TESTOSTERONE AND DAYLENGTH-DEPENDENT DEVELOPMENT OF COMB SIZE AND BREEDING PLUMAGE OF MALE WILLOW PTARMIGAN (*LAGOPUS LAGOPUS LAGOPUS*)

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ABSTRACT.—Photostimulation of male Willow Ptarmigan resulted in a rapid molt from the white winter plumage to the pigmented plumage of the breeding bird. In castrated ptarmigan the breeding plumage was omitted, resulting in a slow molt from white to pigmented summer (postnuptial) plumage. Feathers were plucked from the head and back of castrated and intact birds kept on short daylength to investigate the effects of testosterone on feather pigmentation. Both castration and testosterone treatment resulted in pigmentation of regenerating feathers, while the untreated, intact birds regenerated white feathers.

Pigmented feathers that regenerated on short daylengths in castrated or testosterone-treated birds were similar to each other, but were not the same as any type of pigmented feather seen in intact or castrated birds exposed to long daylengths. Pigmented feathers that generated in testosterone-treated intact or castrated birds on long daylengths were the same as feathers in breeding males. When compared with control birds, testosterone treatment shortened the interval between photostimulation and the beginning of the molt, while castration markedly lengthened this interval.

Together with the photostimulated development of pigmented breeding plumage in intact males, there was a 100% increase of comb height. Castrates did not show any comb growth, whereas testosterone treatment always resulted in a rapid comb growth, both in intact males on short daylengths and in castrates on short daylengths and on long daylengths.

In the male Willow Ptarmigan, testosterone and perhaps gonadotrophins (LH) affect the pigment producing system. There is a daylength dependent testosterone induction of molt from winter to breeding plumage, and a testosterone-stimulated and a testosterone-dependent comb growth. *Received 15 March 1978, accepted 28 September 1978.*

TOGETHER with a number of arctic and hyperboreal birds and mammals, Willow Ptarmigan (*Lagopus lagopus lagopus*) show a pronounced seasonal dimorphism, displaying a white winter and a pigmented summer plumage. Through the summer there may be several stages, and Johnsen (1929) described as many as four attires in the male and three in the female throughout the year.

Both male and female Willow Ptarmigan show a white *winter plumage,* normally lasting from the end of October to the end of March. The male then begins to molt the white winter feathers and develops a conspicuous pigmented *breeding plumage.* This is characterized by molt and formation of new feathers on the head, upper neck, upper anterior breast and on the back, while the ventral and wing feathers remain. The pigmentation is reddish-brown and black and the feathers are shed in a sequence so that feathers on the back are affected last. This part of the body may attain full coloring at the time when actual mating takes place, or it may not be fully colored at all. The naked wattle or comb over the eye enlarges and appears bright red during this period.

At the end of the breeding period, the male begins to molt into a pigmented *summer plumage.* This may be initiated even before the breeding plumage is completed, and the remaining feathers from the winter and breeding plumage are replaced by bright yellowish and brown feathers with black bars.

In the female, the pigmented plumage starts to develop a little later than in the male, and the feather replacement is not as sequential. The garb is very much like that of the male's summer plumage and is completed at the time of breeding. It is not changed during the periods of egg-laying, incubation, and the first 2–3 weeks of brooding chicks. After brooding, molt starts again, and the female together with the male, who has now more or less completed the summer plumage, gradually change into a pigmented *fall plumage,* consisting of dark brown and black feathers. This stage shows great variations mainly because of the varying number of remaining feathers from the preceding plumages.

The main difference between the sexes, therefore, lies in the breeding plumage of the male, and while the female shows a rather constant feather garb while incubating eggs and rearing young, the male molts continuously from the end of March until the winter plumage is completed at the end of October.

The dramatic change from white to brown in the spring coincides with the annual activation and growth of the gonads. In arctic and subarctic regions, this part of the year is characterized by a rapid and pronounced increase in the daylength. A great number of investigations have described the causal relationship that seems to exist between daylength and gonadal activity in birds (see Farner and Follett 1966, Lofts and Murton 1968, 1973 for reviews). Høst (1942) and Novikov and Blagodatskaia (1948) showed that during late autumn and mid-winter, male Willow Ptarmigan responded to artificially increased daylength by a rapid development of breeding plumage and gonadal activity. Within a few days after being transferred to long days, the birds began to replace their white winter feathers with feathers of the pigmented breeding plumage. The activation of the gonads was reflected by increased comb size and by the onset of aggressive behavior. All these events took place in unheated outdoor cages, with snow covered ground, and an ambient temperature far below the freezing point (Høst 1942).

