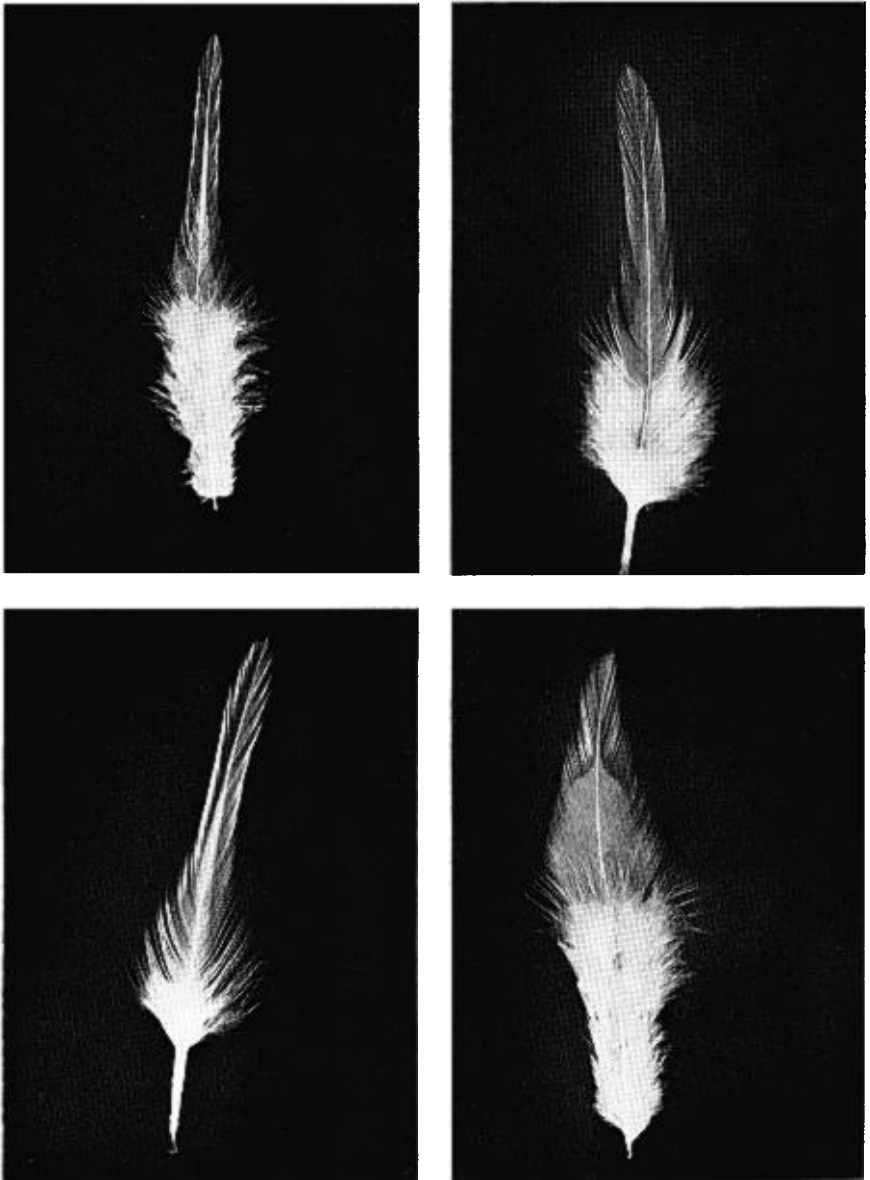


AN EXAMINATION OF SOME INTERPRETATIONS OF MOLT WITH ADDED DATA FROM PROGESTERONE AND THYROXINE

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A recent and extensive review by Assenmacher (1958) is devoted to hormonal mechanisms as the determinants controlling molt in birds. Although the problem is presented as being as yet incompletely clarified, surges of thyroidal activity are thought on the whole to set molt in motion, although these surges may trace to factors further back. There is most ample evidence that exogenous thyroid administration will initiate new feather growth in the greater number of cases studied; there is far less proof that the bird's own thyroid exhibits comparable and measurable activations at the appropriate period. These lacks have caused Assenmacher to suggest that a time prior to the onset of molt may be of greater importance than the molt period itself in an evaluation of endogenous thyroid physiology.

