

# PTILOCHRONOLOGY: FEATHER GROWTH BARS AS INDICATORS OF NUTRITIONAL STATUS

THOMAS C. GRUBB JR.

*Department of Zoology, The Ohio State University, Columbus, Ohio 43210 USA*

**ABSTRACT.**—Ptilochronology is the study of the growth rates of feathers by the measuring of growth bars. Growth bars are cross-bands on feathers that denote 24-h periods of growth. If a rectrix is plucked from a bird that is released, and then recaptured more than a month later, the width of the growth bars on the replacement (or induced) rectrix can provide a day-by-day record of the nutritional regime under which the bird had lived.

Growth rate of induced retrices varies among ages, sexes, and species of birds. I measured growth bars on feathers induced in Downy Woodpeckers (*Picoides pubescens*) that wintered in Ohio woodlots without supplemental food. On a daily basis, females grew feathers significantly more slowly than males. In other woodlots, where the woodpeckers were given supplementary food, daily feather growth did not differ between sexes. I concluded that male Downy Woodpeckers normally have a better nutritional status than females during the winter. A difference in nutritional status may explain why male Downy Woodpeckers use their social dominance to exclude females from parts of the species niche during winter.

Ptilochronology could permit new insights into the nutritional ecology of free-ranging birds. Hypotheses that predict even minor variation in the nutritional status of birds should become accessible to testing. *Received 5 April 1988, accepted 7 October 1988.*

BIRDS molt their plumage at yearly or more frequent intervals (Mathew and Naik 1986, Rohwer 1986). When birds lose feathers, however, replacements are promptly grown (Hall-Craggs and Evans 1985, Payne 1972). Selection apparently favors the expenditure of energy and specific nutrients (*sensu* King and Murphy 1985) to maintain a complete complement of body and flight feathers. However, feather growth can be reduced to compensate (*sensu* King and Murphy 1985) for the nutritional demands of other activities. Molting periods tend not to overlap with either breeding or migration. In some species, the molting sequence brackets reproductive episodes (Mathew and Naik 1986) or migratory periods (Stresemann 1967). Replacement of feathers is slowed or deferred during times when feather production would compete for limited resources.

For several weeks after a rectrix is lost (either during molt or mechanically) or is plucked by an experimenter, a new rectrix grows from that follicle if the intake of energy and specific nutrients is adequate for feather formation. A feather grows from the collar zone of the papilla (Watson 1963, Lucas and Stettenheim 1978) to produce "growth bars" on the feather oriented roughly perpendicular to the rachis. Growth bars are alternating darker- and lighter-appearing bands (Riddle 1908). Darker bands are ap-

parently derived from material laid down during the day and lighter bands consist of material laid down during the night (Wood 1950). Wood (1950) suggested that the appearance of these bands is due to differences in optical properties brought about by differential pigment incorporation into the keratin matrix of the feather during the day and night. However, darker- and lighter-appearing bands are found on white feathers (pers. obs.) and white feathers apparently do not contain pigments of any kind. Whatever their cause, each pair of bands constitutes a 24-h period of feather growth (Michener and Michener 1938).

The breadth of a growth bar along the axis of the feather seems to be related to the bird's nutritional status. During a 24-h period if a bird is stressed nutritionally, it produces a growth bar deficient in barbules. This growth stage has a "fault bar" noticeable to the unaided eye (Newton 1968). Fault bars are observed commonly in the retrices of young raptorial birds with sporadically insufficient food supplies during feather growth (J. A. Smallwood pers. comm.). Under more severe nutritional conditions, there may be insufficient energy or specific nutrients available even for adequate deposition of keratin in the central rachis and the entire feather may break off where the rachis is "pinched" (Riddle 1908).

