

DOES LONGEVITY INFLUENCE THE EVOLUTION OF DELAYED PLUMAGE MATURATION IN PASSERINE BIRDS?

Recently, Studd and Robertson (1985) used Wittenberger's (1979) model for the evolution of delayed breeding as the basis for a new model of the relation between longevity and the cost of breeding by subadult male passerine birds. From this new model they proposed a multiple-factor breeding-threshold hypothesis (BTH) to explain the general pattern of delayed plumage maturation (DPM) in North American passerine birds. They suggested that, everything else being equal, longer-lived species should be more likely than short-lived ones to delay the maturation of their plumage.

In passerine birds, DPM is evidenced by a distinctive, dull subadult male plumage in the first potential breeding season. In many nonpasserine birds, the subadult male plumage is retained into the first one-to-several breeding seasons, but these subadult males do not attempt to breed (Lack 1968). Because, in passerine birds, subadult males in dull plumage often attempt to breed, DPM is of particular interest in this taxon. Several hypotheses have been proposed to explain DPM in passerines (Selander 1965; Rohwer, Fretwell, and Niles 1980; Procter-Gray and Holmes 1981; Rohwer, Klein, and Heard 1983; Lyon and Montgomerie 1986), each suggesting a different proximate function for the distinctive subadult plumage (see Lyon and Montgomerie 1986).

The BTH is a new kind of hypothesis about DPM because it focuses on a life history characteristic that might favor DPM rather than suggesting a proximate function for the dull subadult male plumage. Previous hypotheses about DPM have assumed that there is intense competition among males for mates and that the relative costs and benefits of such competition determine the adaptive value of DPM (Rohwer, Fretwell, and Niles 1980; Procter-Gray and Holmes 1981; see also Lyon and Montgomerie 1986). Unlike other hypotheses, the BTH suggests that the expected life span of males interacts with these costs and benefits of competition to determine whether a facultative delay in breeding will be adaptive. Life span is thought to be important because any delay in breeding is relatively less costly for longer-lived species with respect to their lifetime reproductive success. Thus, in short-lived species, more-intense intermale competition for mates would be needed to favor DPM.

To test the BTH, Studd and Robertson focused specifically on the analysis of longevity patterns in North American passerines and made the following predictions: (1) species with DPM should have a longer potential life span than those without, and (2) species with short potential life spans should require more-

intense male-male competition to favor the evolution of DPM than would species with longer life spans. They tested these predictions indirectly using wing length as an index of longevity (following Lindstedt and Calder 1976) because few data on longevity were available. For their analysis they used only those 68 North American passerine bird species classified by Rohwer et al. (1980) as strongly sexually dichromatic. This group of species is commonly used in analyses of DPM because it includes almost all cases of distinctly dull subadult male plumage among the North American passerines.

Studd and Robertson found that species with DPM had, on the average, longer wings than those without, and among species with DPM, dull subadult males in smaller species tended to be more femalelike. They concluded that both life span and competition are important factors influencing the evolution of DPM in passerine birds. Competition among males for reproductive opportunities has previously been implicated as an important factor in the evolution of DPM (Selander 1965, 1972; Rohwer, Fretwell, and Niles 1980; Procter-Gray and Holmes 1981); the novel contribution of the Studd-Robertson model and analysis is thus to focus attention on the influence of longevity.

Although Studd and Robertson (1985) have clearly demonstrated some correlations between wing length and DPM, these patterns can be better explained by a new hypothesis about the proximate function of DPM, the status-signaling hypothesis (SSH; Lyon and Montgomerie 1986). This hypothesis suggests that a distinctive subadult male plumage is a reliable signal of subordination, allowing young males to settle near adult males in nesting areas or mating flocks, where their presence is not threatening to the mating success of adults. We postulated that this situation would most likely obtain for type-B territorial systems, in which territorial males and their females forage mainly away from their territories (Nice 1941). In such situations, female choice would be based on male traits (like plumage color) rather than attributes of the territory. Thus, adult males would have little to lose from the presence of dull subadults nearby; territory quality should not be affected and females should be unwilling to mate with dull subadults if there are bright adults available. In contrast, for type-A systems, in which males defend all resources for breeding, female choice should be influenced by territory quality, and all males, irrespective of color, pose a threat to territorial males.

As predicted from the SSH, we found a strong correlation between DPM and the defense of type-B territories (Lyon and Montgomerie 1986); 88% (22 of 25) of species defending type-B territories exhibited DPM, whereas DPM occurred in only 33% (14 of 43) of species defending type-A territories. We also found that 7 of the 39 species originally classified by Rohwer, Fretwell, and Niles (1980) as lacking DPM (i.e., brown-headed cowbird, *Molothrus ater*; hepatic tanager, *Piranga flava*; house finch, *Carpodacus mexicanus*; red crossbill, *Loxia curvirostra*; white-winged crossbill, *Loxia leucoptera*; lesser goldfinch, *Carduelis psaltria*; and American goldfinch, *Carduelis tristis*) actually do have a distinctive subadult male plumage. We use this new information about the occurrence of DPM in the present analysis. Wing lengths were taken from sources listed by Studd and Robertson (1985).

