seven from Elk River, Minn. The former include specimens taken in summer and autumn, while the latter were taken during the spring molt.
at Rutland, Vt., and in New Brunswick, are already quite white, while others taken at the same locality and on the same day show very little change from the summer coat. Most of the specimens taken the last week in November are in nearly full winter dress, but in some the change is much less advanced. March and April specimens also show a wide range of variation in respect to the spring molt, some individuals changing much earlier than others.

Autumnal Change.

The early stages of the autumnal change are well shown in five New Brunswick specimens taken Oct. 27-30. In two of these only the sides of the nose, the ears and the feet have become white, the white extending, however, on the fore limbs nearly to the body, and on the hind limbs over the inner edge of the leg to the thigh, with a strong admixture of white hairs all around nearly to the knee. Another specimen is similar except that the ears are much less white and the white extends higher on the sides of the nose. The fourth specimen (No. 6737) is more advanced, the whole top of the nose, nearly to the eyes, being quite whitish, while a broad whitish streak extends backward from this whitish frontal area to the base of the ears. On parting the fur an abundance of short white hairs is seen along the sides of the body and across the rump and lower part of the back. A close examination of the light areas on the front and sides of the head shows that the whiteness is due to a new growth of hair, which in places has almost wholly replaced the brown coat, but is generally mixed with it; on parting the adjoining and still superficially unchanged area an abundance of short white hairs is found which have not yet reached the surface. In the fifth specimen (No. 6739) the change is less advanced on the head, but more advanced on the sides and posterior part of the body, which parts are already more or less whitish, particularly on the thighs, where the greater part of the long hairs of the summer coat have fallen out and the white winter coat begins to show, though it is still largely concealed within the underfur. On the right side of the median line, in front of the hips, are several small irregular patches of white, due to the almost entire falling
out of the summer pile, although the thick winter pile here developed is still much shorter than the surrounding pelage.

The next set of twelve specimens was taken some two weeks later (Nov. 14-17), yet, through individual variation, they continue by insensible gradations the stages of change, almost to the full winter coat. No. 6788 of this series is even less advanced than Nos. 6737 and 6739, already noticed. Three or four others are so nearly like these two as not to call for special mention. No. 6791 is a little more advanced, and shows beautifully the progress of change on the head. The whole top of the head, from between the base of the ears to a point somewhat in front of the eyes, is apparently unchanged, forming a large crown patch about twice as long as broad, bounded in front by a pure white nose patch, and on the sides by a broad whitish ocular band, leaving on either side below this a broad, nearly unchanged, malar region, extending forward in a point toward the nostril. The hairs forming the white nose patch are still short, though the longer brown hairs of the old coat have entirely disappeared. The transition to the brown crown patch is abrupt, but on parting the hairs at its anterior border the pelage is found to be thickly set with short, pure white hairs that have not yet reached the surface. The tawny pectoral ruff has become considerably whitened by the incoming white hairs, some of which have nearly reached their full length. One or two of the other specimens already mentioned show the pectoral ruff in about the same condition; in others only a few white hairs have appeared, while in still others it remains practically unchanged at the surface, although on separating the pelage white hairs are found beneath the surface.

No. 3240 (Rutland, Vt., Nov. 17) carries the change considerably further. The whole pelage has become more or less whitened, but there is still a sufficient remnant of the summer coat over the dorsal region to give the prevailing tint to the central portion of the back, gradually fading thence laterally till white becomes the prevailing tint at a point quite high up on the sides of the body. The white nose patch extends laterally to the eyes and centrally in a broad point to the middle of the interocular space, while the whole crown is irregularly whitish, small
patches where white prevails being mixed with patches of the summer coat, which is one-third to one-half longer than the new winter coat. This results in giving to the whole top of the head the ragged, patchy appearance so often seen in molting animals, and shows at a glance and beyond question that the change of color is due to a replacement of the summer coat by a winter coat of a different color, and that the whiteness of winter is not due to a change of color in the summer coat. The whole dorsal region is thickly set also with white hairs, but few of which have reached the surface, although a considerable part of the long pile of the summer coat has been shed, except over a narrow band along the median line, extending from the loins to the head and widening anteriorly. The sides of the head have still undergone little change.

