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Ptilochronology: A Consideration of Some Empirical Results and "Assumptions"

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Recently, I (Grubb 1989) introduced a technique, termed ptilochronology, for indexing the nutritional status of free-ranging birds by measuring the width of growth bars on an induced feather. Murphy and King (1991) have presented results of feeding trials

using White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) and a critical evaluation of what they concluded are assumptions inherent in the technique. Here, I comment on their empirical results and then consider several of their "assumptions."

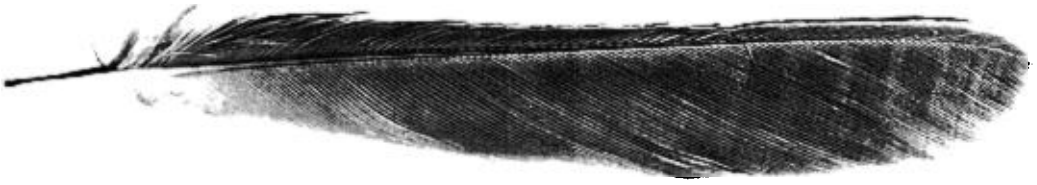


Fig. 1. Growth bars on R6 rectrix of a Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*; OSUMZ 6978). Analysis of growth-bar width indicated that this feather grew at a rate of 3.35 mm day⁻¹.

Although Murphy and King (1991) claimed that their feeding experiments were germane to ptilochronology, they calculated daily growth of flight feathers from periodic measurements of the growing feather rather than from the actual width of growth bars. They stated that they did not measure the width of growth bars, "which are difficult to see and often invisible in *Z. l. gambelii*." Apparently, this statement applies both to the original feather grown during the preceding molt and to the induced feather grown during the feeding experiments. Lack of discernable growth bars on the original feathers of their birds is puzzling. I found discernable and measurable growth bars on the (R6) rectrix of all 14 *Z. l. gambelii* skins in The Ohio State Museum of Zoology collection (Fig. 1). While growth bars usually are quite apparent on newly induced feathers, Murphy and King (1991) were not able to see them clearly enough to measure. Growth bars are difficult to see on abraded feathers, and the rectrices of birds housed in the very small cages they used (0.03 m³) were "often frayed or broken." In an experiment demonstrating that a deficient diet caused narrower growth bars in Carolina Chickadees (*Parus carolinensis*; Grubb 1991), I purposely used relatively large cages (0.42 m³) to reduce abrasion of induced feathers.

In commenting on some of what Murphy and King (1991) concluded are assumptions inherent in the technique of ptilochronology, I will begin each section by quoting them. "Assumption 1: Each pair of growth bars results from 24.00 hours of elongation of the feather." There is good evidence supporting this assumption and none refuting it. Murphy and King (1991) must accept this assumption for their feather-growth measurements, made at intervals while the feather was growing, to have relevance to discussion of growth bar widths, the focus of ptilochronology.

"Assumption 2: There is a predictable, exclusive, and direct relationship between the growth rate and final length of feathers and the bird's nutritional status while the feathers are growing, regardless of the type of malnutrition." Several parts of this statement are incorrect. In Grubb (1989), I was careful to maintain that reduced nutritional status was only a sufficient cause of reduced

growth-bar width. We (Murphy and King 1991, Grubb 1991) have now demonstrated in controlled experiments that a "restricted adequate" diet is sufficient to cause reduced feather growth, but there was never any assumption that it was both sufficient and necessary (i.e. exclusive). In fact, I devoted fully a third of my 1989 paper to a detailed consideration of factors other than nutritional status that might affect growth bar width. Since then, coworkers and I have detected an apparent circannual rhythm in growth-bar width, as well as correlations of daily feather growth with a bird's age and/or sex (Grubb et al. 1991). In a controlled experiment, we have failed to demonstrate any statistically significant effect of temperature and wind on induced feather growth (Zuberbier and Grubb, in press).