The purpose of this investigation was to find out whether the development of breeding plumage in male Willow Ptarmigan is regulated by sex hormones, or if the plumage development and the coinciding activation and growth of the testes may be controlled through more or less separate mechanisms initiated by the same external stimulus (i.e. long days). To this end castration and testosterone treatment of male Willow Ptarmigan were performed, and the effects of such treatment, alone or combined, on photostimulated plumage changes and comb growth were observed.

Methods

Forty-four farm-bred male Willow Ptarmigan were used for the experiment. The birds were individually caged with free access to water and a modified, pelleted chicken food. When the experiment started on 17 November 1976, all birds were exposed to a light regimen of short days (6L:18D) and had white winter plumages. Previously, they had all experienced a normal autumn with decreasing daylength, controlled by electrical timers and synchronized to the changes outdoors. The illumination was by 80W fluorescent lamps (4400–4600 Lum, 3600°K), each bird situated 1–1.5 m away from a lamp.

The birds were divided into groups as described in Table 1. Castration was carried out under Equithesin anesthesia by bilateral laparotomy between the last two ribs, the testes being removed intact by a pair of fine forceps. Photostimulation was performed by increasing the daylength from 6 to 18 h of light (18L:6D, i.e. long days). The light was always turned on at 0900. The experiment lasted until the beginning of February, when most of the intact photostimulated birds had developed fully pigmented backs. Testosterone treatments were given by daily injections in the pectoral muscle of 1 mg testosterone-oenanthate (Sigma) in 0.05 ml Sesame oil.

Plumage observations were carried out in three ways: 1) *Pigmentation and growth of developing*

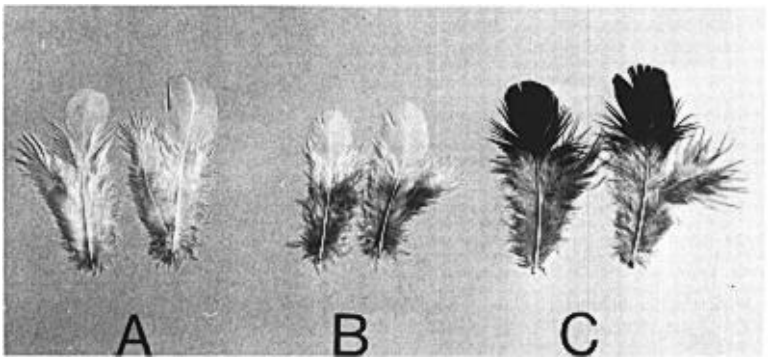

Fig. 1. Feathers plucked from the back of a male Willow Ptarmigan. **A**. from the winter plumage; **B**. from feathers regenerated after first plucking of a testosterone treated bird; **C**. from feathers regenerated after second plucking of a testosterone treated bird.

feathers. Before molting had started, about 60 feathers from one area in the neck and about 30 feathers from one area on the back were plucked on each bird, thereby stimulating regrowth of new feathers. In groups 2, 4, and 7 (Table 1), the feathers were plucked 7 days before the beginning of testosterone treatment. In group 9, the feathers were plucked 7 days after the beginning of testosterone treatment. The plucked feathers regenerated and were plucked a second time, and this took place before photostimulation in groups 3, 4, 6, 7, and 8. 2) *Time of onset of molting*. Molting was manifested by general loss of white feathers and the appearance of pigmented featherpulps outside the plucked areas. 3) *The percent of the birds' back and head appearing pigmented*. The development of pigmented plumage on the head and back was separately judged, and the percent pigmentation was subjectively assessed. The head is the area from above the shoulders, and the plucked area in the neck, therefore, belongs to the head region of the bird. The total height of the comb was measured to the nearest 0.5 mm.

