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Plumage Coloration and Reproductive Success in Male Chestnut-sided Warblers

David I. King,[1,3] Richard M. DeGraaf,[1] and Curtice R. Griffin[2]

ABSTRACT.—We studied Chestnut-sided Warblers (*Dendroica pensylvanica*) to determine whether there exists any relationship between plumage coloration and reproductive success in this species. We observed that males with more extensive chestnut breast coloration initiated nests significantly earlier than males with less chestnut, and had marginally larger clutch sizes as well. However, there was no significant relationship between the number of young fledged or the condition of the young and the extent of chestnut breast coloration, nor were there any significant relationships between any of these measures of reproductive success and the extent of yellow crown coloration. The extent of chestnut coloration on the breast was significantly less for males in their first breeding season, suggesting that the relationships between the extent of breast coloration and reproductive success may reflect age specific differences in these parameters. *Received 6 Sep. 2000, accepted 20 Aug. 2001.*

Numerous hypotheses have been developed regarding the evolution of bright or conspicuous plumage in birds (Savalli 1995). Plumage characteristics may affect fitness by affecting the attractiveness of an individual to prospective mates (Darwin 1871, Fisher 1930,

[1] U.S.D.A. Forest Service Northeastern Research Station, Univ. of Massachusetts, Amherst, MA 01003 USA.

[2] Dept. of Natural Resources Conservation, Univ. of Massachusetts, Amherst, MA 01003 USA.

[3] Corresponding author; E-mail: dking@fs.fed.us

Andersson 1982) or their success in contests with conspecifics over resources (Rohwer 1982, Studd and Robertson 1985). Intraspecific variation in male plumage brightness may be the result of balancing selection between the advantages of bright plumage (e.g., attracting mates, dominating competitors) and disadvantages of bright plumage (e.g., susceptibility to predation; Rappole 1983). Alternatively, intraspecific variation in male plumage characteristics may be partially attributable to delayed plumage maturation (Rohwer et al. 1980, Thompson 1991).

Chestnut-sided Warblers (*Dendroica pensylvanica*) exhibit extensive variation in plumage characteristics, particularly in the extent of the chestnut patches on their breasts and in the amount of yellow in the crown, and subadult individuals generally have less extensive coloration that adults (Richardson and Brauning 1995). We studied Chestnut-sided Warblers to evaluate whether plumage coloration is associated with reproductive success, and thus potentially fitness, and whether variation in plumage characteristics and reproductive success were potentially attributable to delayed plumage maturation.

STUDY AREA AND METHODS

We studied Chestnut-sided Warblers from May to August, 1996–1998, at three sites in the White Mountains of New Hampshire (44° 03′ N, 71° 15′ W). Chestnut-sided Warblers were captured with mist nets and marked with a unique combination of colored leg bands. The extent of breast and crown coloration were measured in the field using a 25 dot/cm^2 grid by holding the bird with head and body in a natural posture, holding the grid over the patch of color and counting the number of dots within the color patch. Three measurements of each color patch were made and the means used in the analyses. We aged as many individuals as possible using the shape of the outer rectrices. In general, birds in their first breeding season (SY) have rectrices that are noticeably pointed and worn, and birds in their second or later breeding season (ASY) have relatively blunt rectrices with little wear (Pyle et al. 1987). Each bird was measured only once during the study.

The following variables were used as measures of Chestnut-sided Warbler reproductive success: nest initiation date, clutch size (first clutches only), the number of young fledged by a pair over the course of the breeding season, and the condition of the young at fledging. We included nest initiation date as a measure of reproductive success because later nesting likely is associated with lower nestling recruitment, and allows less time for the laying of replacement clutches (Verhulst et al. 1995). We used only first clutches in these comparisons to provide a measure of adult fitness while avoiding the potentially confounding effects of replacement clutches, which are significantly smaller than first attempts at our sites ($Z = 3.96$, $P < 0.001$, $n = 117$). Nests were located by following adults carrying nesting material or food. For nests found with a full clutch, initiation dates were calculated by back dating. On the eighth day after hatching, nestlings were weighed to the nearest 0.1 g with a spring balance, and wing chord was measured to the nearest 0.1 cm with a vernier caliper. Nestling condition for each chick was calculated by dividing body mass by the cube of the wing chord (Searcy 1979), and mean condition measurements were used in the analyses.

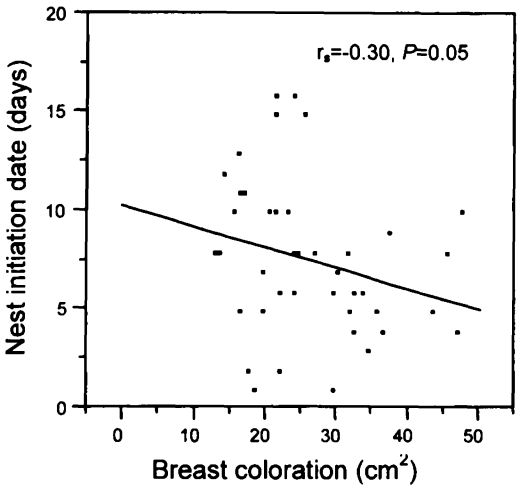

FIG. 1. Correlation of nest initiation date with extent of breast coloration of male Chestnut-sided Warblers in the White Mountains, New Hampshire, 1996–1998.

