

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-

dened with uncertainty, conceivably serviceable only under closely controlled conditions, and then acceptable only to practitioners who have an affirmative opinion about Assumption 7" (bearing on the relationship between the diminished rate of growth of a single feather and fitness). At the outset I will state that, in my opinion, all the concerns raised and conclusions drawn in Murphy and King (1991a) are valid. In responding to Grubb (1992), I will attempt to deal with the specific issues he raises; a more extensive review of this subject is, however, found in Murphy and King (1991a).

Implicit in ptilochronology are two general assumptions (also recognized by Grubb et al. 1991): (I) feather-growth rates can be compared accurately among birds by comparisons of growth-bar widths; and (II) a reduction in the rate of feather growth reflects a period of undernutrition. Grubb (1992) reiterated each of the seven specific assumptions outlined by Murphy and King (1991a), and so I will refer to them below only by their ordinal designations.

At the outset Grubb (1992) suggested that our study may not be germane to ptilochronology because we *directly* measured feather-growth rates rather than using the *indirect* measure of average growth-bar width. Because feather-growth rate is precisely the measure on which ptilochronology relies, it seems to me that direct measures of feather-growth rates in variously nourished birds are indeed germane to the topic. Furthermore, directly measuring growth rates bypasses the first implicit assumption of ptilochronology (I above) and allowed us specifically to evaluate the second assumption (II above).

As Grubb (1992) pointed out, the Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in our study did not exhibit well-defined growth bars in either the original or the induced feathers. This difference between our birds and the skins of Gambel's White-crowned Sparrows he examined is consistent with Michener and Michener's observation (1938: 149) that growth bars "are not equally visible in the corresponding feathers of all birds even of the same species, but grade from absent, at one extreme, to easily apparent, at the other." Causes for the variable clarity of growth bars noted by Grubb and others (for references, see Murphy and King 1991a) remain unknown. In our experiments, however, it was not attributable to abrasion as Grubb suggested; perhaps mineral or pigment content of the diet influenced their visibility. Grubb's emphasis on variability in the clarity of growth bars, nevertheless, is well placed because it illustrates a limitation of ptilochronology. This variability among, and even within, birds is particularly troublesome in attempts to discern as many as 10 consecutive growth bars at nearly the same locations on feathers from several birds. If ptilochronology is used to compare within-day or between-day nutritional condition (Grubb 1989), variability in the clarity of growth bars could be even more trouble-

some. In these cases, the width of individual growth bars, or segments of growth bars, would need to be measured with exceptional accuracy, an especially difficult task in the proximal two-thirds of a feather (e.g. see Grubb 1992:fig. 1). Indistinct bars and unexplained variance in bar width both were identified by White et al. (1991) as "risks" of ptilochronology.

Like Grubb, we concluded that a growth bar probably represents *about* a day's growth (assumption 1, Murphy and King 1991a). Despite our shared view, I believe this assumption deserves further scrutiny. The literature reveals scant attention—and virtually none in the last four decades—to the mechanisms of growth-bar formation. Little is known about: (1) the metabolic and biochemical events underlying the formation of growth bars; (2) the time course of these events; and (3) the factors influencing these events (Lillie and Wang 1940, but also see Murphy and King 1986, Murphy et al. 1989). Meeting the assumption that growth bars delineate one day's growth (i.e. some invariable time period) is crucial for ptilochronology because the technique relies on this indirect measure of feather-growth rate. We acknowledged that our own results only indirectly addressed this assumption (Murphy and King 1991a). As we pointed out, however, we circumvented the need to meet this assumption by directly measuring the lengths of growing feathers at exactly 72-h intervals. This protocol allowed us to address specifically the more tenuous assumption in ptilochronology—the growth rate of a single feather reliably indicates nutritional status (the crux of assumption II).

