THE EFFECT OF PERMANENT SHORT DAYS AND CASTRATION ON PLUMAGE AND COMB GROWTH IN MALE WILLOW PTARMIGAN (*LAGOPUS LAGOPUS*)

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ABSTRACT.—Intact and castrated male Willow Ptarmigan (*Lagopus lagopus lagopus*) were kept on spring-like increasing daylengths or permanent short days (6L:18D) from December to July. During this period, plumage changes were recorded and comb height was measured. Both intact and castrated males exposed to increasing daylengths began to molt from white to pigmented plumage in late February. The intact males first molted into the rich brown breeding plumage, and then, in late May, they began to develop the mottled brown summer plumage. The castrated males omitted the breeding plumage and slowly developed a summer plumage. At the end of June, the heads and backs of the intact birds were fully pigmented, but were still 60% white in the castrated birds. The intact and castrated males exposed to permanent short days had identical plumage changes. In early April, scattered, dark brown and black feathers, lacking the barred pattern of normal plumages, began to grow on the head, and by the end of June both pigmented and white feathers were growing on both the head and back. The height of the combs in intact birds on increasing daylengths had a well defined maximum at the peak of the breeding period. This was not observed in the intact birds on short days, where only a slight increase could be detected. Castrated males always had low and unchanging comb height, irrespective of the daylength. *Received 23 January 1979, accepted 21 May 1979.*

THE male Willow Ptarmigan (*Lagopus lagopus lagopus*) has four plumages throughout the year (Johnson 1929). From October to March, he has a *winter plumage,* which is all white except for the black rectrices. During March and April, he undergoes a partial molt into the pigmented *breeding plumage*. Reddish-brown and black feathers replace the white feathers on the head, neck, upper breast, and parts of the back, while the rest of the body remains white. At the same time, the combs over the eyes enlarge and become conspicuously red. This change in plumage and comb size has been shown to be stimulated by increasing daylengths (Høst 1942, Novikov and Blagodatskaia 1948). At the end of the breeding period, the comb size declines, and the male Willow Ptarmigan molts into a pigmented *summer plumage*. This may often be initiated even before the breeding plumage is completed, and the remaining feathers from the winter and breeding plumages are replaced by bright yellowish and brown feathers with black bars. In August, the *fall plumage* develops with dark brown and black feathers. In the female, the pigmented plumage starts to develop a little later than in the male, and the feather replacement is not as sequential. Her garb is very much like that of the male's summer plumage and is completed at the time of breeding. Except for the breeding plumage therefore, the plumage changes are the same in the male and female Willow Ptarmigan.

Høst (1942) suggested that the development of the breeding plumage of the male is stimulated by hormones secreted by the growing testes, while Nowikow (1939) reported that castrated male Willow Ptarmigan developed normal breeding plumage in the spring. Stokkan (1979), however, showed that artificially photostimulated castrates molted slowly into a summer plumage. In both studies comb growth did not occur in photostimulated castrates. Stokkan (1979) showed that testosterone injections given to photostimulated castrates caused comb growth and the devel-

opment of breeding plumage. Testosterone injections given to castrates or intact males on short days also stimulated comb growth and pigment production in feathers growing after plucking, but did not stimulate molt.

In the present study, I have investigated the possibility that the development of pigmented plumage or comb growth may be independent of increased daylengths and/or testicular function. I also investigated the apparent contradiction between Nowikow (1939) and Stokkan (1979) by describing the plumage changes in castrated and intact males exposed to spring-like increases in daylength.

Methods

Willow Ptarmigan were hatched from machine-incubated eggs laid by captive females at the Wildlife Research Station, University of Tromsø. After hatching, the chicks were raised outdoors in groups. From about the age of 5 months, the birds were individually caged indoors under daylength conditions closely synchronized to the changes outside (Tromsø, 69°N).

A group of five males, aged 14 months, was castrated in August. From November until the end of June, they were kept on a constant light regimen of 6L:18D together with four intact controls. Another group of 5 males, aged 19 months was castrated in December, and, together with 9 intact controls, was exposed to increasing daylengths synchronized to changes outside throughout spring.

To prevent extraneous light from entering during the short-day period, the photoperiodic rooms were built inside another room, where the daylength was fixed at 6 h. Castration was carried out with the birds under Equithesin anesthesia by bilateral laparotomy between the last two ribs, the testes being removed intact using a pair of fine forceps. About every 2 weeks from December onward, the plumage of the head and back of each bird was inspected and the percent pigmentation was subjectively assessed. At the same time the comb height was measured to the nearest 0.5 mm. At the end of June, all the birds were killed. The length and width of the left testis were measured in the intact birds, and the castrates were inspected for remaining testicular tissue.

A further group of 7 intact males was kept on permanent short days (6L:18D) from December, and they remained on this light regimen for 19 months. About every month from May onward, the plumage was inspected and the height of the comb was measured. The testicular sizes, however, were not measured on these birds.