There were no significant differences in plumage measurements or reproductive parameters among years (Kruskal-Wallis tests, $P > 0.10$), so we combined data among years for analyses. We analyzed the relationship between reproductive success and plumage patch size using Spearman rank correlation, and tested for age-related differences in the extent of plumage coloration and reproductive parameters using median tests.

RESULTS

We collected both plumage characteristics and reproductive data for 46 male Chestnut-sided Warblers. Nest initiation date was negatively correlated with the extent of male chestnut coloration ($r_s = -0.30$, $P = 0.05$, $n = 43$; Fig. 1), indicating that males with more extensive patches of chestnut coloration initiated nests significantly earlier than males

TABLE 1. Comparisons of mean (SE) plumage characteristics and reproductive parameters between ASY and SY Chestnut-sided Warblers in the White Mountains, New Hampshire, 1996–1998.

	ASY	SY	Z[a]	P	n
Breast color extent[b]	1.24 (0.08)	0.80 (0.08)	3.98	<0.001	42
Crown color extent[b]	0.87 (0.03)	0.87 (0.02)	0.02	0.99	40
Nest initiation[c]	5.83 (1.14)	7.82 (0.96)	2.07	0.04	29
Clutch size	3.90 (0.13)	3.88 (0.10)	0.21	0.83	28
Number fledged	3.42 (0.54)	3.41 (0.49)	0.77	0.44	31
Nestling condition[d]	2.62 (0.42)	2.64 (0.30)	0.00	1.00	12

[a] Normal approximation of the median test.
[b] cm^2.
[c] Number of days after the first nest initiation within the population.
[d] (Body mass)/(wing chord)$^{1/3}$.

with less chestnut coloration. Clutch size was marginally positively related to the extent of male chestnut coloration ($r_s = 0.28$, $P = 0.07$, $n = 42$); however, there were no significant relationships between the extent of male chestnut coloration and the number of young fledged ($r_s = -0.17$, $P = 0.38$, $n = 42$) or the condition of the young ($r_s = -0.05$, $P = 0.74$, $n = 13$). There were no significant relationships between the extent of male yellow crown coloration and nest initiation date ($r_s = 0.07$, $P = 0.63$, $n = 32$), clutch size ($r_s = -0.05$, $P = 0.74$, $n = 40$), young fledged ($r_s = 0.09$, $P = 0.58$, $n = 42$) or fledgling condition ($r_s = 0.08$, $P = 0.79$, $n = 13$). ASY males had significantly more chestnut coloration than did SY males, and initiated nests significantly earlier (Table 1). There were no significant differences between ASY and SY males in crown coloration, clutch size, fledging success, or fledgling condition (Table 1).

DISCUSSION

Our observation that males with pointed rectrices had significantly less chestnut coloration is consistent with the view that differences in the extent of plumage coloration in Chestnut-sided Warblers are associated with age (Richardson and Brauning 1995). Our finding that less colorful, younger Chestnut-sided Warblers fledged similar numbers of young as more colorful, older individuals is similar to other studies of the relationship between age, plumage characteristics, and reproductive success. Proctor-Gray and Holmes (1981) reported that SY male American Redstarts (*Setophaga ruttacilla*), which have less black coloration than older males, achieved reproductive success similar to ASY males. Similarly, Flood (1984) reported that SY male Baltimore Orioles (*Icterus galbula*), which have less extensive orange coloration than older males, achieved reproductive success similar to ASY males. The finding that younger, less colorful males are able to achieve reproductive success similar to older, more colorful males contradicts the view that the less colorful plumage often characteristic of younger individuals is associated with a delay of full reproductive output until after the first breeding season (Selander 1965).

Our finding that SY Chestnut-sided Warblers initiated nesting later in the season than ASY birds is consistent with Flood's (1984) finding that SY male Baltimore Orioles initiated breeding later than ASY males. Breeding later in the season may enable SY males to avoid conflicts with ASY males during the period of intense intrasexual competition during the early portion of the nesting season, conflicts which could subject them to unnecessary risk of injury, and which as subadults they would likely lose anyhow (Hill 1988).

Information on aggression from conspecifics as a function of plumage coloration would be a valuable supplement to our analyses. Flood (1984) reported that older male orioles attacked stuffed mounts with less extensive orange less often than mounts with more orange, and hypothesized that the duller plumage of SY males was advantageous because it served to reduce aggression from older males. In contrast, Proctor-Gray and Holmes (1981) found no evidence that duller plumage in American Redstarts reduced aggression from older males, and concluded instead that duller SY plumage was associated with lower predation. Also, extrapair fertilizations may sub-

stantially increase the fitness of an individual (Yezerinac et al. 1995), and often occur at the expense of the paternity of SY males (Morton et al. 1990). Thus, the inclusion of data on paternity of ASY and SY males also would be helpful in further elucidating the significance of plumage variation in Chestnut-sided Warblers.

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