Another specimen (No. 3242, same date and locality) is a little more advanced, but presents the same general features, including the rough, patchy appearance of the head. There is, however, much less of the summer coat left over the dorsal region. In No. 3241 (same date and locality) the change is nearly complete, only the black hairs of the dorsal region remaining of the summer coat, producing a general grizzled effect.

The New Brunswick specimens furnish a parallel series to those from Vermont, last described. Other specimens of the New Brunswick series taken later (Nov. 20, 24 and 26) present interesting phases of change. No. 6828 (Nov. 20) has a considerable mixture of the summer coat remaining on the crown, cheeks, ears and shoulders, and less (but still enough to produce a grizzled, dingy effect) over much of the dorsal region. No. 6831 (Nov. 26) has a large part of the top of the head still brown, with much brown hair over the shoulders and along the median line of the back, extending as a narrow band from the nape posteriorly for about two-thirds the length of the body, decreasing in width posteriorly and becoming gradually obsolete. No. 6829 (Nov. 24) has the crown almost unchanged, forming a cap of brown hair projecting above the surrounding white pelage; and there is a very slight admixture of the summer coat over the middle of the back. A specimen taken later (No. 6837, Dec. 6) is nearly white throughout, but is slightly tinged with brown hairs.
on the back, while the head is piebald through the presence of small spots of brown on the white ground. The hind feet, particularly near the base of the toes, are streaked with fawn color on a white ground, while the anterior surface of the fore limbs is mainly deep fawn color. But it does not follow that the fawn-colored pelage of the feet is a remnant of the summer coat, since this is found also in specimens killed in January and March, the series of specimens covering the period from November to March showing that this is an individual peculiarity, different specimens presenting a gradation from white to fawn-colored feet independently of season.

The December series (Nov. 29 to Dec. 15) shows that after the white color is practically assumed it increases in purity, as does the coat in softness and fullness, by the maturing or lengthening of the white overhair and the thickening of the soft underfur. The long black hairs of the summer coat are the last to disappear, being retained, apparently to give firmness and stability to the pelage, till the white overhair of the winter coat is fully developed.

From the foregoing it will be seen that the Varying Hare has an autumnal molt, not unlike that occurring in other mammals, to which alone the change of color is due; and, furthermore, that the change begins and proceeds in the manner, so well known to every one who has given careful attention to the subject, common to other mammals; it beginning with the nose, feet and ears, extending gradually, sometimes somewhat irregularly, over the head, up the limbs and along the flanks, creeping gradually up the sides toward the median line of the back, and from the rump anteriorly, leaving the crown, the sides of the head (malar regions), and the anterior and median portions of the back as the parts last to undergo the change of coat. Indeed, so simple and so matter of course is the whole process, that the only excuse for giving so detailed an account of the change is the fact that exceedingly erroneous statements of the process have not only found their way into print, but have also been made the basis of other generalizations.

In addition to the evidence of a molt afforded by skins, as already given, I am assured by Mr. Rowley and Mr. Granger, independently of each other, that they noticed in preparing the skins of the fall specimens in change that the long brown hairs came out very freely, while there was no noticeable shedding of the white hairs.
VERNAL CHANGE.

My studies of the vernal change are based primarily on specimens taken in the vicinity of Hartland, Vermont, during the present spring (1894)—a season remarkable for the great and almost unprecedented warmth of the first three weeks of the month of March. Hence the molt may have begun this year somewhat earlier than usual for this locality. This series is admirably supplemented by a series from Elk River, Minn., taken March 24 to May 11, 1886, kindly loaned me by Dr. C. Hart Merriam from his private collection for use in the present connection.

