

PTILOCHRONOLOGY REVEALS DIFFERENCES IN CONDITION OF CAPTIVE WHITE-THROATED SPARROWS

KENDELL D. JENKINS, DANA M. HAWLEY, CHRISTOPHER S. FARABAUGH AND DANIEL A. CRISTOL¹

Dept. of Biology, P.O. Box 8795, College of William & Mary, Williamsburg, VA 23187

Abstract. Ptilochronology is a technique in which the growth rate of a feather is used as an assay of a bird's condition. Two important questions remain regarding this decade-old technique: (1) Does the daily rate of feather growth correspond very closely with changes in nutritional status during feather growth? and (2) For which stressors can ptilochronology be used as a reliable assay? Using an experimental manipulation of diet, we tested the effectiveness of ptilochronology for assessing nutritional condition in male White-throated Sparrows (*Zonotrichia albicollis*). Our hypothesis was that birds given an ample diet would be in better condition than those given a subsistence diet, as indicated by faster feather growth. In a second experiment, we examined the effect of a stressor, low social status, on feather growth. We expected that dominant birds would be in better condition and regrow feathers faster than subordinates because of their priority of access to food. Birds fed an enriched diet weighed more, grew longer feathers, and had wider growth bars than birds receiving a diet lower in protein and calories. Dominants retained more fat than subordinates, but did not grow significantly longer feathers or wider growth bars. However, within flocks, the differences in social status between the birds corresponded to differences in growth-bar width. Our results support the validity of ptilochronology for directly detecting differences in nutritional status during feather regrowth, and point to a likely influence of social status, a density-dependent ecological stressor, on feather growth rates.

Key words: dominance, feather growth, nutrition, ptilochronology, social status, *Zonotrichia albicollis*.

La Ptilocronología Revela Diferencias en la Condición de Individuos de *Zonotrichia albicollis* en Cautiverio

Resumen. La ptilocronología es una técnica en la que la tasa de crecimiento de una pluma se utiliza para examinar la condición física de un ave. Dos preguntas sobre esta técnica desarrollada hace una década permanecen abiertas. Primero, ¿está la tasa diaria de crecimiento de las plumas relacionada estrechamente con cambios en el estatus nutricional de las aves durante el crecimiento de las plumas? Segundo, ¿para cuáles agentes causantes de estrés puede usarse la ptilocronología como un examinador confiable? Mediante una manipulación experimental de la dieta, pusimos a prueba la efectividad de la ptilocronología para determinar la condición nutricional de machos de *Zonotrichia albicollis*. Nuestra hipótesis era que aves con una dieta rica estarían en mejor condición que aves con una dieta de subsistencia, lo que sería indicado por un crecimiento más rápido de las plumas. En un segundo experimento, evaluamos el efecto de un factor de estrés (bajo estatus social) en el crecimiento de las plumas. Esperábamos que las aves dominantes estuvieran en mejor condición y que sus plumas crecieran más rápidamente que las de aves subordinadas debido a su acceso prioritario al alimento. Las aves con dieta rica pesaron más, desarrollaron plumas más largas y tuvieron barras de crecimiento más amplias que las aves que recibieron una dieta con menor contenido de proteínas y calorías. Las aves dominantes retuvieron más grasa que las subordinadas pero no desarrollaron plumas significativamente más largas ni barras de crecimiento más amplias. Sin embargo, al interior de bandadas, las diferencias en estatus social entre las aves se reflejaron en diferencias en la amplitud de las barras de crecimiento. Nuestros resultados apoyan la validez de la ptilocronología para detectar diferencias en estatus nutricional durante el período de crecimiento de las plumas directamente y apuntan a una probable influencia del estatus social (un factor ecológico denso-dependiente causante de estrés) sobre las tasas de crecimiento de las plumas.

INTRODUCTION

During the last decade, ptilochronology has been

adopted as a technique for evaluating nutritional condition in birds based on the width of sequential bands, called growth bars, on feather vanes (Grubb 1989). Dark and light bands are generally assumed to be produced during the day and night, respectively, so each set of bars represents

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¹ E-mail: dacris@facstaff.wm.edu

24 hr of growth (Riddle 1908, Michener and Michener 1938), and their width represents the rate of growth of the feather. Ptilochronology assumes that feather growth is related to nutritional status, and has been used as a proxy for overall condition and an assay for ecological stressors (Grubb 1995).

