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The Condor 96:214–217

PTILOCHRONOLOGY: FOLLICLE HISTORY FAILS TO INFLUENCE GROWTH OF AN INDUCED FEATHER[1]

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Key words: Follicle history; habitat monitoring; House Sparrow; Passer domesticus; *ptilochronology.*

Ptilochronology uses the width of daily growth bars on a feather as an index of a bird's nutritional condition while the feather was being grown (e.g., Grubb 1989, Waite 1990, White et al. 1991, Hogstad 1992). The validity of this index has been supported by two manipulative studies employing, respectively, supplemental feeding (Grubb and Cimprich 1990) and food deprivation (Grubb 1991). See Grubb (1992) for a photograph of daily growth bars. Among other uses (Grubb 1989, in press), this index has considerable potential for monitoring habitat quality. For example, comparison of growth bar widths has indicated that Loggerhead Shrikes (*Lanius ludovicianus*) living in citrus groves were in poorer nutritional condition than conspecifics in three other habitat types in southern Florida (T. C. Grubb, Jr. and R. Yosef, unpubl. ms.). In any protocol for long-term monitoring of habitat quality, an appealing design feature would employ daily growth bar widths on successive feathers pulled from the same follicle, thus controlling for any inter-follicular variation in feather growth. However, before such a design could be employed, possible effects of follicle history and other factors on feather growth should be investigated. Here, we report on a controlled laboratory test of whether follicle history influenced the growth characteristics of a series of induced rectrices grown by House Sparrows (*Passer domesticus*). We arranged for various sparrows to grow a first, second, or third induced rectrix from the outermost right (R6) follicle of the tail at the same time that each of the birds grew a first induced rectrix from the outermost left (L6) follicle. We tested the prediction deduced from the null hypothesis that there should be no differences among the daily growth bar widths, total feather lengths, or total feather masses of first, second or third rectrices induced from the same follicle over a period of months.

METHODS

During October, we captured male House Sparrows in central Ohio and housed them individually in cuboidal wire-mesh cages 0.75 m on a side. From previous studies, we knew that cages this large were needed to minimize feather wear during long-term experiments. Our approved animal-holding facility at The Ohio State University, Columbus, Ohio, could only accommodate 12 such cages, so we replicated the experiment twice, during the winters of 1991–1992 and 1992–1993.

[1] Received 7 June 1993. Accepted 9 August 1993.

TABLE 1. General linear models for body mass and feather characteristics of captive House Sparrows (n = 22). The first number in each cell is the F statistic and the second number is the level of statistical significance. Regression degrees of freedom were 3 and 2 for influence of treatment group on body mass and feather characteristics, respectively. Error degrees of freedom were 83 for body mass and 17 for feather characteristics.

Characteristic	Covariate or factor			
	OL6	IL6	Year	Treatment group
Body mass (g)	–	–	7.01; 0.01	2.45; 0.07
First induced L6 rectrix				
Daily growth (mm)	0.11; 0.74	–	0.03; 0.86	0.30; 0.75
Total length (mm)	6.42; 0.02	–	0.05; 0.83	4.47; 0.03
Mass (mg)	6.98; 0.02	–	0.87; 0.36	1.08; 0.36
Induced R6 rectrix				
Daily growth (mm)	–	23.30; <0.001	1.16; 0.30	0.84; 0.45
Total length (mm)	–	11.36; 0.004	0.02; 0.89	0.81; 0.46
Mass (mg)	–	153.20; <0.001	0.87; 0.36	2.72; 0.09

Each year, the 12 sparrows were initially ranked by body mass from lightest (1) to heaviest (12). To minimize the possible effects of variation in body mass on feather growth, we randomly assigned each bird in each "trio" (1–3, 4–6, 7–9, and 10–12) to one of the three treatment groups. For the eight birds in group 1 (four birds each year), we pulled the original R6 and L6 rectrices on 1 November, and the first induced R6 and L6 rectrices on 21 December after these replacement feathers were fully grown. For the eight birds in group 2, we pulled the original R6 on 1 November, the first induced R6 and original L6 on 21 December, and the second induced R6 and first induced L6 on 13 February. Finally, for the eight birds in group 3, we pulled the original R6 on 1 November, the first induced R6 on 21 December, the second induced R6 and original L6 on 13 February, and the third induced R6 and first induced L6 on 9 April. The three successive intervals between pulling feathers were 51, 54, and 56 days in 1991–1992, the last interval one day longer than in 1992–1993 because of Leap Year. At each pull date, the birds' body masses were recorded to the nearest 0.1 g.