Three specimens, taken March 25, present the following conditions: No. 7289, ♂, differs little in superficial appearance from midwinter specimens. A close examination, however, shows that it has already lost the long soft white overhair from the ears—so conspicuous a feature of the basal portion in winter examples—and that a portion of the long white overhair of the body has been lost. On separating the pelage a few small patches of the summer pelage can be found here and there, where by accident, or in fighting, the old hair has been torn out, and the new coat has come in, as on the shoulders and hips. Here the summer coat, only a few millimeters in length, is coming in in a uniform, compact mass. It presents all the characteristics of the summer coat, as far as it has advanced, generally showing only the black tips and a portion of the broad subapical zone of fulvous.

A second specimen (No. 7290, ♂) is almost precisely similar, except that the hairs of one of the small patches of new fur on the middle of the back are more than half grown, thus showing a part of the black basal portion below the fulvous zone. A third specimen (No. 7288, ♀) is quite different, having shed nearly all of the long overhair, only a few scattered white bristly hairs remaining, so few that they might be easily counted. The heavy coat of long thick underfur, however, remains apparently intact, and, strange to say, the animal looks nearly as white as before it lost its overhair. It serves to show in a striking manner that the surface of the underfur is also white, as well as the overhair; and having seen it thus demonstrated, it is easy now to discover on careful
examination, that the surface of the underfur is generally white in winter specimens. This specimen also shows numerous patches of new hair on the back where the old coat has been violently removed.

Two specimens, taken April 1 and 2, exhibit the progress of ten days. In both of these (No. 7285, ♂, and No. 7286, ♀) the greater part of the overhair has been shed, and there has evidently been a great reduction in the amount of underfur. In addition to this the new summer fur can be seen coming in somewhat uniformly over most parts of the body; though somewhat thinly dispersed it can be easily seen on parting the underfur.

Two specimens killed April 9 (Nos. 7291 and 7292) carry the change much further. No. 7291, ♀, has lost all of the winter coat of overhair, except here and there a few remotely isolated hairs. The patches of new hair, replacing bunches lost by accident, have now reached the level of the still heavy coat of underfur. There is less short new hair generally dispersed over the body than was found in the two specimens of a week earlier date, above described; but very interesting changes have taken place on the head, and on the summit of the shoulders, where a large increment of the summer fur has risen to the surface of the underfur. A large part of the white hairs of the winter coat still cover the sides and top of the nose and extend back in a triangular patch to a point between the orbits; but on either side of this median line, from a point considerably in advance of the eyes back nearly to the crown, the summer pelage is quite fully developed, and the winter hair has disappeared. A similar patch occupies the upper part of the cheeks, just below the eyes, and new summer hair is abundantly dispersed throughout the crown.

No. 7292, ♂, is much more advanced. There are scattered new hairs over much of the body, as yet concealed by the overtopping underfur; the feet, particularly the hind feet, are more advanced in change, and the whole head, including the cheeks, has become invested with the summer coat. The pelage is still short, and in places presents a patchy appearance, as over the nose and on the posterior part of the cheeks, where irregular tufts of the winter coat remain, conspicuous by its greater length and white color. The ears appear practically unchanged, retaining an unusual
amount, compared with the other April specimens, of the long, white winter hair. Over the shoulders and on the hinder part of the back are numerous patches of the nearly full-grown summer pelage, with its characteristic mixture of fulvous-barred and black-tipped hairs.

Of two specimens taken April 15 one (No. 7295, ♂) is less advanced than No. 7292 (described above), taken a week earlier, it still retaining much of the long white overhair over the posterior third of the back, and the ears are nearly as white as well clothed in winter; and generally the specimen is in a very backward condition of change. The other (No. 7294, ♂) is in a very advanced stage of change, excepting the ears and feet, which still remain nearly as in midwinter. The entire head, the pectoral ruff, and the whole central part of the dorsal region nearly back to the hips, have taken on the characteristic dress of summer, the summer pelage protruding above the underfur, though not yet of mature length. There still remain, however, many long white hairs over the middle of the back, especially posteriorly, and there are small tufts of white hair on the sides of the head. On the sides of the body and over the posterior part of the back the summer coat is largely concealed beneath the still persistent winter underfur.