If one plucks a rectrix and releases the bird, then recatches the same individual more than a month later and plucks the newly grown replacement feather, that replacement (or induced) feather can provide a day-by-day record of the nutritional regime of the bird during the previous weeks. Individual growth bars (one dark band plus one light band) can be counted and measured to establish the number of days taken to grow the feather and which days were more nutritionally constrained than others. Correlations can be sought between daily increments of feather growth and mean daily temperature, wind velocity, day length, and other factors. Matching induced rectrices from two birds that had feathers plucked at the same time and were then released in the same habitat could be used to determine the relationship of species, sex, age, dominance status, kinship, and other factors to nutritional status.

The induced feather is retained until the next molt. In the case of most temperate- and boreal-zone birds, rectrices are replaced annually during the pre-basic molt of late summer and autumn (Svensson 1975, Pettingill 1985). A bird plucked in late autumn will grow the induced feather and will carry this record of nutritional status to be collected any time during the next 6-8 months.

I use *Ptilochronology* (literally, the study of feather time) to define the study of the growth rates of feathers. *Ptilochronology* focuses on the daily growth bars of feathers from much the same perspective that dendrochronology focuses on the annual growth rings of trees (Fritts 1976). The potential of ptilochronology as an experimental method stems from its ability to detect variation in the rate of experimentally induced feather growth. Artificial diets below the maintenance requirements of White-crowned Sparrows (*Zonotrichia leucophrys*) molting in captivity reduced the rate of feather growth (Murphy and King 1987). Because each growth bar delimits one day's feather growth (Michener and Michener 1938), it seems logical to conclude that the captive sparrows on an inadequate diet must have grown feathers with narrower than normal growth bars. Nevertheless, controlled experiments are needed to verify the quantitative relationship between inadequate diets and the width of growth bars on induced feathers.

*Ptilochronology* uses the growth rate of

feathers to assess the nutritional status of birds. The extent to which feather growth in nature falls below that of birds living in optimal, artificial conditions could be used as an index of nutritional status. Furthermore, comparisons of feather growth could be used to indicate the probability of starvation. King and Murphy (1985) lump energy (in the form of stored lipids), protein, minerals, and vitamins under the term, nutrient. It seems probable, however, that feather growth is constrained primarily, if not entirely, by the amount of available energy.

During the winter of 1987-1988, I tested the hypothesis that the ultimate cause of sex-specific foraging in Downy Woodpeckers (*Picoides pubescens*) is the increase in nutritional status to be gained by foraging in the males' microhabitat. Sex-specific foraging niches have been found in reptiles (Schoener 1974) and mammals (Bartholomew 1970, Krebs and Davies 1981), and are particularly well-known in woodpeckers (Selander 1966). In Downy Woodpeckers, both males and females wintering in deciduous woodland changed their foraging behavior in response to ambient weather conditions (Grubb 1975, 1977, 1978), but males generally foraged higher in the forest and on smaller diameter branches than did females. When tested individually in a laboratory aviary, however, females preferred smaller diameter branches than did males (Pierce and Grubb 1981). Finally, when all males were removed from a woodlot, the females foraged on branches of smaller diameter and greater height above the ground than did females in a control woodlot. Reciprocally, males in the absence of females foraged like control males (Peters and Grubb 1983).

These studies support the hypothesis that sex-specific foraging niches in Downy Woodpeckers are caused by female avoidance of the foraging microhabitat of socially dominant males. I predicted that under normal circumstances the growth bars on induced feathers would be wider in males than in females, but that the difference should lessen or disappear if woodpeckers were provided with supplemental food.

#### METHODS

My general technique involved capturing a bird and plucking the right outermost rectrix. Removing this feather caused no visible trauma to the bird and

had no observable effect on flight. The growth bars were most evident on the outer rectrices.

During February 1988, I obtained induced feathers from Downy Woodpeckers wintering in Morrow County, Ohio. Because the outermost pair of the twelve rectrices in woodpeckers is reduced in size (Short 1982), I collected the second to the outermost right rectrix (designated R5). Starting in late November, I attracted woodpeckers to feeders in ten 25–40 ha woodlots. During the first week of January, I banded, plucked the rectrix, and released the birds. Over the course of the next 6 weeks, I kept feeders in 5 of the woodlots so that woodpeckers had continual access to an unlimited supply of sunflower seeds and beef suet, but I left empty feeders in 5 other woodlots over the same period. During the last week of February, I refilled the feeders that had been empty, recaptured birds at both supplemented and unsupplemented sites, and collected the induced R5 rectrix from each bird.

