

## TESTIS MASS AND SUBADULT PLUMAGE IN BLACK-HEADED GROSBEAKS<sup>1</sup>

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**Abstract.** Like males of approximately 30 other species of North American passerines, male Black-headed Grosbeaks (*Pheucticus melanocephalus*) do not attain complete definitive alternate plumage until their second breeding season. I collected yearling and adult male Black-headed Grosbeaks in the Rio Grande valley in central New Mexico to test the hypothesis that delayed plumage maturation in Black-headed Grosbeaks is one manifestation of a general, hormonally-mediated developmental pattern. I compared the mass of testes to the degree of plumage maturation in eleven yearling males and found a significant positive correlation. Moreover, the mean testis mass of yearling males was significantly lower than the mean testis mass of older males. In contrast, I found no significant relationship between plumage brightness and testis mass among seven adult males in definitive alternate plumage. These observations support the idea that delayed plumage maturation in Black-headed Grosbeaks is part of a general delay in investment in first-year reproduction.

**Key Words:** *Delayed plumage maturation; hormones; life history; plumage color; Pheucticus melanocephalus.*

### INTRODUCTION

Males of most species of temperate passerine birds attain a definitive alternate plumage in the first spring after their birth and attempt to breed. In approximately 31 species of sexually dichromatic North American passerines, however, males fail to attain a complete definitive alternate plumage in their first breeding season and may or may not attempt to breed (Rohwer et al. 1980, Rohwer and Butcher 1988). In species with such delayed plumage maturation, the extent to which yearling males develop definitive plumage is variable, with some individuals achieving a more adult-male-like appearance than others (e.g., Flood 1984, Hill 1988a, Enstrom 1992). Moreover, whether or not subadult males attempt to breed is often related to the degree of plumage maturation that they display—yearlings with a more adult-male-like appearance are generally more likely to breed than those with a more female/juvenile appearance (Flood 1984; Hill 1988a, 1988b; Butcher and Rohwer 1989). Thus, the patterns of reproductive behavior and plumage development are linked in many species.

Numerous studies have addressed the adaptive function of subadult plumage in the breeding

season, and, in recent years, a growing number of studies have also begun to focus both on non-breeding functions and constraints to producing ornamental plumage (Rohwer and Butcher 1988, Butcher and Rohwer 1989, Zack and Stutchbury 1992). Despite the effort that has been devoted to understanding delayed plumage maturation, however, there is still no consensus on why this developmental pattern evolved and is maintained (Thompson 1991, Zack and Stutchbury 1992) or much data on the proximate factors that determine the extent of plumage development in yearling males.

Black-headed Grosbeaks (*Pheucticus melanocephalus*) are typical of temperate passerines that show delayed plumage maturation. They are sexually dichromatic with ASY (after second year: in a second or later breeding season) males displaying a complex, brightly colored nuptial plumage and with females having a much drabber streaked brown plumage (see Hill 1987 for a detailed description of plumage). Yearling male Black-headed Grosbeaks are intermediate in appearance between females and ASY males but highly variable: a few nearly resemble females, showing only a few features of male definitive-alternate plumage; a few look much like ASY males, showing only a few features of female/juvenile plumage; most show a more balanced mix of ASY male and female/juvenile characteristics (Hill 1988a). Previous research has shown