Ptilochronology is described as a *technique* that "uses the width of daily growth bars on an induced feather as an index of a bird's nutritional condition" (Grubb et al. 1991) in order ultimately to understand the "causes of avian nutritional condition and relative fitness" (Grubb 1992). It has not been presented as an *hypothesis* to be modified and qualified and ultimately accepted or rejected as evidence accumulates. I think most would agree that for any technique to reliably measure a variable (in the case of ptilochronology, nutritional condition) it is mandatory to have a change in some measured index of that variable (in this case, average growth-bar width) correlate reasonably well with a change in the variable. Any confounding influence on the measured index by other variables reduces the accuracy and reliability of the technique. As Grubb (Grubb et al. 1991, Grubb 1992) has reported, sex, age, and season (the results on temperature are equivocal) influence the rate of growth of feathers as measured by average growth-bar width; at least a seasonal effect is further substantiated by our direct measures (Murphy and King 1991a). These differences in feather-growth rates are unrelated to nutritional condition. Grubb (1992) emphasized that he indicated (Grubb 1992) that nutritional status was only a sufficient cause, not a necessary or exclusive cause, of reduced growth-bar width. It follows that,

even if reduced growth bars can be detected accurately among an adequate sample of birds, the investigator can only conclude that undernutrition *may* have occurred. Confounding even this conditional conclusion is the observation that differing types and degrees of undernutrition do not influence growth rates of feathers in a consistent fashion (Murphy and King 1991a).

As Grubb proposed (Grubb et al. 1991, Grubb 1992), limiting the use of ptilochronology to measures of feathers grown by birds in the same season could control for many of the potentially interfering variables. For others, it may not. Before assessing the reliability of ptilochronology as an index of nutritional status, these other potentially interfering variables need to be explored. For example, these include: (1) the influence of physiological, metabolic and endocrine adjustments entrained in annual cycles of birds; (2) the potential inhibition of feather regeneration by reproductive hormones that may vary with stage of breeding cycle and fecundity; (3) the cyclic changes in physiology and responsiveness of feather papillae (Lucas and Stettenheim 1972); and (4) the potential inhibitory influences on growth rates of feathers by chronic nonnutritional stressors (a corollary to acute induction of fault bars; King and Murphy 1984, Murphy et al. 1989). The amount still unknown about these potentially confounding influences is both worrying and reminiscent of the reasons prompting Chamberlin's (1897:839) classic caveat: "First the full facts, then the interpretation thereof, is the normal order." Otherwise, the usefulness of ptilochronology as a technique will remain burdened by uncertainty. For example, Hogstad (1992:326) suggested that significant differences between DGI and DGO (daily growth induced and daily growth original) in tits (*Parus montanus*) were "a strong indication that the nutritional status of the juveniles was better in summer and that of the adults was better during the moult in August than in winter." However, slower growth rates of feathers in winter, as compared with molt, have been reported for well-nourished adult Northern Cardinals (*Cardinalis cardinalis*, Grubb et al. 1991) and Gambel's White-crowned Sparrows (Murphy and King 1991a). In contrast, well-nourished juvenile Northern Cardinals grew an induced rectrix more quickly "during shorter days" (Grubb et al. 1991). The foregoing results illustrate how difficult it is to draw robust conclusions about nutritional status from ptilochronology alone.

I agree with Grubb's (1992) statement that "there is no information yet on the response latency of feather growth to nutritional shortfall [assumption 3] in free-ranging birds." Data from captive birds suggest that in many species this latency exceeds one day (see Murphy and King 1991a and references cited therein). I also agree with Grubb's (1992) suggestion that body reserves might ameliorate any reduction in growth rates of feathers. Such capacity for amelioration, how-

ever, indicates that ptilochronology would not accurately gauge the day-by-day nutritional regime of an animal but rather, *when* the reduced growth rate is attributable to undernutrition, would potentially integrate several days.