Despite wide acceptance, criticism has been leveled at the technique of ptilochronology. Growth bars are often difficult to see, and the majority of successful applications of the technique have been carried out by only a few investigators. More importantly, Murphy and King (1991) found that "Only lethal kinds or levels of nutritional privation consistently slowed feather growth. Moderate or even severe sublethal privation did not produce consistent effects on feather growth." In addition, Murphy (1992) argued that the technique involves too many untested assumptions and unresolved limitations, and that not enough is known about the role of nutritional condition in feather growth rate.

Two fundamental questions must be resolved before ptilochronology can be applied as a technique rather than a hypothesis (Murphy 1992). First, does growth-bar width correspond closely enough to nutritional status to be used as a reliable record of condition during feather regrowth? Second, if ptilochronology does measure these changes in nutritional status, which types of ecological stressors, if any, can be reliably detected with this technique?

To evaluate the reliability of ptilochronology as an indicator of nutritional status, we measured feather growth rates in captive White-throated Sparrows (*Zonotrichia albicollis*) using a manipulation of diet. We predicted that feather growth rates would be higher for birds of better nutritional status, which would support the use of ptilochronology as a direct assessment of condition. In a separate experiment, we examined whether ptilochronology could detect stress resulting from low social status in captive flocks of White-throated Sparrows. This species is known to establish dominance hierarchies on the wintering grounds (Falls and Kopachena 1994). Dominant birds have greater access to resources because they can feed at safer sites and times of the day and can supplant subordinates from food (Schneider 1984, Piper 1990, Piper and Wiley 1990). Free-living dominant White-throated Sparrows had greater fat reserves and higher survival between years than subordinates (Piper

and Wiley 1990), but no one has measured the direct effect of social status on feather growth rates in this species. We tested the prediction that dominant birds would have higher feather growth rates than subordinates.

METHODS

EXPERIMENT 1: DIET AND FEATHER GROWTH

The purpose of experiment 1 was to determine whether differences in nutritional status could be detected as differences in feather growth rates. From 18 January to 2 February 2000, 72 White-throated Sparrows were captured in a 4-ha woodlot in Williamsburg, Virginia. Unbaited mist nets and baited ground traps were used at three trapping stations 100 m apart along the edge of the woodlot. Only birds with ≥ 74 -mm unflattened wing length were used, which eliminated variation due to sex since birds this size are known to be males (Piper and Wiley 1991). Age could not be determined reliably in late January when we caught most of these birds (Pyle 1997). We randomly assigned the birds to one of two large outdoor cages located adjacent to the woodlot ($8.3 \times 2.4 \times 2.1$ m [height]). The birds acclimated to the cages for 10–14 days before the diet manipulation commenced.

Beginning 10 February, one cage of birds ($n = 36$) received a subsistence diet for the duration of the experiment, while the other group ($n = 36$) received a diet more than sufficient in quantity and quality. The group receiving the subsistence diet (hereafter Low) was given 200 g daily of food containing four parts cracked corn, three parts white millet, and two parts red millet in eight food dishes. This quantity was slightly in excess of the birds' caloric needs, based on the observation that there was a small amount of grain, usually just corn, left in the dishes each morning. Spilled grain was always removed before refilling dishes so that a consistent amount of food was available, and so that less-preferred seeds would not accumulate. The birds receiving the ample diet (hereafter High) were given 500 g daily of a mixture containing four parts cracked corn, three parts white millet, two parts red millet, two parts sunflower hearts, one part thistle, and one part high-protein turkey starter, as well as 2–3 *Tenebrio* larvae per bird, and *ad libitum* carrots, boiled eggs, and parsley, also in eight food dishes, such that preferred foods were available to all birds at all times.

This quantity was far in excess of the birds' caloric needs based on the amount of seed left at the end of each day. Spilled food was allowed to remain for several days to increase availability away from the food dishes. Both groups received *ad libitum* vitamin/mineral fortified water, grit, and cuttlefish bones.