Feathers were stored individually in envelopes. To measure the width of growth bars, I first taped a rectrix by its calamus to an index card. I then pushed a size 0 insect-mounting pin perpendicularly through the feather at the distal edge of each dark growth bar, piercing the underlying card each time. I also pierced the underlying card at the proximal and distal ends of the feather.

Because feathers often differ in the number of growth bars that can be seen clearly, I developed a standard technique to determine the width of growth bars. I used a caliper to measure the total length of the feather to the nearest 0.01 mm. Then I calculated and marked on the card the point two-thirds of the feather's length from the proximal end. My normal procedure with passerine birds was to determine the average width of 10 growth bars. These included the growth bar on which the "two-thirds" point falls plus 4 proximal and 5 distal bars. I divided the total length of this 10-bar segment by 10 to obtain an average value of daily growth. On the R5 rectrix of Downy Woodpeckers, it was often impossible to see 10 growth bars clearly. The rectrices were often worn and dirty. However, I could generally determine 6 growth bars centered on the "two-thirds point," and I used the average width of these 6 to compare the daily growth of the induced feather (DGI) in males and females.

As an index of nutritional status, induced feather growth must be comparable across birds of different size. To obtain a standardized index, I determined the daily growth of the original feather (DGO) collected in early January. I assumed that all of these feathers were grown during the previous molting season because they were all faded and worn to about the same extent. I then divided the daily growth rate of the induced rectrix by the daily growth rate of the original rectrix (DGI/DGO) to obtain the proportion of the growth rate during the normal molting period that occurred in a rectrix induced during the winter.

DGI/DGO was also taken to be positively correlated with nutritional status. I used two-tailed *t*-tests to compare categories of feather growth and accepted statistical significance at the 0.05 level. For analysis, proportions were transformed by arcsine (Sokal and Rohlf 1981).

## RESULTS

In early January, I plucked the original R5 rectrix from 6 male and 8 female Downy Woodpeckers at food-supplemented sites, and from 7 males and 9 females at unsupplemented sites. At the end of February, I recaptured 3 males and 4 females at food-supplemented sites, and 5 males and 7 females at unsupplemented sites. Within each sex, neither the total length nor the daily growth of the original feather differed significantly between food-supplemented and unsupplemented birds (Table 1). Food supplementation had no statistically significant effect on the total length or daily growth of the induced feathers of males, but it caused a significant increase in both of these measures in females.

The standardized index of daily growth (DGI/DGO) in the induced rectrices of males was unaffected by added food. In food-supplemented females, DGI/DGO was 0.84, which was not significantly different from the value for either the food-supplemented or unsupplemented males. In the unsupplemented females, however, the DGI/DGO index (0.70) was only 83% as large as that for food-supplemented females. This value of daily growth in unsupplemented females differed significantly from that in either food-supplemented females or in both categories of males.

## DISCUSSION

In the example, unsupplemented female Downy Woodpeckers grew an induced feather significantly more slowly than did either unsupplemented male woodpeckers or food-supplemented females. This supports the hypothesis that the social dominance of male Downy Woodpeckers confers a significantly higher nutritional status. Larger sample sizes will be required to check for correlations between growth rates of induced feathers and such factors as habitat type and age of woodpecker.

As an index of nutritional status, induced

TABLE 1. Relationships of original and induced R5 rectrices of food-supplemented and unsupplemented male and female Downy Woodpeckers wintering in Ohio woodlots (1987-1988).