The correlation between territory type and DPM can also explain the correla-

TABLE 1

LOGISTIC REGRESSION STATISTICS FOR THE EFFECTS OF (A) WING LENGTH AND TERRITORY TYPE AND (B) MAXIMUM LIFE SPAN AND TERRITORY TYPE ON THE PROBABILITY OF DELAYED PLUMAGE MATURATION

	Coefficient	Improvement	<i>P</i>	Goodness of Fit	<i>P</i>	<i>n</i>
A. Constant	0.63					
Territory	1.36	$\chi^2 = 21.4$	<0.001	$\chi^2 = 72.6$	0.27	68
Wing		$\chi^2 = 0.95$	0.33			
B. Constant	0.60					
Territory	1.24	$\chi^2 = 14.9$	<0.001	$\chi^2 = 49.3$	0.17	51
Longevity		$\chi^2 = 1.55$	0.21			

NOTE.—Wing length is used as an index of longevity. Tests are for the probability of the occurrence of DPM in strongly sexually dichromatic passerine birds. Regression coefficients estimate the effect of a single unit increase of each variable on the natural logarithm of the odds of a correct prediction. Improvement (χ^2) is used to test whether each variable provides an additional contribution to the model's ability to predict the pattern of occurrence of DPM. In this stepwise analysis, the variable with the highest *P*-to-enter value is entered into the model at each step. Coefficients are given only for those variables that significantly entered the model. The nonsignificant goodness-of-fit tests for these models indicate that the predicted values adequately fit the data (Hosmer tests, see Dixon 1983).

tion between wing length and DPM that Studd and Robertson suggested was due to longevity. The 25 species defending type-B territories have significantly longer wings than the 43 species defending type-A territories (Mann-Whitney $U = 312$, $P = 0.004$). Thus, the correlation between DPM and wing length may simply be due to the correlation between DPM and the type of territory defended. To determine whether territoriality or wing length (as an index of longevity) is the better predictor of DPM within these species, we performed a stepwise, logistic regression analysis with the presence or absence of DPM as the dependent variable. This technique is a categorical analogue to multiple regression (Fienberg 1981) that allows us to assess how a response variable (i.e., the occurrence of DPM) is affected by two or more explanatory variables (e.g., territory type and wing length). For this analysis we used the PLR procedure in BMDP (Dixon 1983), which permits explanatory variables to be either categorical (e.g., territory type) or continuous (e.g., wing length). The stepwise method that we used is analogous to stepwise multiple regression in that it allows us to select those independent variables that make statistically significant ($P < 0.05$) contributions to the model.

Only territory type significantly entered the linear-logistic regression model (table 1), and it makes a correct prediction for the occurrence of DPM in 75% of the cases ($n = 68$ species; see also Lyon and Montgomerie 1986). We conclude, therefore, that territory type significantly affects the probability of occurrence of DPM but longevity does not, when these two factors are considered together. This relationship between wing length and territoriality is expected because omnivores tend to be relatively large and usually defend type-B territories (Schoener 1968).

We can also perform a more direct test of the prediction that species with DPM live longer, by using recently available data on passerine longevity from banding records (Clapp et al. 1983; Klimkiewicz et al. 1983; Klimkiewicz, pers. comm.). Longevity data are available for 51 of the 68 species of strongly sexually di-

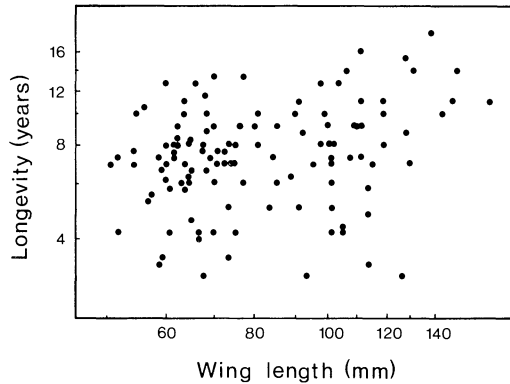


FIG. 1.—The relationship between maximum longevity and wing length for 78 species of passerine birds (longevity data from Klimkiewicz, pers. comm.). Both variables were log-transformed to help linearize the relationship. Wing length explains only 6.7% of the variation in maximum longevity ($r = 0.26$, $P = 0.02$).