RESULTS

Untreated, intact birds on short daylength (groups 1 and 3, Table 1) showed new feather pulps 7 days after plucking, both on the back and in the neck. All the feathers regenerated, and they were all white, both from the first and from the second plucking and regeneration.

Testosterone treatment affected the regrowing feathers in two ways: first, the feather replacement process was slowed down to a varying but considerable degree—

TABLE 1. The number of birds in each group, and the treatment they received throughout the experiment. The dates (day/month) indicate when the testosterone injections started, when the feathers were plucked, and when castration and photostimulation were performed. An asterisk indicates that the above listed treatment was not performed in that group.

Group	Number of birds	Feathers plucked[a]	Castrated	Testosterone-treated[b]	Photo-stimulated[c]
1	5	17/11 and 1/12	*	*	*
2	5	17/11 and 1/12	*	24/11	*
3	6	17/11 and 1/12	*	*	8/12
4	7	17/11 and 1/12	*	24/11	8/12
5	5	17/11 and 1/12	30/11	*	*
6	6	17/11 and 1/12	30/11	*	8/12
7	3	17/11 and 1/12	30/11	24/11	8/12
8	2	17/11 and 1/12	30/11	12/1	8/12
9	5	1/12	*	24/11	*

[a] One area of the neck and one area of the back were plucked two times (except group 9) to allow regrowth of new feathers.
[b] Testosterone treatment was given by daily injections in the pectoral muscle of 1 mg testosterone-oenanthate in 0.05 ml Sesame oil.
[c] Photostimulation was preformed by increasing day length from 6 to 18 h of light.