On 7 February, between 09:00 and 12:00, we weighed each bird and scored their furcular fat deposits (on a scale of 0–5), and then plucked their two outermost right rectrices (in case of damage to one of the replacement feathers). Thereafter, birds were handled only once every seven days, at approximately 10:00, to check health and obtain a fat score and mass. After 52 days in captivity, one induced rectrix was pulled, allowing us to measure the length and growth-bar widths of the original and induced feathers. We measured the outermost rectrix unless it was damaged ($n = 3$), in which case we used the penultimate original and induced feathers. Birds were released at site of capture at the end of the experiment.

To measure feather growth rate we followed Grubb's (1989) procedure: (1) the feather was attached to a card; (2) a point one-third of the distance from the distal end was marked; (3) the edges of the ten growth bars centered on this point were marked on the card with size 0 insect-mounting pins; and (4) the width of each growth bar was measured to the nearest 0.1 mm with dial calipers and the mean calculated. If fewer than ten growth bars could be detected, the mean of all detectable bars was used instead. This procedure was carried out by an observer who was blind to the treatments, with original and induced feathers for all birds. In addition, the length of all feathers was measured from the distal end to the superior umbilicus. Since most of the feathers from Low birds had not completed regrowth, while most of those from High birds had recently completed regrowth, total length produced in 52 days provided a highly conservative comparison of growth rate.

EXPERIMENT 2: SOCIAL STATUS AND FEATHER GROWTH

Because we found a strong relationship between nutritional condition and feather growth in experiment 1, we examined the data from a previous study (experiment 2) for evidence of a relationship between social status and feather growth rate. As there is ample evidence from

free-living White-throated Sparrows that dominants have greater access to food, we predicted that ptilochronology would detect lower feather growth rates in subordinates. White-throated Sparrows were caught between 6 January and 28 February 1999 in the same woodlot as described above. Our sample consisted mainly of males (all wings ≥ 72 mm) that were either yearlings caught early enough to detect incomplete skull ossification ($n = 42$) or of unknown age ($n = 14$). Fourteen flocks of four sparrows with unique color-band combinations were established in outdoor cages adjacent to the woodlot (3.1 m \times 2.4 m \times 2.1 m). A separate study had established with reasonable certainty that the colors of bands we used did not have detectable effects on dominance status (Johnson 1999). Dominance hierarchies were observed from 09:00–12:00 for two days (until all birds had interacted aggressively at least five times and one member of each dyad had won $>90\%$ of the interactions). Each bird was then given a dominance score based on the proportion of flockmates dominated. The difference in proportion of flockmates dominated by the highest and lowest-ranked birds differed between flocks as a result of ties and nonlinearities and is a measure of the degree of despotism.

The penultimate rectrix on both sides of the tail was pulled. This method left the outer rectrix in place to prevent abrasion of replacement feathers, but was not used in experiment 1 because it was difficult to monitor accurately the replacement of penultimate feathers without handling birds. Replacement feathers were allowed to regrow for 36 days, during which the flock was left entirely unhandled and undisturbed except for brief, twice-daily feedings (09:00 and 14:00). Flocks were given a total of 35 g of corn, millet, sunflower hearts, thistle, and turkey starter mash, and eight *Tenebrio* larvae daily in one dish. This resulted in *ad libitum* availability of less preferred food items such as corn, while preferred items such as *Tenebrio* larvae, sunflower hearts, and thistle ran out approximately one hour after each feeding. We provided 9.5 g of extra seeds on cold days (high temperature $< 0^\circ\text{C}$).

To determine if dominance hierarchies resulted in differential access to food, we conducted foraging observations three times per flock between 09:30 and 12:00 at seven-day intervals. Each flock was deprived of food for one hour,

and then the following variables were recorded for each bird: time spent waiting within 0.2 m of food while another bird occupied the dish, time spent on food dish, number of visits to food dish, latency to enter food dish, number of *Tenebrio* larvae obtained, latency to eat first *Tenebrio* larva, and number of pecks while on food dish.