chromatic passerines analyzed by Studd and Robertson. Although the BTH is based on the average expected life span, such data are not available for many species nor are they likely to be in the foreseeable future because birds have long life spans relative to the duration of most studies. The banding data are maximum life spans (i.e., the oldest recorded individual of each species) rather than average life spans, but across four orders of magnitude of body size, these two variables are strongly correlated ($r = 0.88$, $P < 0.01$, $n = 13$; data from Calder 1984, table 11-4). We assume, therefore, that maximum life span is a good predictor of average life span. Note, however, that such assumptions are particularly important to test further because trends that are clear over variation of several orders of magnitude may be relatively weak within a more restricted size range, such as that found within passerine birds. For example, though Studd and Robertson used wing length as an index of longevity, the relation between these variables is particularly weak within the passerine birds (fig. 1). Note also that Studd and Robertson (1985) implicitly used maximum rather than average life span in their analysis because they refer to the correlation between body size and maximum life span (Western and Ssemakula 1982) to support their claim that body size (i.e., wing length) is a reasonable index of longevity.

The banding data confirm that the maximum life span of species with DPM is, on the average, significantly longer than the life span of those without DPM (fig. 2; Mann-Whitney $U = 193$, $P = 0.02$, $n = 29, 22$). Although this prediction from the BTH is supported, the correlation between longevity and DPM can also be explained by the type of territory defended: type-B species are significantly longer-lived than type-A (Mann-Whitney $U = 211$, $P = 0.04$, $n = 22, 29$). To examine the relative influence of territoriality and longevity on DPM we again performed a stepwise, linear-logistic regression analysis and found that only territory type significantly entered the regression model (table 1). Thus, again, territory type is sufficient to explain much of the variation in DPM among these

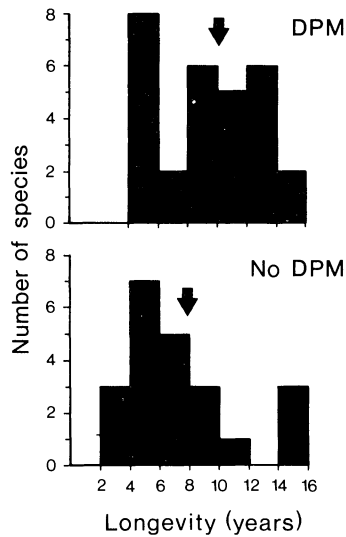


FIG. 2.—Maximum longevity of strongly sexually dichromatic passerine birds with ($n = 29$) and without ($n = 22$) delayed plumage maturation. Medians are indicated by arrows.

birds; the explanatory power of this statistical model is not significantly improved by the addition of longevity.

As further support for the BTH, Studd and Robertson also showed that wing length (again as an index of longevity) correlated significantly and negatively with the resemblance of subadult males to adult females. They argued that this was expected from the BTH because more-intense competition among males would be required to favor the evolution of DPM in species with relatively short potential life spans. Thus, in short-lived species with such intense male-male competition, subadult males would benefit from reduced aggression of adult males by more closely resembling females. Note, however, that the pattern described by Studd and Robertson is expected whenever there is a negative interspecific correlation between body size and the intensity of male-male competition, irrespective of longevity. It is important, therefore, to look directly at the relation between longevity and the resemblance of subadult males to females. Maximum longevity data are available for 24 of the 29 species with DPM, but the analysis does not support this prediction from the BTH; the correlation between maximum longevity and subadult-male-plumage score is not significant (fig. 3; Spearman rank correlation, $r_s = 0.15$, $P = 0.48$). Clearly some correlate of body size other than longevity (e.g., sex ratio or territory size) is responsible for the observed pattern.

Despite the apparent attractiveness of the BTH as an explanation for some of the observed patterns of DPM in passerine birds, there is little evidence that longer-lived birds in general are more likely to have a distinctive subadult male plumage, when everything else is equal. Thus, among passerine birds, which are relatively short-lived anyway, such ecological factors as reproductive competition

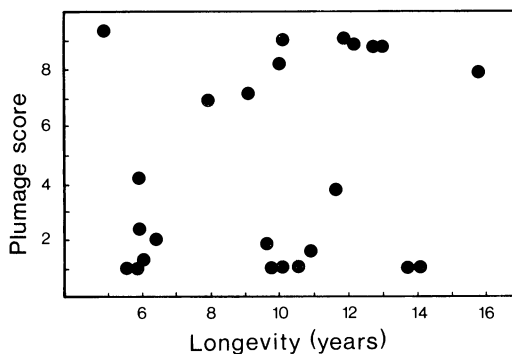


FIG. 3.—Relationship between plumage score and maximum longevity for subadult males in 24 passerine bird species with delayed plumage maturation. Plumage score of 0 is adult female and 10 is adult male.

may be more important in determining the optimal plumage for a bird in its first breeding season.

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