These are the last of the Vermont series received up to the date of this writing, but fortunately the specimens from Elk River, Minn., already mentioned as received from Dr. Merriam, carry the change forward to almost full summer pelage. These will be described somewhat in detail, although covering in part the ground already traversed, the locality rendering them of especial interest in this connection. The seven specimens were taken at such well chosen intervals (March 24 to May 11) that they show the leading stages of change throughout the whole period of molt.

No. 2545 (Coll. Dr. C. Hart Merriam), ♂ ad., March 24, has begun to lose the long white overhair, particularly on the ears, sides of the shoulders and middle of the back, and patches of the new summer coat have appeared on the front of the head near the eyes, that on the left side being about twice as large as the one on the right side. Another specimen (♀), taken March 27, is slightly more advanced, having lost most of the long white over-
hair from the back, and over which area considerable new hair has just appeared above the skin, as can be seen by carefully parting the underfur.

No. 2546, ♀, April 1, has lost nearly all of the long white overhair, except from the ears and feet, and the new summer pelage is coming in abundantly and quite evenly over nearly the whole dorsal surface, including the sides of the body as well as the back, much of it being already 5 or 6 millimetres in length; while little patches here and there have reached the surface of the underfur, and over a large part of the head it has quite replaced the winter coat. No. 2551, ♀, April 7, is a little more advanced, the summer pelage being well developed over the whole head, except a small central area in front, over the nasal bones, and has attained considerable length over the whole dorsal surface, though still buried in the winter underfur. A few long white hairs are scattered over the dorsum—remnants of the winter coat of long white overhair.

In No. 2549, ♀, April 8, the summer pelage thickly clothes the head, sides of the shoulders and a very broad area on the back, extending as far back as the hips. Over all these parts it overtops the underfur, and gives to the surface of the pelage the characteristic color and texture of the summer dress. From the hips, posteriorly, and along the sides of the body, it is much less abundant and still concealed beneath the underfur.

The next specimen in the series (No. 2555, ♂) was taken April 23, and is nearly in full summer dress, except on the feet and ears, although the pelage is still short. There are little tufts of white hairs—remnants of the winter coat—still remaining here and there on the back and sides. This is the first specimen of the Elk River series that shows much change in the pectoral ruff or on the feet, the ruff in this example having taken on the character of the summer dress. On the forearm the summer pelage has advanced on the outer side to a point about half way between the elbow and wrist, superseding the winter coat, and below this point much of the winter coat has either fallen out or worn off. On the hind feet a nearly complete change has advanced as far as the ankle joint, and the feet are ragged and worn, having lost much of the winter coat.
The last specimen of the Elk River series (No. 2553, ♂, May 11) has practically attained, so far as the head and body are concerned, the summer dress, except that the pelage appears not to have attained its mature length. The ears and tail still show traces of the winter pelage, and the feet are but little more advanced in change than in the specimen last described.

From the foregoing it is obvious that the spring molt, like the autumnal, occupies a period of from fully four to six weeks, the latter probably being about the average length of time required for the complete change of dress.

In tracing the change from the winter to the summer coat we have spoken only of the change of the overhair. A comparison, however, of the specimens last mentioned with those first described in the Elk River series, or of summer with winter specimens, renders it evident that the underfur is changed as well as the overhair. The summer underfur is at least three-fourths less in amount, is shorter, and apically quite different in color. It appears to grow simultaneously with the overhair, the old coat of underfur being retained as a protection from cold for some time after the winter overhair has fallen out, and much later giving place gradually to the new coat, as the latter becomes sufficiently developed to afford the necessary amount of warmth. Whether or not the summer underfur is molted in autumn it seems almost impossible to determine, but that there is at this season a heavy growth of new underfur is plainly obvious.