Throughout their months in captivity, the sparrows were housed under the constant conditions of 22°C and 8:16 LD, and were maintained on ad libitum water and wild bird seed mix supplemented with fresh vegetables and hard-boiled eggs. At the end of each replicate, the birds were released.

RESULTS AND DISCUSSION

Analyses utilized general linear regression models (Cohen and Cohen 1983, Anonymous 1991). Following GLM procedure with qualitative variables, we used t-test comparisons of regression coefficients between each treatment group and the mean of all treatment groups (Neter et al. 1989). Such a procedure allowed us to avoid the loss of statistical power resulting from correcting for experimentwise error (Anonymous 1991). Using standard analysis of residuals, we determined that our data met the assumptions for using GLM mod-

TABLE 2. General linear model comparisons, using t-tests of regression coefficients, between each of three induction dates, one each in November, December and February, and the mean value for the three dates for characteristics of the first induced L6 rectrix in captive male House Sparrows. For body mass, the date in April when induced feathers were last collected was also used in the analysis. Within each cell, the upper line is the adjusted mean ± standard deviation, the first number in the lower line is the t value, and second number in the lower line is the level of statistical significance. t-test degrees of freedom were 83 for body mass and 17 for feather characteristics.

Characteristic	Rectrix induction and/or collection date			
	1 November	21 December	13 February	9 April
Body mass (g)	27.4 ± 0.4	28.4 ± 0.4	27.2 ± 0.4	28.2 ± 0.4
	−2.06, 0.04	1.80, 0.08	−1.97, 0.05	1.23, 0.22
First induced L6 rectrix				
Growth bar width (mm)	2.56 ± 0.05	2.56 ± 0.05	2.61 ± 0.06	–
	−0.42, 0.68	−0.35, 0.73	0.77, 0.46	–
Total length (mm)	60.98 ± 0.51	62.43 ± 0.57	63.17 ± 0.57	–
	−2.58, 0.02	0.49, 0.63	2.11, 0.05	–
Mass (g)	12.4 ± 0.22	12.31 ± 0.23	12.76 ± 0.23	–
	−0.55, 0.59	−0.91, 0.38	1.45, 0.16	–

TABLE 3. General linear model comparisons, using t-tests of regression coefficients, between each of three induction dates, in November, December and February, and the mean value for the three dates for characteristics of the first, second and third feather induced from the same follicle. Within each cell, the upper line is the mean $\pm$ standard deviation adjusted for covariates, the first number in the lower line is the t value, and the second number in the lower line is the level of significance. t-test degrees of freedom were 17.

Characteristic	Induced R6 rectrix number		
	First	Second	Third
Growth bar width (mm)	2.51 ± 0.04 −0.59, 0.56	2.50 ± 0.04 −0.72, 0.48	2.57 ± 0.04 1.29, 0.21
Total length (mm)	61.69 ± 0.50 −1.19, 0.25	62.09 ± 0.50 −0.19, 0.85	62.72 ± 0.55 1.18, 0.25
Mass (mg)	12.4 ± 0.1 −1.92, 0.07	12.8 ± 0.1 1.95, 0.07	12.6 ± 0.1 0.01, 0.99

els (Cohen and Cohen 1983, Neter et al. 1989). Statistical significance was accepted at the 0.05 alpha level.

We discarded from the analysis two sparrows which lost additional rectrices during the course of the 1991–1992 replicate. Thus, the following results are based on sample sizes of eight, seven, and seven, respectively, for treatment groups 1–3.

Year was significantly related to body mass (Table 1), with the birds used in 1991 (27.30 ± 0.27 g) about 3% lighter than those used in 1992 (28.28 ± 0.25 g). Over the course of the experiment each winter, the overall variation in body mass adjusted for the year effect was not significant (Repeated-measures GLM; Table 1). However, body mass in November and February was significantly lower than the mean for all four dates, while body mass in December was almost (P = 0.08) significantly higher than the overall mean (Table 2).

During each of the two winters, four sparrows grew their first induced L6 rectrix at each of three different times. Total length and mass of the original L6 rectrix were significant covariates (Table 1), but growth bar width of the original L6 was not. There was no relationship with year. Of the three feather characteristics measured, only total length was significantly related to induction date (Table 1), with the average L6 rectrices induced in November and February significantly shorter and longer, respectively, than the overall mean for the three induction dates (Table 2).