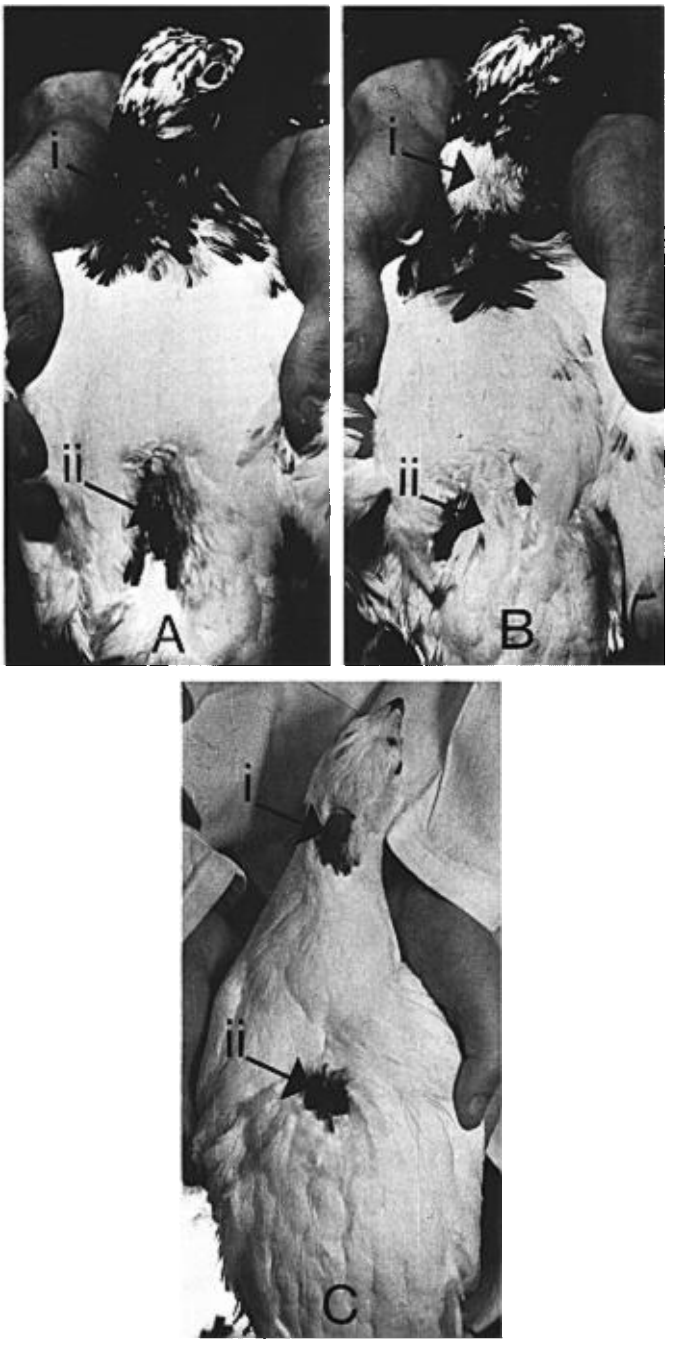

Fig. 2. Feathers regenerated on the plucked areas in the neck (i) and on the back (ii). **A**. photostimulated, testosterone treated male; **B**. photostimulated, untreated male; **C**. testosterone treated male on short daylength.

only a few to none at all regenerated, and the growth of the few that came was retarded; second, pigmentation was generally stimulated. In groups 2, 4, and 7, where feathers had been growing for a week before testosterone treatment started, there was no pigmentation of neck feathers. The proximal half of the regenerating back feathers, however, was pigmented (Fig. 1B). In group 9, where testosterone treatment started one week before plucking, the regenerating feathers were pigmented, but with a white 1–3 mm tip.

The second plucking and regeneration resulted in pigmentation of the whole feather in all the treated groups, both in the neck and on the back (Fig. 1C and 2A and C). In groups 3 and 4, the photostimulated molt began before the second regeneration was completed, leaving a white spot on the dark neck of the control birds (Fig. 2B, i), and a whole dark neck in the testosterone-treated birds (Fig. 2A, i).

Castration in no way affected the regeneration and growth of plucked feathers. However, the pigment-producing system was affected, and castrated birds regenerated pigmented feathers to a considerable extent from the very first plucking. These pigmented feathers on the plucked areas of castrates were not unlike the regeneration observed from the second plucking of the testosterone-treated birds (Fig. 2C, i and ii).

The intact birds of group 3 responded to the changing daylength by molting of white feathers and development of pigmented breeding plumage. The molt started 8–9 days after the change of daylength.

Neither testosterone treatment nor castration had any molting effect on the birds during short days. This was shown in groups 4, 6, 7, and 8 before photostimulation, and during the entire study in groups 2, 5, and 9, which remained on short days.

Both castration and testosterone treatment, however, affected the onset of photostimulated molt. The castrated birds of groups 6 and 8 showed no signs of molting until after 2–3 weeks of long days (i.e. molting was delayed). The testosterone-treated birds of groups 4 began to molt significantly earlier than untreated birds (6–7 days after photostimulation in testosterone-treated birds, 8–9 days in untreated birds). The castrated but testosterone-treated birds of group 7 behaved as the normal testosterone-treated birds. The birds of group 8 behaved as castrates and showed no normal male molt until 7 days after the testosterone treatment started. Then a normal molt ensued, and a normal male breeding plumage developed.

After the molting had started, the testosterone-treated birds of groups 4, 7, and 8 developed a breeding plumage not significantly different from the control birds of group 3. Before the testosterone treatment started the castrated birds of group 6 and group 8 showed a development much unlike group 3. Two to three weeks after transference to long days the birds started to develop a pigmented plumage, but in a way more like a female than a male ptarmigan. The replacement of white feathers was slow, and was initially not restricted to the head as in the male, but affected both back and head to nearly the same extent. These birds did not develop the conspicuous dark crop-region band normally present in the breeding plumage of the male (Johnsen 1929), and the pigmentation on the whole was more like that of the summer plumage.

Testosterone treatment always resulted in a rapid growth of the comb, and within 3 weeks the height of the comb increased 100% (Fig. 3). The birds on continuous short days did not grow larger combs unless they were testosterone-treated. Photostimulation resulted in a rapid comb growth, and within 4 weeks the height had