Results

Both intact and castrated birds exposed to a spring-like increase in daylength began to grow pigmented feathers in late February (Fig. 1A). The molt proceeded at the same rate in both groups up to the end of March. Thereafter, intact birds molted faster than the castrates. By the end of June, the heads and backs of intact birds were 100% pigmented, while the castrated birds were still 60% white. Thus, the intact birds had completed the breeding plumage while the castrates were still molting. There was also a striking difference between the type of pigmented plumage developed by the two groups. The intact birds developed a breeding plumage, with fully pigmented head and a speckly pigmented back. During late May, they began to develop summer plumage, replacing the breeding plumage and the remaining white feathers of the winter plumage. The castrated males, on the other hand, began directly to develop a summer-like plumage in February. It was a light brown, heavily barred plumage, lacking the band of dark feathers across the crop region that is characteristic of the breeding plumage.

The comb size of intact birds increased from 10.6 mm (±0.2 SE) on 25 February, to 15.6 mm (±0.4 SE, $n = 9$) on 18 May. Thereafter, the comb size stayed constant for a month, and then it decreased during June (Fig. 2A). The castrated males, on the other hand, did not show any increase in comb size but had combs less than 10 mm during the whole period (Fig. 2).

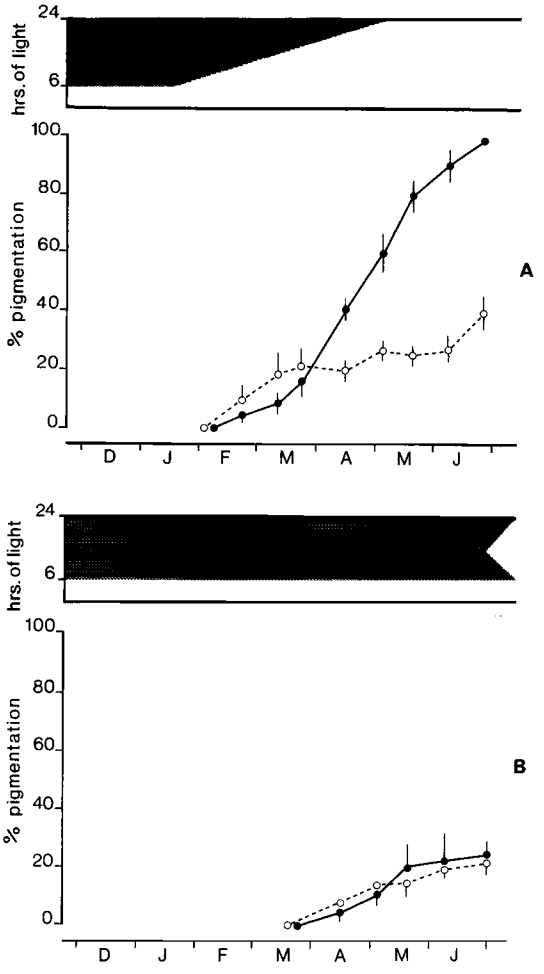

Fig. 1. Percent of head and back appearing pigmented in intact (● ——, n = 9) and castrated (o ----, n = 5) male Willow Ptarmigan experiencing spring-like increase in daylength (**A**), and intact (● ——, n = 4) and castrated (o ---, n = 5) male Willow Ptarmigan exposed to permanent short (6 h) daylengths (**B**). Vertical bars indicate one standard error of the mean (SE).

Birds kept on permanent short days throughout spring did not start to molt until the beginning of April. The molt proceeded slowly but at the same rate in both castrated and intact birds (Fig. 1B). The growing pigmented feathers were first scattered evenly over the head and later on the back, and they had an unusual mixture of dark grey, dark brown, and black pigmentation. They lacked the distinctive barred patterns of normal summer plumage and were more like the dark feathers in the crop region of the breeding plumage. By the end of June, the plumage of castrated and intact birds was indistinguishable, and about 20% of the feathers of the head and back were pigmented. The feathers of the head and back were continually molting, and about one third of the replacement feathers had the odd pigmentation described above; the remainder were white. The comb size in intact males on permanent short days was variable (Fig. 2B), and no significant growth