Ptilochronology was carried out as described for experiment 1, except that two rectrices were measured instead of one. When birds regrew both rectrices the average of the two feathers was used. If only one rectrix regrew ($n = 2$) that one measurement was used. When either the dominant or subordinate did not replace either plucked feather ($n = 10$), the next closest bird in the dominance hierarchy was used as a substitute. Because all induced feathers were collected before growth was complete, we used total length produced in 36 days to determine growth rate. Stored fat reserves and mass were measured at approximately 10:00 on the days that the original and induced feathers were pulled. Because all birds in each flock replaced their feathers under identical conditions, but flocks may have differed somewhat in environmental factors (for example exposure of cages to sunlight) we used a paired statistical design comparing only the differences between the dominant and subordinate in each flock. To eliminate any differences between flocks that might have arisen from differential degrees of despotism, we used linear regression to examine whether flocks with greater differences in dominance scores between the dominant and subordinate birds also had greater differences in feather growth rate between these birds.

STATISTICAL ANALYSES

Analyses were performed using JMP (SAS Institute 1995). Two-tailed t -tests were used for two-sample comparisons except where data did not conform to a normal distribution. We used nonparametric Wilcoxon rank-sum tests when data could not be normalized. We used ANCOVA to compare length or growth-bar width of induced feathers between treatments in experiment 1 using length, or growth-bar width, respectively, of the original feathers as the covariate. We used paired t -tests to compare variables for dominant and subordinate birds from the same flock in experiment 2. When comparing induced feathers we divided by the corre-

sponding measurement from each bird's original feather to correct for size, and then proceeded with paired tests. We used linear regression to examine the relationship between difference in rank and difference in induced feather length or growth-bar width in experiment 2. For these regression analyses we corrected induced length or growth-bar width by the corresponding values from the original feathers to correct for size differences. Data are presented as untransformed means \pm SD in the text (means \pm SE in the figure).

It should be noted that experiment 1 was pseudoreplicated: all birds from one treatment were housed together in a large cage, while those from the other treatment were housed together in an adjacent cage of identical dimensions and layout. We used this experimental design because we wanted to measure the responses of birds living in a semi-natural setting where, for example, they could engage in social interactions with familiar flockmates, experience normal weather fluctuations, compete for food, and exercise their flight muscles extensively. As a result, we violated the assumption that every bird was an independent data point and our statistical conclusions must be interpreted with caution. We hope that what we sacrificed in statistical rigor by not caging birds separately was more than balanced by increased applicability of our results to free-living birds.

RESULTS

EXPERIMENT 1: DIET AND FEATHER GROWTH

The High and Low diet birds did not differ in fat scores at either the beginning or end of the treatment (Table 1). Both groups of birds declined in fat score, and this change did not differ significantly between groups (Wilcoxon rank-sum test, $Z = 1.5$, $n = 71$, $P = 0.13$). At the start of the experiment there was no difference in body mass of the two groups; however, by the end the High birds weighed significantly more than their Low diet counterparts (Table 1).

All birds replaced their plucked rectrices. While the lengths of the original feathers of the two groups did not differ, the induced feathers of the High birds grew significantly longer than those of the Low birds (Table 1). Likewise, there was no difference between groups in the width of the growth bars of the original feathers ($t_{69} = 1.6$, $P = 0.13$), but the induced growth bars of

TABLE 1. Comparisons of fat, mass, and feather growth for White-throated Sparrows receiving an ample diet (High, $n = 36$) or subsistence diet (Low, $n = 35$) in experiment 1.

	Treatment	Mean \pm SD	Test statistic	P	
Fat score	Start	High	1.9 \pm 0.7	1.9 ^a	0.06
		Low	1.5 \pm 0.9		
	End	High	0.3 \pm 0.8	0.3 ^a	
		Low	0.3 \pm 0.5		
Mass (g)	Start	High	28.1 \pm 1.9	0.4 ^a	>0.5
		Low	28.4 \pm 2.2		
	End	High	25.9 \pm 1.9	2.9 ^b	
		Low	24.6 \pm 1.9		
Feather length (mm)	Original	High	70.6 \pm 2.4	1.2 ^b	0.23
		Low	71.3 \pm 1.9		
	Induced	High	69.1 \pm 2.7	36.5 ^c	
		Low	62.5 \pm 6.1		

^a Wilcoxon rank-sum tests, Z .