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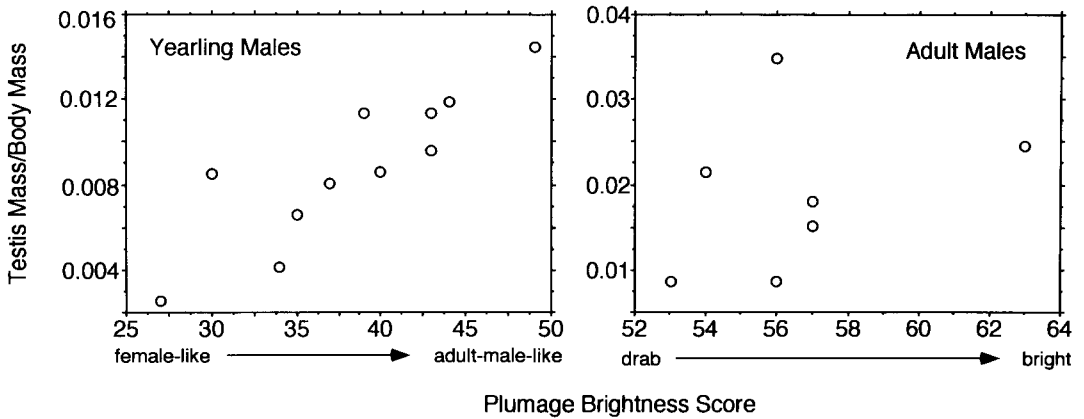


FIGURE 1. The relationship between plumage brightness and testis mass corrected for body mass. Plumage brightness of yearling males reflects extent of first prealternate molt. Plumage brightness of ASY males reflects brightness of orange and yellow ventral plumage.

that most yearling male grosbeaks forego breeding and that only those yearlings with adult-male-like plumage defend territories and attempt to breed (Hill 1988a, 1988b, 1989). The purpose of the present study was to test the idea that degree of plumage development is related to the degree of testes development and thus to test the hypothesis that there is a proximate (hormonal) mechanism for the association between breeding behavior and plumage coloration in subadult males.

#### METHODS AND RESULTS

I collected seven adult and 11 subadult male Black-headed Grosbeaks (*Pheucticus melanocephalus*) along the Rio Grande in the vicinity of Los Lunas, New Mexico in May and June 1985. For each bird that I collected, I scored the plumage brightness as outlined in Hill (1987, 1988a). For 16 plumage regions I assigned a score of 0 (dullest/most female-like) to 3 (brightest/most adult-male-like). The 16 scores were then summed to give an estimate of overall plumage brightness that ranged from 0 to 48 (see Hill 1987, 1988a for details). Immediately after being collected the birds were weighed to the nearest 0.1 g, and within a few hours after they were collected, the birds were dissected and both their right and left testes were removed and weighed to the nearest 0.01 g.

To see if there was a relationship between the plumage development and testis development in

yearling Black-headed Grosbeaks, I compared the plumage score and testis mass of the 11 SY males. To correct for the potential confounding effects of body size, I used testis mass divided by body mass in the comparison. I found a significant positive correlation ( $r_s = 0.91$ ,  $n = 11$ ,  $P = 0.004$ , Fig. 1)—yearling males with brighter plumage (i.e., more extensive definitive alternate plumage) tended to have larger testes.

All ASY male Black-headed Grosbeaks display definitive alternate plumage and thus show the same pattern of nuptial plumage, but they vary substantially in plumage brightness (intensity of ventral orange and yellow) (Hill 1987, 1988a). Therefore, I also compared the plumage brightness and testis mass of adult males. I found no significant relationship between the plumage brightness of ASY males and testis size ( $r_s = 0.40$ ,  $n = 7$ ,  $P = 0.33$ , Fig. 1). The small number of males on which this last comparison was based made the power of the test weak and the chance of detecting a significant relationship low.

Grosbeaks were collected over a 32-day interval during the peak period of nesting. To test for the potential effects of season on testis size, I compared testis mass and collecting date for both ASY and yearling males. There was no significant relationship between collecting date and testis size for either ASY ( $r_s = -0.33$ ,  $n = 7$ ,  $P = 0.42$ ) or yearling ( $r_s = 0.02$ ,  $n = 11$ ,  $P = 0.93$ ) males. I also compared the testis mass of subadult and ASY males, again correcting for body size. Adult males had significantly heavier testes than year-