This seemingly ambiguous relationship between feather-growth rates and nutritional status is further complicated by insufficient evidence on whether feather growth slows in direct proportion to the magnitude of a nutritional shortage (assumption 4; i.e. the wider the growth bars the better the condition). Inconsistencies in the responses of Gambel's White-crowned Sparrows to undernutrition (Murphy and King 1991a) caused us to conclude that it is not possible at present to predict either the trophic conditions in which assumption 4 might be valid, or the form of a calibration curve when a correlation exists. The experiments in which Gambel's White-crowned Sparrows were fed diets deficient in an essential amino acid (Murphy and King 1991a) should not be discounted (cf. Grubb 1992). The loss of body mass by these birds was caused mainly by reduced food intake; these results, therefore, are more applicable to free-living birds than Grubb suggested. In a study of the effects of nutrition on the regeneration of feathers of Carolina Chickadees (*Parus carolinensis*; Grubb 1991), the growth rates (DGI and DGI/DGO) and masses (MI and MI/MO [mass induced/mass original]) of induced rectrices of birds fed 90% *ad libitum* did not differ significantly from birds fed 100% *ad libitum*; the ratios of growth rates of induced and original feathers (DGI/DGO, but not DGI) of birds fed 80% *ad libitum* differed from birds fed 90% or 100% *ad libitum*, and the feather mass and mass ratios (MI and MI/MO) of birds fed 80% *ad libitum* differed significantly from birds fed 90% *ad libitum*, but not from those fed 100%. Thus, these birds did not show a clean relationship between the plane of nutrition and the growth rate or mass of an induced rectrix. The data are further confounded by the absence of any independent measure of nutritional status (e.g. changes in body mass of control birds compared with underfed birds) to substantiate the extent to which the feeding protocol actually created a nutritional deficit. The birds were subsisting on an *ad libitum* diet before the experimental period and, as pointed out earlier, could have relied temporarily on endogenous reserves. Also unknown is whether these birds made a compensatory adjustment in their energy budgets, such as in activity. While I agree that the data from chickadees lend some support to the assumption that growth-bar width can be influenced by a bird's nutritional condition, they do not provide an adequate test of this relationship to support assumption 4. Consequently, I reiterate our earlier conclusion: too little is known about the relationship between the type, degree, and (I add) duration of a nutritional challenge and the rate of feather growth (in different phases of the annual cycle) to establish the presence *or absence* of a nutritional

challenge using ptilochronology without other indices of nutritional condition.

I agree with Grubb that the index DGI/DGO might be functional in controlling for differences in bird size if it can be established that the birds were "equally" nourished while the original feathers were growing (assumption 5). This situation is most easily established if all birds are well nourished (cf. Grubb 1992). In addition to establishing similar nutritional conditions during the postnuptial molt, it also would be prudent to establish that the date of onset of the normal molt does not influence individual feather-growth rates. For instance, often a late breeder that starts molt late, or one that inhibits molt rate until breeding is completed, later molts more quickly. This inhibition and later acceleration of molt may be accommodated mainly by altering shedding intervals, but growth rates of feathers may also be involved (Murphy et al. 1988, Morton and Morton 1990).

I also agree with Grubb that in some instances a feather grown during the normal molt and one grown as a replacement after the molt can be distinguished from each other, thereby avoiding an error in the DGO term (assumption 5). However, the detectability of these different-aged feathers would vary with the species, the lifestyle of the bird, and the elapsed time from when the feather was replaced and when the "original" feather is collected.

Grubb's observation that the mass of the feather positively correlates with the estimated growth rate of the feather potentially broadens the measurement period for ptilochronology (assumption 6), but also potentially complicates interpretations of ptilochronology data. This problem arises when data on mass and growth rates conflict. Also, it would be prudent to scrutinize the relationship between feather mass and nutritional condition. Like feather-growth rates, mass of newly formed feathers also appear to vary (at least) with season, sex, and age of a bird—independently of nutrition (Grubb et al. 1991).