Such hypotheses of prior increases in circulating thyroid levels cannot be examined in the feathering where the onset of the molt is violent and spreads with rapidity over the entire plumage since the time of effect could well be restricted to activation of the papillae alone. These rapid molts may occur but they are not the rule. In general, the molt is prolonged, assuring a coincident series of feathers in various stages of regeneration, and of various papillae coming into function. Feathers during their growth are demonstratively susceptible to some hormonal alterations and furnish records of these events when later collected. Witschi (1936), for example, could show in this manner that the nuptial plumage of a weaver finch, *Pyromelana franciscana*, traces to the pituitary luteinizing hormone. Certain feathers of the domestic fowl give a peculiarly clear and unmistakable reaction to thyroid hormone administration and they do this toward dosages far below those effectively stimulating molt (Juhn and Barnes, 1931). Lacy feather portions being laid down in treated fowl are displaced by barbulated areas; where the bird happens to be parti-colored, the pigmentation shifts in correspondence to structure but this is secondary. Feather series grown during the normal molt period never show the least evidence of such modifications and surely these should be expected if the bird's own thyroid were hyperactive then. This same reasoning was taken to speak against progesterone-caused molt as *via* the thyroid (Shaffner, 1954), but the point seems not to have been quite clear (Assenmacher, 1958:261). Accordingly, an illustrative test was set up whereby progesterone and thyroxine are compared in birds so prepared that feathers in growth were present while molt stimulation in other standing parts of the plumage was effected by either compound.



EXPLANATION OF FIGURES 1-4

Comparison of the feather type regenerated by adult White Rock capons under progesterone and under thyroxine dosages similarly effective in molt as measured in the number of primaries experimentally shed and replaced.

FIG. 1 (UPPER LEFT). Normal control saddle hackle.

Progesterone amounts anticipated to give about maximal response were set against a range of dosages for thyroxine. The amounts employed were estimated from earlier experience and allowance was made for the far heavier body weights, average 5.47 kg, of the birds in the present series. These were White Plymouth Rocks, surgically castrated at about eight weeks of age. Treatment was made at about 15 months of age, during midsummer. The capons were housed by pairs in large adjacent cages; each had a square patch of plumage removed from the left saddle. Three weeks later all individuals were found in suitable regeneration for feather record—treatment by single injection was made as follows:

- Pair 1, 50 mg repositol progesterone in 2 ml, intramuscularly;
- Pair 2, 100 mg progesterone in 2 ml sesame oil, subcutaneously;
- Pair 3, 0.5 mg thyroxine in 1 ml distilled water, subcutaneously;
- Pair 4, 5.0 mg thyroxine in 1 ml distilled water, subcutaneously;
- Pair 5, 10.0 mg thyroxine in 1 ml distilled water, subcutaneously.

There were no ill effects to be noted at any treatment level. Heavy molt became evident within 14 days or somewhat less with progesterone in either carrier and with 0.5 and 10.0 mg thyroxine. The 0.5 mg dosage caused little response to be clearly differentiated from the sporadic small feather loss common to the castrate. The saddle hackles in enforced regeneration during the respective injections were collected when growth was approximately completed. Samples were photographed and grouped on the basis of similarity in the number of primaries experimentally renewed. Figure 1 is from an untreated control; Figs. 2 and 3 are from repositol progesterone and progesterone in oil; Fig. 4 is from 5.0 mg thyroxine. The thyroxine-treated feather shows the expected usual structural responses; the absence of similar modification in the progesterone cases is clear.

If the positive action of progesterone upon molt in the castrate were indeed through an increased output of the bird's thyroid secretions, one should reasonably look for some approximation at least of the specific structural changes experimentally produced by thyroxine: there was none. Questioning the occurrence of "thyroidal surges" in no way detracts from the gland's normal role in differentiation; this attribute may explain the experimental effectiveness in feather papilla activation. It is a property not shared by the

FIG. 2 (UPPER RIGHT). Saddle hackle regenerated under repositol progesterone treatment; 8 primaries experimentally renewed.

FIG. 3 (LOWER LEFT). Saddle hackle regenerated under progesterone in oil administration; 6 primaries experimentally renewed.

FIG. 4 (LOWER RIGHT). Saddle hackle regenerated under thyroxine administration (5.0 mg); 8 primaries experimentally renewed.

metabolism stimulation of dinitrophenol: unpublished data from this laboratory showed that the drug's administration to adult cocks, carried in graded doses to the lethal level, affected neither the regenerating feather structure nor caused molt.