Irregularities in Change of Color, etc.

An examination of the present series discloses various irregularities in the development of the white winter dress, in respect especially to the color of the feet, ears and head. In most specimens that have completed the winter dress the feet, except the soles, are superficially white, the whiteness varying greatly in purity in different specimens, while others, particularly on the fore feet, present large areas of fulvous. In those with the whitest feet, the hairs are wholly white to the base, and the underfur is pale plumbeous, with no tinge of fulvous. In other specimens the underfur varies from pale fulvous to deep rich
fulvous, and in these latter the hair basally, in part or wholly, has the same tint, the hairs varying, in different specimens and also over different parts of the same foot, from pure white nearly or quite to the base to wholly fulvous, or fulvous with a white tip of variable extent in different hairs situated in close proximity. In this way the dorsal aspect of the foot varies from uniform clear white to white mixed more or less irregularly with fulvous, or to nearly deep pure fulvous, shading off laterally or at the edges into white.

The ears vary similarly except that the underfur is more commonly dusky, and the white surface is varied with dark chestnut or rusty brown rather than fulvous.

Usually in the specimens with brownish ears and fulvous feet the whole head shows a tinge of fulvous, which proves to be due in part to the shortness of the white tips to the hairs, as well as to the fulvous underfur. In specimens with a yellowish cast to the nose it is found that only the extreme tips of the hairs are white, all of the subapical portions being fulvous, passing at the extreme base into dusky. Often in specimens with very white heads the underfur is mostly dusky. In spring the ears lose their winter covering very irregularly, it being sometimes shed very early in the molt, and sometimes remaining till the summer pelage is well developed over the whole body.

Unfortunately there are no specimens at hand representing the partial change to white supposed to frequently occur at southern points in the habitat of this species, and is known to be the case in _Lepus campestris_. Reasoning, however, from analogy, and from the condition of the specimens just described, there is no ground for supposing the lack of complete change in color to be due to an imperfect autumnal molt, but rather to the fact that the new hair comes out largely of some other color than white.

Whether or not the soft underfur is also shed in autumn cannot readily be determined, but from its increased length and abundance in winter, as compared with summer and early autumn, it is evident that if not wholly renewed it at least is very greatly augmented.

In the case of the spring molt, there is little doubt that the whole pelage is renewed, the underfur quite as completely as the overhair.
In the case of wounds from fighting or other cause, resulting in the violent removal of large bunches of fur, it is interesting to note that in the autumn the new hair comes out white, often weeks in advance of the general change, and that in spring, under similar circumstances, the hair comes out brown, like the summer coat, much in advance of the general change from winter to summer pelage.

**Conclusions.**

From the foregoing it is evident (1) that the change of color, both in autumn and in the spring, is due to a change of pelage, and not, even in the fall, to a change of color in the hair itself. (2) Further, that this change is gradual, occupying many weeks, both in fall and spring; and that while it may be doubtless more or less accelerated or retarded by temporary climatic conditions, it is not intimately connected with phases of weather, but is as regularly periodic as the seasons themselves.

(3) That the method of change, as regards the parts first affected, is the reverse in spring of the order characterizing the autumnal change: in the fall the change beginning with the feet and ears, the sides of the nose and front of the head, which often become radically changed before the body is much affected; while as regards the body, the change begins first at the base of the tail and extreme posterior part of the back, and at the ventral border of the sides of the body, working thence upward toward the median line of the back and from behind anteriorly, the crown of the head and a narrow median line over the shoulders and front part of the back being the parts last changed. In the spring the order of change is exactly the reverse, the molt beginning on the head and along the median line of the anterior half of the dorsal region, extending laterally and gradually to the ventral border of the sides of the body and posteriorly to the rump, and then later to the ears and down the limbs to the feet, which are the parts last affected, and which often remain but little changed till the head and body have pretty completely assumed the summer dress.