Assumption 7 poses the greatest challenge in ptilochronology. Under what circumstances and at what level of inhibition of feather growth can it be concluded reliably that a bird experienced a nutritional challenge sufficient to affect its fitness? Grubb's clarification of assumption 7 is enigmatic to me. I am uncertain what he means by "comparisons of feather growth could be used to indicate the probability of starvation, where it was understood that the probability could be zero." In my estimation, this implies a graded and defined response between the rate of growth of an induced feather and nutritional status, an implication that is unsupported (Murphy and King 1991a, Grubb et al. 1991, Grubb 1992). It is the predictability of the relationship between feather-growth rate and nutritional status and its susceptibility to confounding influences (i.e. accuracy and reliability of ptilochronology) with which I am concerned. I do not doubt that seriously malnourished birds would

replace a growing feather at measurably slower rates and, also, that their fitness would be in jeopardy. Such circumstances can probably be found in nature. I have reported comparable instances from laboratory studies (Murphy et al. 1988, Murphy and King 1991b). However, it does not follow that—because such circumstances can be found—all instances of diminished feather growth rate can be interpreted as reflecting periods of lowered nutritional status and reduced relative fitness. This line of reasoning nevertheless recurs in studies employing ptilochronology (Grubb 1992 and references cited therein). Practitioners of ptilochronology generally draw conclusions about the nutritional status of the birds they study, in some cases even after acknowledging that causes other than nutrition might account for the reduced rates of feather growth. In some instances, such conclusions will certainly be correct. In other instances, however, they will not. The question that needs to be addressed is how often will conclusions about nutritional status based on ptilochronology be confounded by undetected influences. Only when this question is comprehensively answered can the "heuristic" (cf. Grubb 1992) value of ptilochronology be assessed fairly.

My objective has been to identify some of the unresolved limitations ("risks" in the lexicon of White et al. 1991) associated with ptilochronology. Some of these limitations may be resolved by following the recommendations of Grubb et al. (1991) and conforming to the study "characteristics" outlined in his final paragraph (Grubb 1992). The conclusion of Grubb et al. (1991:444) that their results (which reveal that several factors other than nutrition can influence feather growth rate and mass) "limit the freedom with which ptilochronology can be used" is conceptually related to the conclusion we drew "that ptilochronology is conceivably serviceable only under closely controlled conditions" (Murphy and King 1991a). Similarly, I agree with Grubb that the study characteristics he outlined for using ptilochronology begin to address some of the "physiology-based" concerns we raised in our evaluation. Specifically, avoiding day-by-day analyses of growth-bar width (his characteristic 2) will reduce errors associated with assumption 3. Careful consideration of conclusions about the magnitude of undernutrition (his characteristic 3) and, ideally, a supporting measure of nutritional status may reduce errors associated with assumptions 2, 4, and 7. Maximizing sample sizes to reduce the effects of atypical original feathers (his characteristic 4) will reduce errors associated with assumption 5.

In conclusion, the future of ptilochronology lies not in what Grubb or I currently believe, but rather in systematic and thoroughly controlled studies of the origin of growth bars, and the factors that influence feather-growth rate. Grubb's effort to identify a useful field technique for assessing nutritional status is commendable. The uncertainty burdening his tech-

nique underscores the need for a concerted effort by avian nutritional ecologists to better define the components of nutritional condition, nutritional plasticity, and the physiological and behavioral consequences of undernutrition.

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Furthering Avian Conservation in Latin America

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The Neotropical realm is the most diverse in tropical forest avifauna, and one of the most depauperate in current avian research (James 1987). It also is in desperate need of avian conservation on both national and international levels. Recent estimates indicate that nearly one-eighth of Neotropical bird species are either threatened or endangered (Collar and Andrew 1988, World Resources Institute 1990). A number of authors have outlined both the urgent need for tropical field biologists and the training of Latin American students in ornithology and conservation (Short 1984,

Mares 1986, James 1987, Duffy 1988). Additional, specific activities and programs can be undertaken by North American ornithologists to further the goals of conservation in developing countries.

James (1987:348) stated that "developed nations have long sent researchers to this region; it is now time for Latin Americans to become much more involved." Conservation efforts certainly need national participation, but I point out (as did Duffy 1988) that there is no lack of interest among Latin Americans in either Neotropical conservation or ornithology. At the III