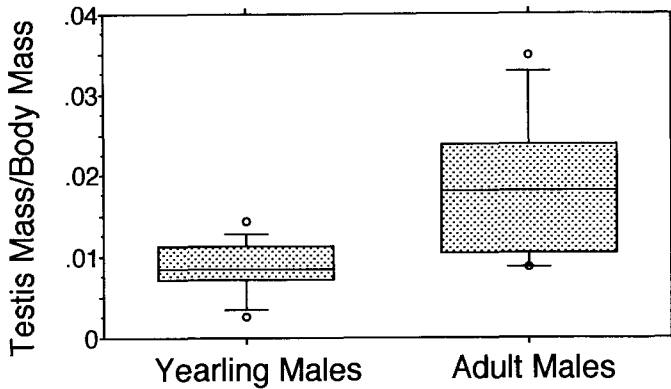


FIGURE 2. Testis mass of yearling ( $n = 11$ ) and ASY ( $n = 7$ ) male Black-headed Grosbeaks. Box plots illustrate 10th, 25th, 50th, 75th and 90th percentiles with horizontal lines and show all data points outside this range.

lings ( $U = 67$ ,  $n = 11$ ,  $7$ ,  $P = 0.01$ , two-tailed Mann-Whitney  $U$  Test; Fig. 2).

## DISCUSSION

This is the first report linking extent of yearling male plumage development to testis mass in a species with delayed plumage maturation. Møller and Erritzøe (1988) found a similar positive relationship between testis volume and the size of the black throat patch in House Sparrows (*Passer domesticus*), a species in which yearling males are on average less well ornamented than adults but lack a distinctive subadult plumage. Observations presented in this paper as well as previously published studies of Black-headed Grosbeaks support the idea that delayed plumage maturation is part of a general reproductive strategy in which many features of breeding—testes size, pre-alternate molt, timing of migration, aggressiveness, song output, etc.—are reduced in yearling males (Hill 1988a, 1988b, 1989). Such a simultaneous depression of multiple traits that function in reproduction suggests some common, controlling mechanism that may simultaneously depress all of these morphological and behavioral traits.

Most of the behavioral and morphological traits associated with reduced reproductive effort in yearling male grosbeaks appear to be under hormonal control (Murton and Westwood 1977). Testis growth is primarily under control of gonadotropic hormones (Murton and Westwood 1977, Payne 1972, Morton et al. 1990). In turn, Leydig cells of the testis produce androgens that

stimulate the development of additional structures and behaviors related to reproduction (Eisner 1960, Murton and Westwood 1977). The endocrinological control of molt is less clear. In at least one tropical species, molt is stimulated by testosterone: subadult male Satin Bowerbirds (*Ptilonorhynchus violaceus*) implanted with testosterone produced definitive plumage years before untreated males in the same age cohort (Collis and Borgia 1992). Yearling male Black-headed Grosbeaks derive their female/juvenile plumage characteristics from the retention of first basic feathers, not by molting drab feathers during their first pre-alternate molt (unpubl. data). Thus, it is the extent of the first pre-alternate molt that determines the degree to which yearlings attain definitive plumage. For temperate bird species, fall molt seems generally to be stimulated by thyroxin and inhibited by androgens such as testosterone (Payne 1972). In the spring, androgens likely do not inhibit molt but it is unclear whether or not they might directly or indirectly stimulate molt (Payne 1972). As stressed by Murton and Westwood (1977:183) “. . . moult requires synergism and hence appropriate phasing of several hormones.” Thus, although details of the mechanism remain to be worked out and may vary among species, it seems quite reasonable that through hormone releases yearling males might coordinate expression of reproductive behaviors and structures. In this way, males that invest more in first-year reproduction produce larger testes, grow more adult-male-like plumage and are aggressive, while those males that invest less produce smaller testes, retain a female-like

appearance, and show reduced aggressiveness. Such hormonal control might be simultaneous, so that yearling males arrive on the breeding grounds with an aggression level that matches their plumage, or it might be offset. In the latter case, a bird's appearance would affect how other birds reacted to it, which could affect hormonal release and hence behavior. Either way, hormones would coordinate behavior and appearance.