Also, contrary to the above quotation, I did not assume any effect of nutritional status on the total length of an induced feather. Apparently, there sometimes is such an effect (Grubb 1989, Waite 1990, Grubb et al. 1991) and sometimes not (Grubb and Cimprich 1990, White et al. 1991).

"Assumption 3: Feather growth rate slows immediately upon the onset of a nutritional shortage (i.e. there is no metabolic latency)." This statement is not correct. The actual assumption was that the response latency of feather growth to nutritional shortage is sufficiently brief for the effect of the shortage to be detected on a diurnal or daily basis. Murphy and King (1991) claimed to have cast doubt on this assumption. In their experiment, feather-growth rate of sparrows on an otherwise *ad libitum* diet was not depressed by 3.5-h fasting periods on two consecutive days. However, all of their birds had been on *ad libitum* diets for several weeks and, during the brief fasts, may have resorted to a fat supply not available to birds under chronic stress in nature. Also, those birds subjected to the short fasting periods actually gained more body mass over the feather-growth period than any other treatment group, except for the one group recovering from an earlier diet abnormally low in protein. Such a compensatory increase in fat could have ameliorated the effects of short-term deprivation, and has been predicted for risk-sensitive foragers (Lima 1986, Rog-

ers 1987). There is no information yet on the response latency of feather growth to nutritional shortfall in free-ranging birds.

"Assumption 4: Feather growth slows in direct proportion to the magnitude of a nutritional shortage." The two experiments with "restricted adequate" diets support this assumption (Murphy and King 1991, Grubb 1991). Murphy and King's only evidence contrary to this assumption comes from the failure of a synthetic diet deficient by one-half in certain amino acids to slow feather growth; diets three-fourths deficient did slow feather growth. Such results with synthetic diets are difficult to interpret because, in nature, any diet adequate in metabolizable energy also is likely to be adequate in specific amino acids (Murphy and King 1984, Grubb 1989).

"Assumption 5: The daily growth rate of the original feather (DGO) occurred when birds were well-nourished and, if two or more birds are being compared, in otherwise identical environmental conditions." Daily growth of the original feather is used to standardize results among conspecifics of different body size (Grubb 1989). The method does assume that the original feather was grown during the normal molt. Feathers not grown during the molt can be detected by their unusual color, degree of abrasion, and/or growth-bar width. However, the method does not assume that a bird was "well-nourished" during growth of an original feather, only that birds in different treatment groups were equally nourished. Daily growth of original feathers can be compared among treatment groups (e.g. Grubb 1991) or designated as a covariate (Grubb et al. 1991, White et al. 1991).

"Assumption 6: Episodes of nutritional privation always coincide with the standard segment of growth bar measurement." This statement is not correct. The method of determining daily feather growth consists of finding the average width of 10 growth bars centered on a point two-thirds of the feather's length from its proximal end. The method assumes that a narrowing of growth bars within this feather segment indicates lowered nutritional condition, but would fail to detect episodes of reduced nutrition coinciding with growth of other parts of the feather. Since my 1989 paper, I have found in a number of data sets that mass of the fully grown feather is significantly positively correlated with average width of the 10 standard growth bars. Thus, average growth-bar width and feather mass, respectively, characterize nutritional condition during a 10-day interval and during the entire period of feather growth.

"Assumption 7: Any adjustment of a bird's metabolism that can result in a reduced rate of tissue synthesis, as reflected by DGI or DGI/DGO, indicates the occurrence of a nutritional challenge sufficient to affect the bird's lifestyle and (or) fitness." In the above sentence, the word "occurrence" does not accurately describe my assumption. I assumed that, all else being equal, reduced growth-bar width indicates the possibility of

a nutritional challenge sufficient to affect a bird's fitness. That is, I accepted the possibility that some reduction of growth-bar width could indicate a reduction in nutritional status too insignificant or transitory to cause a reduction in fitness. While I should have stated this assumption more clearly, my intention was evident in the sentence that stated, "Furthermore, comparisons of feather growth could be used to indicate the probability of starvation," where it was understood that the probability of starvation could be zero. Subsequent studies have been more explicit about this assumption (e.g. Waite 1990).