(4) That for some time during the early part of the spring molt, after the white overhair has been shed (except for a few
scattered hairs), the pelage consists chiefly of the heavy coat of soft winter underfur; later this gradually disappears, probably partly by wearing off and partly by falling out, as the summer coat thickens and matures.

(5) That in spring the molt occurs quite as early and proceeds just as rapidly (if not a little more so) in the females as in the males, and that the molt is practically completed before the young are born. This is noteworthy as being just the reverse of what occurs in many of the Sciuridae, especially in the genera Sciurus and Tamias, in which the males molt much earlier than the females, the molt in the latter being delayed not only till after the young are born but till near the close of the nursing period.

**History of the Subject.**

More than a century ago, Thomas Pennant, a most astute naturalist for his time, gave the gist of the whole subject in a short paragraph of five lines, as follows: "From Hudson's Bay, as low as New England, these animals, at approach of winter, receive a new coat, which consists of a multitude of long white hairs, twice as long as the summer fur, which still remains. About the middle of April they begin to shed their winter covering."1 Omitting the last clause of the first sentence, we have the whole case well stated. Later writers, however, conjectured another cause for the autumnal change. Thus, Dr. Richardson (afterwards Sir John Richardson) believed "that the change to the winter dress takes place by a lengthening and blanching of the summer fur."2 This view appears to have been widely entertained by both scientific and non-scientific writers. But no one appears to have made any attempt at a thoroughly scientific investigation of the matter prior to 1869, when Assistant Surgeon Francis H. Welch published an elaborate paper on the subject.3

---

1 Judging by the condition of the embryos in females taken late in April, when the change to summer pelage is well advanced.
Unfortunately it consists of a singular mixture of truth and error, although looked upon as authoritative by subsequent writers. In fact, it is difficult to understand how the author could have been so misled, or could have been so unfortunate in his observations. His detailed statements as to the change in color, so far as its gradual progress is concerned, leave little to be desired, but in accounting for the change, or in attempting to explain the cause and manner of the change, it is evident at once that his observations were faulty and superficial, notwithstanding his apparently extensive use of the microscope in his investigations.

He says: "About the commencement of October the first indications of the hybernal change are to be detected: the nose and lips assume an iron-grey hue, from the presence of white hairs; many of the whiskers are white at the tip or some portion of the shaft; a patch of white hairs, twenty to thirty in number, of the size of a split-pea, forms on the centre of the forehead; white hairs become apparent on the edges of the ears outside and at their junction with the neck, while on the inside a crop of downy white fluff springs up; a few of the longer hairs of the pile of the back, especially towards the tail, are observed to be blanched wholly, or only at the tips, while the greater part of the smaller kind are brown at the tip, with the tawny band of the shaft much lighter in color or even white; the anterior surface of the feet, especially of the hind ones, is mottled with white. Thus far," he continues, "the most careful examination fails to elicit any addition to the autumnal coat, the change being superficial and entirely dependent on an alteration of colour in existent hairs."

With the material at present before me it is hard to understand how such a conclusion could have been reached. The only explanation that suggests itself is that specimens were casually examined from time to time in the flesh and not preserved for detailed study and comparison in series. For later on he appears to have discovered the new growth of hair, for he says: "During November this surface-change gradually deepens in intensity, ....and is accompanied by a deeper one of a much more potent character; for on separating the fur a thick crop of white stiff hairs (first apparent at the root of the tail) is to be detected
springing up over the back and sides. These hairs, at first extremely minute and entirely of a new growth, rapidly increase in length, accompanied by an advance in the superficial changes above mentioned; soon they are on an equality with the pile of the autumnal coat on the sides, forming a mottled whity-brown band from ears to tail, contrasting strongly with the centre of the back, at present comparatively unchanged; anon they outstrip this, reducing the mottling on the sides to a pure white, and, gradually implicating the mottling on the sides to a pure white, and, gradually implicating the centre of the back in the same process ...they clothe the animal in a thick white outer garment, generally assumed about the first week of December. As soon as the new growth renders itself superficially evident, the change of colour in the old hair, which on the back up to this time has been slow in progress, advances with great rapidity, so that in a few days only a few coloured hairs, generally remaining unchanged throughout the whole winter, can be detected" (l. c., pp. 230, 231).