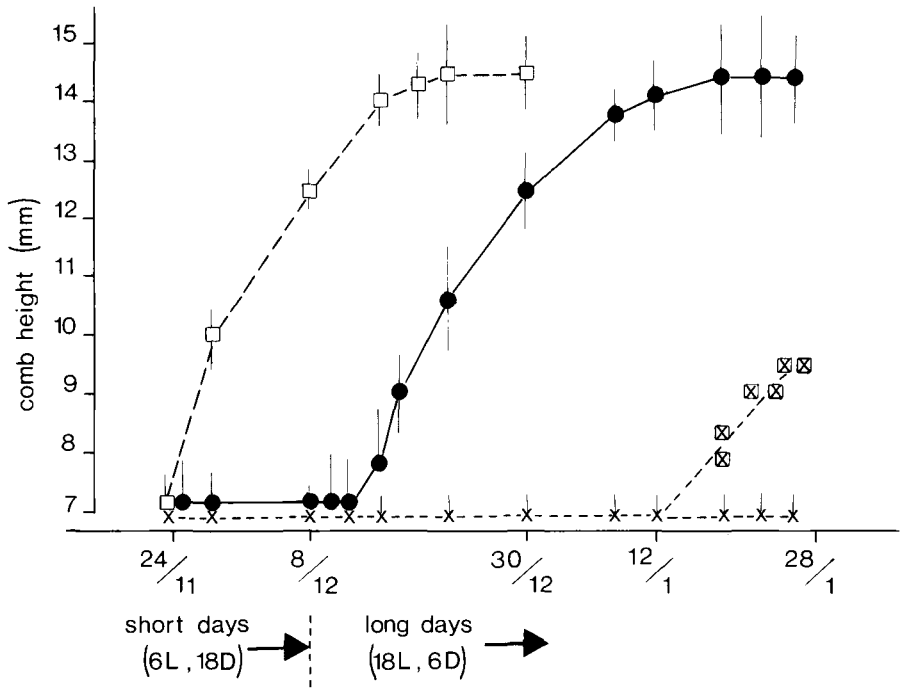

Fig. 3. Comb height variations of male Willow Ptarmigan (height in mm with vertical bars showing ± SE). One group received testosterone treatments from 24 November (⊠, n = 7), one group was castrated on 24 November (□, n = 8), and of these two received testosterone from 12 January (×). One group remained intact and untreated (●, n = 6). At 8 December, all groups experienced an increase in the daylength from 6 to 18 h of light.

increased 100% in the untreated intact birds of group 3. The castrated birds of groups 6 and 8 showed no comb growth at all after being photostimulated, but as soon as group 8 received testosterone a rapid growth ensued.

The pigmentation that resulted from castration and testosterone treatment of birds kept on short days differed from the breeding-plumage coloring resulting from photostimulation. While the normal breeding plumage has feathers with brown, reddish-brown, and black patterns, castration and testosterone treatment induced black and grey pigmentation on short days, and the feathers lacked the characteristic barred patterns.

Only the development of breeding plumage was affected by castration. When castrated birds had reached full pigmentation, they could no longer be distinguished from males wearing summer garb. The development into fall and winter plumage also occurred as in intact normal males. After about 2 weeks in white winter plumage, however, plucking again resulted in pigmented feathers, and photostimulation resulted in a feminine development of pigmented summer plumage.

At the end of the experiment, inspection revealed no testicular regeneration in the castrated birds. The birds were killed in a state where normal birds have enlarged testicles.

TABLE 2. A summary of the results from each group. A dashed line indicates that photostimulation was not performed, and therefore no plumage changes took place.

Group	Feathers regrown on plucked areas	Plumage changes after photostimulation	Comb
1	All white	—	Small—no changes
2	First plucking white, second pigmented	—	Growing after 24/11
3	All white	Molting into breeding plumage	Growing after 8/12
4	First plucking white, second pigmented	Like group 3, but molting began earlier	Growing after 24/11
5	All pigmented	—	Small—no changes
6	All pigmented	Long delay, then a very slow molt into a summer-like plumage	Small—no changes
7	All pigmented	Like group 3, but molting began earlier	Growing after 24/11
8	All pigmented	Like group 6 until 12/1, then like group 3	Small, no changes until 12/1, then growing
9	All pigmented	—	Growing after 24/11

DISCUSSION

The hormonal control of plumage changes in birds has long been a matter of confusion. Depending on the species involved and when experiments with hormones take place relative to periods in the bird's life (e.g. the annual breeding period), a great number of reactions has been recorded from the treatment of most of the normally occurring hormones. In addition, many other chemical and environmental stimuli affect the mechanisms of both molt and pigment production (see Witschi 1961, Ralph 1969, Payne 1972 for reviews).