The responsiveness of the regenerating feather may be applied to similarly guided considerations of the molt period in the normal adult hen. For this aspect no new tests need be devised since the pertinent data have long been in the literature, although not necessarily planned toward this end. The annual molt generally averages from 8 to 10 weeks during which a completely new set of feathers develops in the different feather tracts (Hays, 1957). At this time there is an interruption of lay and the oviduct regresses considerably from its functional development. The state of the oviduct especially suggests a sharp diminution, perhaps even a temporary interruption of oestrogen secretion by the hen's ovary. However, this is not borne out in the feathering regenerated during this period of so-called quiescence. The numerous ovariectomy studies, separately pursued in various laboratories, invariably proved that with complete glandular removal, the original female feathering became displaced by a new and sharply differing type. This castrate plumage is identical in the operated fowl of either initial sex and identical, too, with the plumage worn by the normal cock (Domm, 1924; Goodale, 1916; Pézard, et al., 1925). Further, and this is pertinent here, differences between the hormone requirements of the various feather tracts were early suspected. The suggestions were based on observations that the development of feminized plumage in successful grafts to the male (Zawadowsky, 1926), or its return in ovarian regeneration (Domm, 1931), was a gradual process, a serial spreading. When modification through injected oestrogen became feasible, regionally effective dosages could be established and with this an approach to quantitative appraisals (Juhn and Gustavson, 1930). Effects in the large wing feathers which served in later analyses by Fraps (1938) are particularly relevant to this aspect. Since the feathering formed during her molt by the hen is entirely female, it is clear that all the demonstrated regional demands were being met fully. Hence the ovary must have continued a secretory activity during that period; in fact, to some considerable degree. Perhaps the regenerating plumage may be preferentially avid of circulating oestrogen and so deprive other target organs, such as the oviduct. This, however, is speculation and of no immediate bearing here.

A consideration of the points raised in the preceding discussion suggests some reserve in accepting any one mechanism employed as the determinant of the normal adult molt. In fact, the very range of experimental manipulations that will initiate activation (see Assenmacher, 1958, for reference to which prolactin—Juhn and Harris, 1958—should be added) speaks against

this. Instead, it seems probable that molt is essentially an autonomous process, the primary seat of the cyclical renewals being the feather papilla proper. From this point of view there would be no fundamental distinction between the juvenile and the adult molts, either of which would occur ultimately. The difference present is that between the extreme, although slackening velocity, with which the juvenile replacements follow upon each other and the periods of rest that are interposed in the adult. These differences are, however, of first importance. When a biological activity proceeds at its maximal or near maximal capacity as in the juvenile molts, there is no good prospect of further acceleration. Spontaneously developing gradual declines and renewals on the other hand afford an approach to the various experimental hastening that has been so successfully practiced.

The positive results obtained with hormone treatments have reasonably suggested internal fluctuations of similar nature in explanation of the normal molt. The case for this interpretation is, though, no longer as persuasive as once thought. Within limits, one or another environmental factor could well participate as seasonal trigger. This, however, need not necessarily be because of secretory surges but because of an autonomously changing physiology of the feather papilla which at this time exposes the organ to previously ineffective levels. There is good experimental evidence that increasing sensitivities accompany spontaneous preparatory activations within the papilla: such associations would in any event be reasonable. Van der Meulen (1939), for instance, has found that ever less thyroid substance will stimulate the papilla the closer the treatment is made to the anticipated date of the normal molt. Entirely comparable observations were made by Harris and Shaffner (1957) when progesterone was employed, also, in the domestic hen.

Returning the source of molt in the first place to the papilla makes the adaptive "bunching" or prolongation of the regenerative periods more readily understood; it also speaks against the importance of ascribing pacemaker activities to any particular set of circumstances. These may, in fact, vary from species to species and the problem remains whether an experimental effectiveness in one or another case can be taken as mirroring the normal event.

SUMMARY

It is known that feathers during their growing period will lay down records of certain fluctuations in the hormonal milieu, normal or experimentally caused. This information was used to compare progesterone and thyroxine dosages adequate for induced wing molt in White Plymouth Rock capons with reference to the respective effects in regenerating saddle hackles. Thyroxine caused the well-known structural differentiation in lacy areas; this response was absent with progesterone. The findings support the view that progesterone molt in the fowl is not through an activation of the bird's own thyroid.

Since thyroxine induces the specific feather response with doses far smaller than found essential to experimental molt, lack of its development during the normal molt tends to

discount thyroidal surges at this period. Conversely, the female feathering laid down during molt of the hen is evidence of continued ovarian activity during that time. These considerations, together with the number of manipulations experimentally effective in molt, seem to speak against any one environmental mechanism as causal in all cases. Instead, gradual and spontaneous activations within the papilla, associated with increasing sensitivities, are suggested as the primary seat, the periodicities being adaptive and variable.

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