Measurement (mm)	Male			Female		
	Food-supplemented	P <sup>a</sup>	Unsupplemented	Food-supplemented	P	Unsupplemented
Total length of original rectrix	50.16 <sup>b</sup> 3.95 (3)	NS	50.07 1.56 (5)	52.64 1.77 (4)	NS	50.74 1.61 (7)
Daily growth of original rectrix	2.34 0.08 (3)	NS	2.35 0.18 (5)	2.48 0.09 (4)	NS	2.60 0.15 (7)
Total length of induced rectrix	46.56 4.49 (3)	NS	46.25 2.53 (5)	49.79 1.20 (4)	<0.01	46.42 1.59 (7)
Daily growth of induced rectrix	1.88 0.20 (3)	NS	1.92 0.08 (5)	2.07 0.10 (4)	<0.01	1.81 0.13 (7)
Daily growth of induced rectrix/ daily growth of original rectrix	0.80 0.06 (3)	NS	0.82 0.07 (5)	0.84 0.03 (4)	<0.001	0.70 0.05 (7)

<sup>a</sup> Probability from two-tailed *t*-tests; NS = not significant.

<sup>b</sup> For each measurement and each category of woodpecker, the upper value is the mean, the middle value is the standard deviation of the mean, and the lower value is the sample size.

feather growth appears to have at least three advantages over other indices, such as increase in mass of indeterminate growers (e.g. fish) or regeneration of excised body parts (e.g. many invertebrates, urodele amphibians). First, the loss of one rectrix had no observable effect on a bird's behavior. Second, feather growth can be divided *a posteriori* into units (the dark and light portions of growth bars) that correspond to less than 24-h of growth. Therefore, fine-scale comparisons can be made of feather growth as an index of nutritional status with naturally occurring or manipulated variation in the environment. Third, other than increasing the mass of one induced rectrix, a postfledging bird would remain essentially the same size, so that overall body growth would not confound interpretation of the causes of the degree of feather growth observed.

The extent to which the growth of induced feathers is limited may be related to a host of naturally occurring or manipulated environmental variables. To interpret such studies, it would be useful always to be able to relate differences in induced feather growth among categories of birds directly to differences in the energy shortfall they experience. However, there are at least four possible ways besides direct energy shortage that induced feather growth might be constrained.

*Specific nutrient deficiency.*—The rate of feather growth could be constrained by the availability of dietary nutrients rather than by the availability of metabolizable energy (Dolnik and Gavrilov 1979). In particular, the availability of dietary sulfur-containing amino acids (SAA) has been considered potentially limiting because of their relatively high abundance in feathers and the integral part they play in keratin structure (e.g. Newton 1968, Dolnik and Gavrilov 1979, Murphy and King 1984). However, recent findings by Murphy and King (1984) lead me to conclude that constraints on the regeneration of one rectrix due to insufficient SAA are extremely unlikely. Murphy and King fed groups of molting captive White-crowned Sparrows synthetic diets containing either 0.28% or 0.83% SAA, a range that encompassed the percentage of SAA in the natural foods of this species. They found no differences in the masses either of newly molted feathers in the aggregate or of just the rectrices. Furthermore, there was no difference in the amount of food ingested during molt on either diet, indicating that the low-SAA group did not increase food consumption to obtain sufficient SAA. Thus, there was no evidence that SAA intake constrained feather growth, even when the entire feather coat was replaced during the annual molt. SAA limitation in the regrowth of one rectrix seems even

more improbable. In White-crowned Sparrows, which are about the same size and dimension as Downy Woodpeckers, the rectrices comprise 7.0–8.4% of the total feather mass (Murphy and King 1984). One of the 12 rectrices would constitute 0.6–0.7% of the total feather mass. I assume that the ratio of outermost-rectrix mass to total-plumage mass will be the same order of magnitude for most bird species. Therefore, because SAA did not constrain the growth of a whole plumage coat, I conclude it would not constrain the growth of one rectrix in which an amount of SAA between two and three orders of magnitude less would be required.

SAA constraint of induced feather growth seems even more remote in wintering Downy Woodpeckers, which exist below their lower critical operative temperature, have omnivorous diets, or both. Murphy and King (1984) studied birds at thermoneutrality. Birds living below their thermoneutral zone require considerably more food to meet their maintenance energy requirements, and then would also ingest considerably more SAA.