The lack of comb growth in photostimulated, castrated Willow Ptarmigan was also reported by Nowikow (1939), and the dependency on testosterone for comb growth has now been documented for several avian species (see Parkes and Emmens 1944, Lofts and Murton 1973). The comb is an important secondary sexual character, and Gjesdal (1977) found a positive correlation between the comb height and social rank between male Willow Ptarmigan in captivity.

Most investigators have found that gonadal hormones inhibit molting in birds. Castration often triggers a premature molt, and in a number of species the birds enter a condition of continuous molt after castration. But for the more than 100 species, including Willow Ptarmigan (Høst 1942), where molting and changes in gonadal activity coincide, the action of gonadal hormones on plumage changes is less well understood (see Payne 1972). The present results show that the molting system is not influenced by testosterone as long as the birds are held on short days. After photostimulation, testosterone-treated birds molt earlier than control birds, and castrated birds do not show a normal male molt at all. The time lag between photostimulation and the first signs of molt for testosterone-treated birds is 6–7 days, which is the same time it takes for a plucked feather follicle to regenerate a new visible feather pulp. This indicates a daylength-dependent testosterone induction of molting. In the treated birds the plasma levels of testosterone are high when the daylength is increased, and a stimulation occurs even after the first long day. The control birds have to wait for their own testosterone production, and it is a reason-

able inference that this becomes high enough within 2–3 days. The plasma level of luteinizing hormone (LH), which stimulates the testicles to produce testosterone, has been shown to increase the first day after photostimulation in Japanese Quails (*Coturnix coturnix*) (Nicholls et al. 1973, Gibson et al. 1975), White-crowned Sparrows (*Zonotrichia leucophrys*) (Follett et al. 1975, Lam and Farner 1976), and Willow Ptarmigan (Stokkan in prep.). The finding that regeneration of plucked feathers is retarded in testosterone-treated birds is not understood. The present results conflict with those of Nowikow (1939) who reported that photostimulated castrated Willow Ptarmigan molted into breeding plumage as normal birds. This could be attributed to an incomplete castration since this may result in a normal development of photostimulated breeding plumage, but a reduced comb size (Stokkan unpublished observations). The results of Nowikow (1939) are not quantified.

In male Rock Ptarmigan (*Lagopus mutus*), which also show seasonal dimorphism, testicular hormones seem to suppress the initiation of the molt from white to pigmented plumage (Salomonsen 1950–1951). MacDonald (1970) observed that one male Rock Ptarmigan implanted with testosterone did not change from white to pigmented plumage at the time when normal males did, but remained white through most of the summer, displaying sexual activity long after the normal breeding period was terminated. This difference whereby testosterone acts on the onset of molt between the two ptarmigan species may explain why male Willow Ptarmigan develop a pigmented breeding plumage, whereas male Rock Ptarmigan normally stay white all through the breeding period.

The present study shows that the pigment-producing system is affected by both testosterone treatment and castration independently of daylength. Sex hormones have been shown to affect the production of feather pigments in several species. Both quality and quantity are affected, and the effects have resulted from both gonadectomy and local and systemic administration of hormones (see Ralph 1969). Both testosterone treatment and castration stimulated pigment production, but there was a latency in the action of testosterone. This latency was shown in several ways. The birds of group 9 regenerated pigmented feathers after the first plucking, but they had a white tip. The back feathers of groups 2, 4, and 7 also had a white distal part (Fig. 1B), and the head feathers of these groups were not pigmented until they regenerated after the second plucking. In castrates, however, the feathers were fully pigmented after the first plucking and regeneration.

The different modes of action whereby castration and testosterone treatment affect pigment production suggest different mechanisms. Castration results in increased plasma levels of LH in male Willow Ptarmigan at this time of the year (Stokkan in prep.). Both testosterone (rat scrotum epidermis, Wilson and Spaziani 1976) and LH (weaver finch breast feather follicles, Hall and Okazaki 1966, Hall 1966) have been shown to stimulate melanin production through action on the tyrosinase enzyme system. Thus it could be argued that both increased levels of plasma testosterone, resulting from testosterone treatment, and increased levels of plasma LH, resulting from castration, could stimulate pigment production. The finding that castration and testosterone treatment resulted in regrowth of feathers displaying grey and black colors, which are different from those normally found in the male breeding plumage, suggests a hormone-influenced tyrosinase stimulation. Tyrosinase is the enzyme system catalyzing the conversion of L-tyrosine to DOPA-quinone, generally believed to be the rate-limiting step in the biosynthesis of melanin (Lerner 1953).