Whether an induced R6 rectrix was the first, second or third grown in succession from the same follicle, its daily growth, total length and mass were all significantly positively related to the same values of the first induced L6 rectrix grown at the same time (Table 1). Neither year nor treatment group was a significant factor (Table 1). In particular, after having been adjusted for the covariate, neither the first, second or third R6 rectrix induced from the same follicle differed from the mean value for the three induction dates in growth bar width or total length (Table 3). However, the mass of the first and second rectrices induced from the same follicle was almost significantly lighter (P = 0.07) and heavier (P = 0.07), respectively, than the overall mean feather mass for all three inductions.

That the sparrows used in 1991 were significantly lighter than those employed in 1992 could have been due to sampling error. However, 1991 and 1992 rank among the driest and wettest summers, respectively, ever recorded in Ohio, and the difference in the average body size of sparrows in the two years may have resulted from drought effects on the birds' food base.

Even in the constant conditions under which the experiment was run, there was an indication of a circannual rhythm in body mass. The increase in body mass to the December value followed by the decrease to the February level (Table 2) could have been due to the phenomenon of mid-winter fattening well-known in free-ranging birds (e.g., Lehikoinen 1987).

Total length and mass of the original L6 rectrix grown during the previous molt covaried significantly with the same measures of the first induced L6 feather, but growth bar width did not (Table 1). Similarly, total feather length, but neither growth bar width nor feather mass of first induced rectrices varied significantly with induction date (Table 2). While these differences could have been due to sampling error, they do suggest the possibility that the factors determining total growth were somehow uncoupled from those determining daily growth. In a study of photoperiodic influences on induced feather growth in American Tree Sprarrows (*Spizella arborea*), White and Kennedy (1992) also concluded that total growth and daily growth could have been governed by different control mechanisms. Whether the variation in feather length we detected was a function of a circannual rhythm or was somehow associated with length of time in captivity could be investigated by producing a series of first-induced rectrices at the intervals we used, but over a period longer than a year.

Body mass has often been used as an index of nutritional condition (Harder and Kirkpatrick, in press). However, recent results have cast doubt on the validity of the body mass index. For example, socially subordinate Willow Tits (*Parus montanus*) maintained higher body mass than dominant flockmates, but became lighter in mass after the dominants were removed (Ekman and Lilliendahl 1993). This result showed that dominants were maintaining lower body mass out of choice rather than necessity. According to the body-mass index the tit with more restricted access to food, the subordinate, would be incorrectly considered to be in the better nutritional condition (Ekman and Lilliendahl 1993). Grubb (in press) has argued that measures of induced anabolism, such as daily feather growth, may be less ambiguous indices of nutritional condition than body mass because they are less subject to confounding factors. The present results appear to support Grubb's assertion. Throughout the experiment, the birds were maintained on ad libitum food and water and, therefore, we assume their nutritional condition was uniformly excellent. However, such was not indicated by records of body mass. Compared with the overall mean for all four feather induction/collection dates, body mass was 1.4% less in November, 3.5% greater in December, 2.1% less in February, and 1.4% greater in April. The first and third of these differences were significant and the second was nearly so (Table 2). By contrast, compared with the overall mean for three induction dates, growth bar width was 0.1% less in November, 0.1% greater in December and 1.2% less in February. None of these differences from mean daily feather growth approached significance ($P \geq 0.46$; Table 2). Thus, daily feather growth appeared to reflect more accurately than body mass the constancy of the nutritional condition of the sparrows over the course of the experiment.

The significant covariations between the first, second and third induced R6 rectrix and the first induced L6 rectrix being regenerated at the same time suggest that both feathers were responding similarly to the physiological state of the sparrows. After being adjusted for such covariation, the growth characteristics of the R6 rectrix were not related to whether the rectrix was the first, second or third grown from the same follicle (Table 1), nor was there any suggestion of a biological trend not detected statistically (Table 3).

In summary, in our experiment birds on ad libidum food and water and in constant conditions of photoperiod and temperature grew induced R6 rectrices in a fashion independent of the recent history of the follicle. These results suggest that when employing successively induced feathers to assess habitat quality, researchers may be able to rule out recent follicle history as a confounding variable. However, in addition to other methodological precautions (Murphy and King 1991, Grubb 1992), this assumption should be checked, especially with studies employing larger series of feathers or shorter time intervals between inductions of successive feathers from the same follicle.

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