The possibility that reduced growth-bar width indicates reduced fitness is, of course, what an ecologist finds heuristic about ptilochronology. Therefore, Murphy and King's (1991) conclusion that this assumption is "perhaps untestable" is a serious criticism. By "untestable," I assume that Murphy and King meant not falsifiable. Some reduction in growth-bar width may occur under environmental conditions not severe enough to produce catabolism of body tissues (the conventional measure of nutritional stress; Murphy and King 1984), let alone to reduce fitness. However, if no reduction in some established fitness trait (e.g. survivorship, lifetime reproductive success) were to occur over a substantial number of temporally and spatially separated replicates under conditions that substantially reduced growth-bar width (or eliminated feather regeneration altogether; Waite 1990, White et al. 1991), then the ecological and evolutionary implications of the technique would be gravely weakened.

Present results link induced feather growth to the fitness traits of survivorship and brood size, but only indirectly. Both the width of growth bars on an induced rectrix (Hogstad 1992) and survivorship (Koivula and Orell 1988) increased with increasing social-dominance status within flocks of wintering Willow Tits (*Parus montanus*), but the two trends were found in Norway and Finland, respectively. White et al. (1991) found an inverse relationship between manipulated brood size and the width of growth bars on an induced feather grown by female European Starlings (*Sturnus vulgaris*) feeding nestlings. Another study of the same species found that survivorship was inversely related to brood size (Clobert et al. 1987). In order to test for a relationship between induced feather growth and various fitness traits more directly, ongoing projects involve assessing: (1) induced growth-bar width and survivorship in wintering Carolina Chickadees (*P. carolinensis*) experimentally deprived of associations with Tufted Titmice (*P. bicolor*), their principal heterospecific flock mates (D. A. Cimprich and T. C. Grubb, Jr., in prep.); (2) induced feather growth, breeding age, parental effort and survivorship in Leach's Storm-Petrels (*Oceanodroma leucorhoa*; R. A. Mauck, T. C. Grubb, Jr., and C. E. Huntington, in prep.); (3) induced feather growth, territory size and reproductive success in Loggerhead

Shrikes (*Lanius ludovicianus*; R. Yosef and T. C. Grubb, Jr., in press, in prep.); and (4) daily feather growth and territory-specific survivorship in fledgling Florida Scrub Jays (*Aphelocoma c. coerulescens*; K. K. Harris, T. C. Grubb, Jr., and G. A. Woolfenden, in prep.).

In conclusion, much of Murphy and King's (1991) critique concerns what they regarded as uncertainty and imprecision in the physiological aspects of ptilochronology. While more physiological and biochemical detail about feather growth could be useful, it also may not be helpful in addressing critical points concerning ptilochronology. Current studies share characteristics that allow them to meet physiology-based concerns: (1) experimental and control trials are arranged in a balanced design, thus obviating seasonal effects; (2) treatment effects such as territory size or dominance status occur on the order of weeks, so that any possible metabolic latencies are of diminished importance; (3) evidence is being sought at only the qualitative or ordinal level; and (4) sample sizes are sufficiently large to reduce the effect of any unidentified atypical original feather. Ptilochronology's prospects remain bright for furthering understanding about the causes of avian nutritional condition and relative fitness.

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Ptilochronology: Accuracy and Reliability of the Technique

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After reviewing the assumptions inherent in ptilochronology outlined by Murphy and King (1991a), Grubb (1992) concluded that "Ptilochronology's prospects remain bright for furthering understanding

about the causes of avian nutritional condition and relative fitness." His view contrasts sharply with the conclusion of Murphy and King (1991a) that the method, as originally conceived (Grubb 1989), "is bur-