Later on he says: “Thus the winter hue would appear to be brought about by a change of colour in the pile of the autumnal coat combined with a new hybernal white crop, the latter undoubtedly playing no small part in the colouring process and in the thickening of the fur. There is no indication of shedding." An increase in length ensues over the whole body....The process may be summed up as a combination of colour-change (except in the underparts) of the lengthened outer hairs of the autumnal [=summer] coat, with an additional hybernal growth; the former universal over the body, the latter limited to certain portions”¹ (l. c., p. 232).

There is so much to be corrected in the foregoing quotations that the points may best be taken seriatim.

(1.) First, as to the whiskers, which elsewhere, it is said, “will demonstrate each variety” of the “blanching process” of the hairs. My series of over seventy specimens shows that the color of the whiskers is entirely independent of any seasonal color-change of the general pelage. They may be either all black, as in many of the midwinter specimens, as well as in some

¹ Not italicized in the original.
October and November specimens; or part white and part black, or even the same hair particolored, as happens about equally in early fall specimens and in December, January and March specimens. This feature appears to be a matter of purely individual variation, having no relation to season.

(2.) Secondly, the small white spot in the forehead. This is a mark more or less common to all species of Leporidae, including those that do not change to a white winter dress. It varies in extent from three or four white hairs to much more than “twenty to thirty.” It is especially frequent in Lepus americanus while in the summer coat. It is present in 10 out of 18 fall specimens now before me, in which the crown is unchanged by molt, and also in a large proportion of the April and May specimens in which the head has acquired the full summer dress. Being found all summer, and more or less commonly in all Hares, it evidently is not one of the early stages of change to the winter coat, either by a “blanching process,” or any other.

(3.) As already said, the failure to discover a new growth of white hair about the nose, sides of the head, and on the ears and feet, must have been due to faulty observation, since my specimens demonstrate its presence beyond question. Some show it so plainly that it is impossible not to recognize it on the most hasty inspection; in others the fact that the short white hair is a new growth is not so obvious, so that a mistaken interpretation of the facts might easily be made by one unaware that the absence of a new growth would be an anomaly, and in opposition to what occurs as a rule in mammals. Besides, as already shown, the pelage of the sides of the nose, the feet, and sometimes of the greater part of the head, is often, even in midwinter, only superficially white, even the coarser hairs being only tipped with white, easily leading to the inference that they were undergoing a “blanching process.” This erroneous departure has obviously influenced the author's whole subsequent work, which his discovery later on of the new growth, when more advanced, failed to correct, and led to the false assumption that the change of color over the whole body was due largely to the blanching of the old hair.
(4.) It is assumed that the old hair is not shed, but suddenly assumes new vitality and proceeds to "increase in length," and to take on an entirely changed molecular structure, for he says elsewhere (l. c., p. 233) that "to this [increase in the length of the autumnal hairs] must be added that the blanching shaft, in the majority of cases, has also augmented in thickness.... the increase being consequent upon a more than usual number of series of cells entering into its composition." And again (l. c., p. 234): "It would seem that the rapid development of new hairs .... involves the autumnal outer fur in the same process, leading to an increased length and thickness in the shaft of the hair by the superposition of layers of the same colourless cells entering into the structure of the new growth—perhaps combined also with an arrested production of pigmentary matter." This is further elaborated in such detail of explanation, based on microscopical examinations, that it would seem to rest on a solid basis, but I must confess that to me the case is simply incomprehensible. My material certainly demonstrates that the summer coat is shed, and not transformed, either in structure or color. On the other hand, it does not need even the aid of a magnifying glass to show that the winter coat of long white overhair is of a finer and softer texture, with a much smaller (instead of larger) diameter of shaft than the summer coat, which is coarser, harsher to the touch, and of a different structure, the particolored (not the wholly black to the same degree) hairs of the summer coat being subapically thickened, the thickened portion including the fawn-colored band, and extending slightly above and below it. Hence, the only explanation that occurs to me is that the thickened hairs were a part of the old summer coat, which it was assumed were in process of change, or about to change to white, simply from the fact that the brown hairs were disappearing, and that he compared these old hairs with the new hairs of the winter coat. Again, in specimens well advanced in change, on casually parting the pelage of the back, the new white hairs are so abundant and conspicuous that all of the hairs seem white below the surface, but on removing some of the hairs still remaining of the summer coat they are found to be colored to the base and still unchanged.