This explanation for delayed plumage maturation provides a mechanism for the cryptic hypothesis (Procter-Gray and Holmes 1981, Studd and Robertson 1985), one of the prominent hypotheses that has been proposed to explain delayed plumage maturation. Under the cryptic hypothesis, reproductive opportunities for yearling males are assumed to be limited, so yearling males benefit by reducing their investment in first-year reproduction, thereby increasing their survivorship. Here, I emphasize that a common hormonal mechanism might both depress and coordinate expression of a number of features that affect the cost of first-year reproduction and that subadult plumage is simply the most conspicuous of these features. This echoes a recent paper by Ketterson and Nolan (1992) that emphasized the controlling and coordinating effects of hormones on diverse suites of morphological and behavioral characters.

The idea that delayed plumage maturation might be symptomatic of a more general, hormonally mediated developmental pattern is not new. Long before the function and evolution of delayed plumage maturation became a focal point for behavioral and evolutionary research, three studies proposed a link between hormone levels and plumage development. Wright and Wright (1944) found that the testes of subadult Red-winged Blackbirds (*Agelaius phoeniceus*) mature later and were only about two-thirds the size of the testes of ASY males. The Wrights further suggested that this reduction in testes size was related to the subadult plumage displayed by yearlings. Miller (1933) suggested that the variability in the plumage of yearling Phainopeplas (*Phainopepla nitens*) was directly related to variation in circulating testicular hormone during molt. Finally, Ficken and Ficken (1967) formally developed a hypothesis linking testosterone, plumage development, and reproductive behavior in subadult male American Redstarts (*Setophaga ruticilla*). Rather than proposing an

adaptive function for subadult plumage per se, the Fickens proposed that it was advantageous for yearling males to reduce their overall reproductive effort in their first year. The physiological mechanism by which the birds accomplished this was depression of levels of hormones that simultaneously inhibited molt, reduced aggressiveness, changed migratory patterns, and generally reduced the structures and behaviors associated with breeding. The Fickens presented no data on gonad size in redstarts, but they cited the studies by Miller and the Wrights, and clearly they expected reduced testis volume to be one of the effects of decreased first-year reproductive investment. Recent papers searching for a functional explanation for the delayed plumage maturation have generally overlooked these early ideas about hormonal control. For instance, Foster (1987) reported reduced testis size of SY males compared to ASY males in Long-tailed Manakins (*Chiroxiphia linearis*) but not Swallow-tailed Manakins (*C. caudata*), but she did not consider the underlying hormonal mechanisms that might produce such a pattern. However, Foster (1987) as well as Lawton and Lawton (1986) did discuss the phenomenon of delayed plumage maturation in the context of heterochrony, with the clear implication that such a developmental pattern would be hormonally mediated.

Finally, the cost of bright plumage has long been assumed to be increased risk of predation (Darwin 1871, Lack 1954), but there is virtually no evidence to support this assumption (see Götmark 1992 for a review). Recently, another cost to displaying bright plumage has been proposed. Ligon et al. (1990) and Foldstad and Karter (1992) pointed out that expression of many ornamental traits is closely linked to levels of circulating testosterone and that elevated levels of testosterone are known to suppress immune response in vertebrates. They proposed that this link between testosterone, ornament expression, and immune response provides a mechanism by which ornamental traits signal individual quality. Only robust, high quality individuals would be able to maintain both their health and the high levels of testosterone needed for maximum ornament expression. Although the role of testosterone in display of bright plumage in species such as the Black-headed Grosbeak is still unclear, it is interesting to speculate trade-offs between hormone levels, immune response, and plumage brightness might affect costs and promote de-

layed investment in reproduction, including delayed plumage maturation.

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