^b t -test.

^c ANCOVA, $F_{2,68}$.

the High group were significantly wider than those of the Low birds ($t_{69} = 6.7$, $P < 0.001$; Fig. 1).

EXPERIMENT 2: SOCIAL STATUS AND FEATHER GROWTH

As predicted, subordinates spent significantly more time than dominants waiting near the food dish while another bird occupied it, and made significantly more visits to the food bowl than dominants (Table 2). There were no rank-related differences in other measured feeding variables

TABLE 2. Comparisons of foraging by the dominant (D) and subordinate (S) individuals from 14 captive flocks of White-throated Sparrows in experiment 2.

	Status	Mean \pm SD	t	P
Time around food (sec)	D	3.1 \pm 6.3	2.2	<0.05
	S	21.4 \pm 35.9		
Time on food (sec)	D	57.3 \pm 32.4	0.9	0.39
	S	68.5 \pm 36.4		
Number of visits to food	D	3.2 \pm 1.6	2.5	<0.05
	S	4.4 \pm 2.2		
Latency to food (sec)	D	186.8 \pm 130.3	0.1	>0.5
	S	183.7 \pm 174.8		
Number of <i>Tenebrio</i>	D	0.6 \pm 0.5	1.2	0.26
	S	0.9 \pm 0.9		
Latency to <i>Tenebrio</i> (sec)	D	440.3 \pm 136.8	0.9	0.38
	S	356.4 \pm 240.7		
Peck rate (pecks sec ⁻¹)	D	0.6 \pm 0.1	0.3	>0.5
	S	0.6 \pm 0.2		

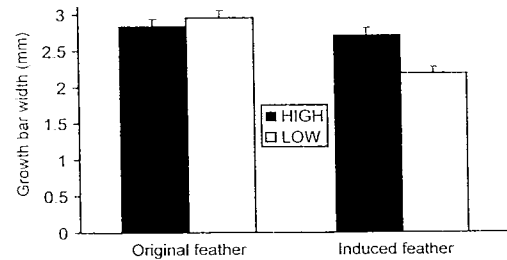


FIGURE 1. Original and induced growth-bar widths (\pm SE) for White-throated Sparrows fed an ample diet (High, $n = 36$) or a subsistence diet (Low, $n = 35$).

(Table 2). Dominant and subordinate sparrows differed in change in fat scores, with subordinates decreasing and dominants increasing levels of stored fat over the 36 days of the experiment ($t_{12} = 2.3$, $P < 0.05$; Table 3). Fat score did not differ by social rank at the start of the study and, although subordinates lost fat during the experiment and dominants gained, this apparent difference was not significant (Table 3). The mass changes of the two groups did not differ ($t_{12} = 1.9$, $P = 0.08$) with the result that dominants did not weigh significantly more than subordinates at the end of the experiment (Table 3). These data suggest that the diet and degree of competition for the food bowl were austere enough to push fat reserves of dominants and subordinates in different directions, but not severe enough to produce significant differences in fat or mass.

The mean length or growth-bar width of induced feathers did not differ between dominant and subordinate birds across all flocks (Table 3).

TABLE 3. Comparisons of feather growth and condition parameters for dominant (D) and subordinate (S) White-throated Sparrows from 14 captive flocks in experiment 2. Means of dominants and subordinates did not differ significantly (all $t < 1.7$, all $P > 0.11$).