This study has focused upon the development of the male breeding plumage. The testes regress in June/July and the plasma levels of testosterone fall (Stokkan in prep.), but the birds still produce pigmented feathers until the end of October, when the winter plumage starts to develop. From the time that the castrates have completed the summer plumage until they again await the development of breeding plumage in winter, they cannot be distinguished from intact birds. Outside the breeding period, therefore, other hormones must control the molt and production of pigments. That such hormones may play a role in the control of seasonal plumages in Willow Ptarmigan has recently been shown by Braun and Höhn (1977). They found that plucked birds grew pigmented replacement feathers if they were injected with any of the hormones alpha-MSH, mammalian posterior pituitary extract, thyroxine, TSH or an FSH/LH mixture.

The complete understanding of the control of seasonal plumage changes of the Willow Ptarmigan is still an unsolved problem. However, the male breeding plumage must be regarded as a secondary sexual character, and the development of it is dependent on the levels of plasma testosterone.

ACKNOWLEDGMENTS

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EDITOR'S COMMENTS

With this issue we initiate what I hope will become a regular feature of *The Auk*: a "Commentary" section. This is intended to provide a forum for brief essays or points-of-view on various matters of interest to ornithologists, or exchanges relating to papers published in recent issues of *The Auk*. In this issue Harold Mayfield addresses some aspects of the role of amateurs in ornithology, speaking from the position of an amateur who has made exceptional contributions to the field. Harold prepared this essay at the invitation of the Editorial Board, and we have invited several other individuals to prepare such personal statements on several other topics of current interest. But "Commentaries" may be contributed as well as invited. If you have strong feelings about some matter of importance in ornithology and wish to submit an essay or position statement, please do so. Alternatively, we would welcome suggestions of topics that you would like to see addressed, and the names of individuals you think the Editorial Board might consider inviting to prepare such a Commentary. The ground rules are these: (1) contributions should generally not exceed 750 words in length, and (2) all contributed material will be reviewed by the Editorial Board, which will advise the Editor of the acceptability of the material.

One other matter: In the January 1978 issue of *The Auk* I drew attention to the rather lengthy time lag between acceptance of manuscripts and their final publication in *The Auk* (17.5 months, on the average, for the papers in that issue). Reducing this time lag has been a major objective during the past year, and we have now lowered it about as far as is practical. The average time lag between acceptance and final appearance of articles in this issue (taking into account the actual date of issue of the "January" issue) is 5.6 months; the time lag for Short Communications is about a month longer.

Because of the large number of inquiries concerning the late delivery of the October *Auk* and therefore of the 1979 dues notices, we feel that we should provide some explanation for this delay. First, the transfer of the editorial offices from Oregon State University to the University of New Mexico in late summer created numerous delays, particularly involving the completion of the index for volume 95. Second, after the October issue was sent to press we experienced additional delays at Allen Press, because their publishing schedule is tight, and material for *The Auk* now had to be worked into other scheduled jobs. Third, because our turn-around time for publication has been reduced significantly, some delays were experienced when some authors did not return galley proofs as expeditiously as possible.

The print order for the 1979 dues notices was submitted to Allen Press early in the Fall and the dates for submission of dues were established to account for a possible delay in publication. Unfortunately, we did not anticipate the magnitude of the delays. We apologize for the inconvenience this has caused the membership, and we trust that in paying dues members will have used their discretion in remitting the appropriate amount.

We should also note that this issue of *The Auk* was delayed for some of the same reasons noted above, but also to allow sufficient time for members to pay their dues and thus enable the Treasurer to establish the press run for the January *Auk*. We intend to return to a regular publication schedule as quickly as possible.—JOEL CRACRAFT, *Treasurer*; JOHN WIENS, *Editor*.