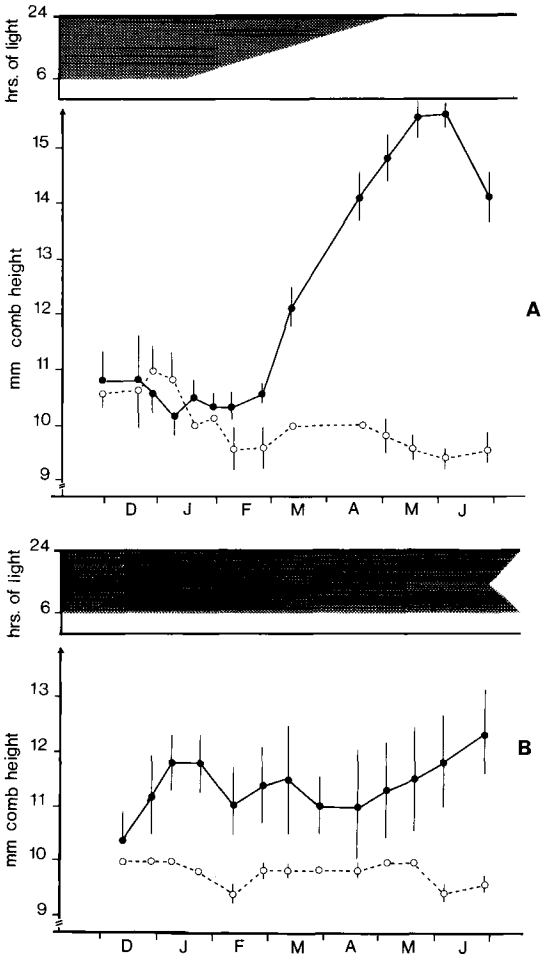

Fig. 2. Comb height in intact (● ——, n = 9) and castrated (○ ----, n = 5) male Willow Ptarmigan experiencing spring-like increase in daylenth (**A**), and intact (● ——, n = 4) and castrated (○ ----, n = 5) male Willow Ptarmigan exposed to permanent short (6 h) daylengths (**B**). Vertical bars indicate one standard error of the mean (SE).

occurred during March and April. Castrated males on permanent short days had comb sizes below 10 mm throughout the whole period.

Autopsy of the castrated birds at the end of June revealed no remaining testicular tissue. In intact controls that had experienced increasing daylengths, the length and width of the left testis were 12.7 mm (±0.7 SE) and 8.3 mm (±0.3, n = 9), while the corresponding values in intact birds on short days were 7.0 mm (±0.6) and 4.3 mm (±0.1, n = 4).

From July and throughout the next 12 months, the 7 males who remained on permanent short days had about 30% (27.3% ± 2.0 SE) pigmented heads and backs, with the pigments of the dark, "short-day" type described above. They had an average comb height of 11.3 mm (±0.2), and they never appeared to enter breeding condition.

DISCUSSION

In some avian species, molt is stimulated by castration and inhibited by injections of gonadal steroids, indicating that gonadal activity normally inhibits the processes of molt. In other species, however, molt occurs while the gonads are active (Payne 1972). The role of gonadal hormones in the control of molt is thus difficult to understand, particularly in species like the Willow Ptarmigan, in which the prebreeding molt occurs when the testes are enlarging and the postbreeding molt occurs when the testes are regressing.

The present observations did not confirm those of Nowikow (1939), who thought that castrates could develop breeding plumage in the spring. His results could be due to incomplete castration, as partially castrated male Willow Ptarmigan can develop normal breeding plumage (Stokkan unpubl. data).

Høst (1942) suggested that the development of the breeding plumage is dependent on reproductive hormones or on some other factors controlled by increasing daylengths. The former suggestion is supported by our observations (Stokkan and Sharp 1979) that the rapid growth of the comb and the development of breeding plumage in the spring begins when the levels of plasma testosterone and luteinizing hormone are increasing. The presence of testes appears to accelerate the rate of molt into breeding plumage in intact birds relative to the molt into summer plumage in castrates (Fig. 1A). The action of testicular hormones on molt during this period is difficult to assess, however, because plasma levels of testosterone are depressed for a brief period in intact birds on normal days, at the time when the back is molting.

The present study, together with that of Stokkan (1979), shows that both the development of breeding plumage and comb growth are dependent on testicular hormones. Because the growth of the testes in the spring is dependent on increased daylengths, the development of breeding plumage and comb growth are indirectly related to the daylength. The observation that castrated birds exposed to long or short daylengths grew pigmented feathers shows that the stimulation of pigmentation and molt *per se* is not dependent on testicular hormones or daylength. The timing of the onset of molt was independent of testicular activity, as it began at the same time in both castrated and intact birds, but was dependent on daylength, as birds on permanent short days began to molt later than birds exposed to increasing daylengths. The type and pattern of pigmentation, however, are determined by both daylength and testicular hormones.

Thus, it seems that in the male Willow Ptarmigan at least three hormonal systems are involved in controlling the growth of pigmented feathers. The stimulation of molt and pigmentation *per se* must be of endogenous origin, or controlled by environmental cues other than the daylength. Increased daylength stimulates the formation of the pigmented summer plumage in castrated males, as in the female, whereas in the intact male, testicular hormones stimulate the development of a breeding plumage. What controls the formation of pigmented plumages outside the breeding season or stimulates molt and pigmentation on short days still remains unknown.

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