Murphy and King's minimum SAA diet was constructed to be below the minimum expected in a granivorous bird such as the White-crowned Sparrow. Omnivores (Martin et al. 1951) ingest at least some animal flesh, which contains approximately twice as high a proportion of SAA as plant material (Newton 1968). I conclude that, under normal conditions, differences in induced feather growth found among categories of birds cannot be caused by differential access to a limiting supply of dietary sulfur-containing amino acids. However, it is important to bear in mind that some other specific nutrient deficiency could limit feather growth even when metabolizable energy is sufficient.

*Day length.*—The daylight portion of each 24-h period varies with season and latitude. As most birds do not forage at night, short day length may result in a shortfall of energy or a specific nutrient. Such a shortfall would cause a reduction in daily growth of feathers even if food was plentiful during the daylight hours. However, reducing the L:D cycle from 20:4 to 12:12 for White-crowned Sparrows (Murphy and King 1986) and from 12:12 to 8:16 for White-breasted Nuthatches (*Sitta carolinensis*; A. P. Marshall and T. C. Grubb Jr. MS) failed to reduce the daily rate of feathers in the laboratory when the birds had access to *ad libitum* food during the daylight

hours. Whether or not day length constrains induced feather growth in free-ranging birds, such a constraint can be controlled by experimental designs in which birds in various treatment groups are plucked at the same time of the year, as was done with the Downy Woodpeckers.

*Temperature.*—A third theoretical constraint is low temperature. Feather growth in the follicle presumably follows the "Q<sub>10</sub> Law" which states that the rate of chemical reactions increases by a factor between 2 and 3 with each 10°C increase in temperature (Davson 1964). I have not found any description of the surface or subsurface temperature of the pygostyle as a function of ambient temperature, but the pygostyle is somewhat removed from the bird's core, and in cold weather the temperature of a follicle in the tail may be so reduced that the rate of induced feather growth slows independently of available energy and specific nutrients. Such direct temperature effects, if present, could confound interpretation of differences in induced feather growth among free-ranging birds. To control for such effects, comparisons among different categories of free-ranging birds can be designed so that birds in different treatment groups are plucked contemporaneously, as was done with the Downy Woodpeckers.

*Wind.*—Air temperature and wind act together to affect metabolic rates and behavior of small birds (e.g. Mayer et al. 1979). As the wind velocity increases, convective heat loss increases and the integrity of a bird's plumage becomes increasingly disturbed, reducing the insulating capability (Bakken et al. 1985). A combination of wind and low temperature could also slow induced rectrix growth by directly cooling the follicle in the pygostyle. Similar to the effect of temperature alone, a combined chilling effect at the follicular level would confound interpretation of differences in feather growth among categories of birds that result solely from differing nutritional constraints. This could affect comparisons among categories of free-living birds if all such categories were not exposed to similar temperature and wind conditions (Glase 1973; Grubb 1975, 1977, 1978; Peters and Grubb 1983). Once a relationship between rectrix growth rate and the combined chilling effect of temperature and wind has been established, correction factors can be applied to growth rates of free-ranging birds where required.

Downy Woodpeckers of both sexes roost at night in cavities where wind velocity must be at or near zero (Grubb 1982, Peterson and Grubb 1983). Because female Downy Woodpeckers tend to forage lower in a woodland and on larger diameter substrates than males, females are generally exposed to lower wind velocities. Therefore, any effect of wind velocity at the level of the follicle would have biased against the observed higher growth rates of induced feathers in males.

Ptilochronology appears to have the potential to reveal new insights into the nutritional ecology of free-ranging birds. Hypotheses of ultimate causation that predict variation in the nutritional status of birds of different age, sex, dominance status, dialect-group, deme, information center, breeding experience, support from helpers, species, niche, habitat, migratory pathway, guild, community, and exposure to environmental toxicants can be tested directly.

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