	Status	Mean \pm SD
Start fat score	D	1.4 \pm 0.5
	S	1.6 \pm 0.6
End fat score	D	1.7 \pm 0.7
	S	1.3 \pm 0.7
Start mass (g)	D	27.0 \pm 1.4
	S	27.4 \pm 1.7
End mass (g)	D	27.2 \pm 2.7
	S	26.8 \pm 2.5
Original length (mm)	D	78.5 \pm 2.3
	S	78.9 \pm 2.5
Induced length (mm)	D	62.2 \pm 10.3
	S	60.0 \pm 11.3
Original growth-bar width (mm)	D	3.2 \pm 0.2
	S	3.2 \pm 0.3
Induced growth-bar width (mm)	D	2.6 \pm 0.3
	S	2.6 \pm 0.2

The difference between dominants and subordinates in feather length was significantly related to the difference in ranks ($r^2 = 0.31$, $F_{1,11} = 5.0$, $P < 0.05$; Fig. 2), indicating that in flocks with a high degree of despotism the dominants grew feathers faster than subordinates, while that was not the case where dominants were less despotic toward lower-ranking birds. However, this pattern was not apparent for measures of growth-bar width ($r^2 = 0.09$, $F_{1,9} = 0.9$, $P = 0.38$), indicating that the daily growth bars we measured were not responsible for the relationship between overall length produced and degree of despotism.

DISCUSSION

As predicted, birds in one large flock provided with more and better food were heavier and grew feathers faster than birds in another large flock held under identical conditions but on a diet lower in quantity and quality. This finding supports the fundamental assumption of ptilochronology, that diet influences nutritional condition, which in turn affects feather growth on a regular basis. Since replacing feathers is a productive process and requires excess energy and nutrients (King 1974, King and Murphy 1985), it is not surprising that feather growth varies according to nutritional condition. However, studies on a congener of our study species failed to find consistent effects of nutrition on feather

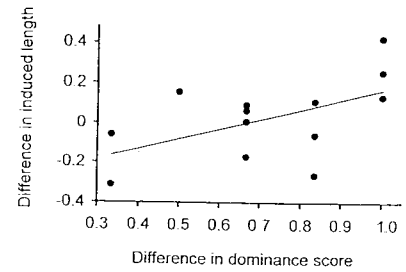


FIGURE 2. Relationship between difference in the size-corrected induced feather length and difference in dominance score within 14 flocks of White-throated Sparrows ($y = 0.59x - 0.33$). Flocks with greater degrees of despotism had greater differences in feather growth rates.

growth rate. White-crowned Sparrows (*Z. leucophrys*) maintained on various marginal diets or deprived of specific amino acids lost body mass, but showed no consistent, significant declines in feather growth rates (Murphy and King 1991). Our results agree with two other studies on captive birds in which inadequate quantity (Grubb 1991) or protein content (Pehrsson 1987) slowed feather regeneration, and thus our data provide additional support for the basic assumption of ptilochronology. The fact that mass differed at the end of the experiment between birds on our ample and subsistence diets, but stored fat reserves did not differ (both were low), suggests that birds on the subsistence diet had metabolized some muscle, but we did not measure muscle mass. We conclude that feather growth rates can be used to assay nutritional condition over periods of weeks or months under semi-natural living conditions ranging from chronic food restriction to *ad libitum* resources.

In a second experiment with 14 small captive flocks, subordinates made more visits to food dishes and spent more time near but not in them, suggesting that they were foraging less efficiently than dominants. Dominant birds gained fat and subordinates lost it during the course of the experiment, consistent with results from free-living White-throated Sparrows (Piper and Wiley 1990). When interflock differences in despotism were controlled, the data supported our prediction that dominants would grow feathers faster than subordinates, although this was true only for feather length, not growth-bar width. Despite these differences, several other measures of foraging success, including time in food dish, failed to indicate greater access to food for dominants

under our experimental conditions. In addition, the rank-related difference in direction of change in fat reserves did not result in differences in mass or fat at the end of the experiment. We conclude that we probably produced only slight differences in access to resources, severe enough that subordinates spent more time waiting for food, but mild enough that nutritional condition and feather growth were affected only in flocks with highly despotic dominant birds.