In a January specimen (No. 3277, Rutland, Vt., Jan. 8) a small proportion of the hairs over the dorsal region are pure white for
rather more than their apical half, and then pass into a broad band of very pale horn-color, which usually fades out basally, or may persist faintly to the base of the hairs. In texture and size they do not differ from the pure white hairs with which they are intermixed. A very few of these basally faintly horn-tinted hairs can be found in another specimen taken at the same time and place, and in one out of three early March (March 2) specimens from the same locality. Also a specimen from Locust Grove, Lewis Co., N. Y., taken March 21, 1884, and kindly loaned me by Dr. Merriam, is a fine example of this phase of coloration. In this specimen many hairs still remain wholly black, others are only black, or more or less blackish, basally. These hairs are evidently, however, in each case, a part of the true winter coat, and not a remnant of the summer coat, any more than are the fulvous hairs on the fore legs and hind feet of certain midwinter specimens, or the basally fulvous hairs on the nose, or the fulvous hairs on the ears, of these same specimens. They simply grew particolored instead of white, and have not either the texture or the form of the particolored hairs of the summer coat. Yet, although so exceptional, they might, considered alone, seem to give some support to the 'blanching' theory of the autumnal change of color.

So much attention would not be given, in this connection, to Mr. Welch's paper, in view of the overwhelming evidence of its erroneous character, were it not that it has recently been made prominent by Mr. E. B. Poulton as the chief basis for his theory respecting 'Variable Protective Resemblance in Vertetrates,' in which he either quotes at length or summarizes from Mr. Welch most of the passages above quoted, and proceeds to theorize from this insecure basis.

In conclusion it may be well to correct a time-honored error respecting the geographical distribution of Lepus americanus, since it figures prominently in the matter of seasonal change of color. Thus Mr. Poulton (l.c., p. 97), in speaking of this species, says: "In Hudson's Bay Territory it changes early and carries the winter coat till June, while no change of color takes place

in the winter in the *southern parts of the United States,*" basing the statement probably on Welch (l. c., p. 235), who in turn quotes it directly from Sir John Richardson. Richardson seems to have derived the statement from Pennant, as he says (Faun. Bor.-Am., I, p. 218): "The white color is less perfect in more southern districts, and to the southward of New England, according to Pennant, the brown dress endures all the year." Pennant, in his 'Arctic Zoology,' recognized only two species of North American Hares—the Varying Hare and the American Hare. The first is the Arctic Hare of the present day; the other was primarily the Varying Hare here under consideration, but included also all other species of North American Hares then known. Hence when he says, "From *New England* southward they retain their brown color the whole year," he is evidently speaking of the 'Cotton-tails' and Swamp Hares of the South, which, as every one knows, never turn white. It is needless to tell intelligent mammalogists that the southern limit of distribution of the Varying Hare is the southern half of the Alleghanian Fauna—in other words, it is not found at ordinary levels south of Massachusetts. Furthermore, there is little evidence to show that it does not practically become white in winter to the very southern limit of its range, although less perfectly so than further north, the change in color sometimes remaining more or less incomplete and superficial, so far as can be determined at this writing.

1 Not italicized in the original.