There have been several previous studies that used ptilochronology to directly measure the effects of dietary manipulation, and the technique has succeeded in detecting the predicted effects in most cases (e.g., Grubb and Cimprich 1990, Waite 1990, Nilssen et al. 1993; but see Murphy and King 1991). Ptilochronology has also been used previously as an assay for the effect of an ecological stressor on condition. For example, numerous studies on social organization or habitat quality have detected the predicted effects (Hogstad 1992, Grubb and Yosef 1994, Carlson 1998, Carrascal et al. 1998). In contrast, a similar number of studies on increased molt or reproductive effort have revealed no effect on feather growth (Mauck and Grubb 1995, Langston and Rohwer 1996, Ogden and Stutchbury 1996, Senar et al. 1998; but see White et al. 1991). Likewise, a number of studies on climatic variables, both specific (wind chill) and more general (region or season) have failed to detect consistent effects. For instance, White-crowned Sparrows grew feathers more slowly in cold temperatures (Murphy and King 1991), but wind chill did not slow growth of White-breasted Nuthatch (*Sitta carolinensis*) feathers (Zuberbier and Grubb 1992). In another example, feather length, but not growth-bar width, was affected by day length in American Tree Sparrows (*Spizella arborea*; White and Kennedy 1992). Thus, ptilochronology has reliably detected ecological stressors originating from changes in density-dependent factors such as territory size, social rank, or degree of competition, but not necessarily those stressors related to density-independent factors such as wind chill or day length, or internal physiological changes such as molt or reproductive effort.

In experiment 1, birds on better diets weighed more and grew longer replacement feathers with wider growth bars than their counterparts maintained on a protein and calorie-restricted, but not lethal, diet. Our results, along with those of oth-

ers in the literature, validate the use of ptilochronology to assay nutritional condition in birds. In experiment 2, we found that under a dietary regime severe enough only to cause subordinates to wait for food, rank-related differences in feather growth were detectable when interflock differences in despotism were controlled statistically. Clearly, ptilochronology can detect changes in nutritional condition, including those brought about by certain stressors, such as subordinate social status, but effects may be subtle. Numerous studies (examples cited above) suggest that some types of ecological stressors, such as those resulting from climate, molt or reproductive effort, are not consistently detected by ptilochronology. We conclude that only certain stressors, possibly those that are density-dependent, diminish nutritional condition in ways that affect feather growth. Practitioners of ptilochronology should use the technique as an assay only for those stressors that it can detect reliably, and future research should be directed at lengthening the list of reliably detectable stressors.

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LITERATURE CITED

- CARLSON, A. 1998. Territory quality and feather growth in the White-backed Woodpecker *Dendrocopos leucotos*. *Journal of Avian Biology* 29:205-207.
- CARRASCAL, L. M., J. C. SENAR, I. MOZETICH, F. URIBE, AND J. DOMENECH. 1998. Interactions among environmental stress, body condition, nutritional status, and dominance in Great Tits. *Auk* 115:727-738.
- FALLS, J. B., AND J. G. KOPACHENA. 1994. White-throated Sparrow. In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 128. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- GRUBB, T. C., JR. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106:314-320.
- GRUBB, T. C., JR. 1991. A deficient diet narrows growth bars on induced feathers. *Auk* 108:725-727.

- GRUBB, T. C., JR. 1995. Ptilochronology: a review and prospectus. *Current Ornithology* 12:89-114.
- GRUBB, T. C., JR., AND D. A. CIMPRICH. 1990. Supplementary food improves the nutritional condition of wintering woodland birds: evidence from ptilochronology. *Ornis Scandinavica* 21:277-281.
- GRUBB, T. C., JR., AND R. YOSEF. 1994. Habitat-specific nutritional condition in Loggerhead Shrikes (*Lanius ludovicianus*): evidence from ptilochronology. *Auk* 111:756-759.
- HOGSTAD, O. 1992. Mate protection in alpha pairs of wintering willow tits, *Parus montanus*. *Animal Behaviour* 43:323-328.
- JOHNSON, K. M. 1999. Timing of spring migration in White-throated Sparrows. M.A. thesis, College of William & Mary, Williamsburg, VA.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds, p. 4-85. In R. A. Payntor Jr. [ED.], *Avian energetics*. Nuttall Ornithological Club, Cambridge, MA.
- KING, J. R., AND M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *American Zoologist* 25:955-964.
- LANGSTON, N. E., AND S. ROHWER. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* 76:498-510.
- MAUCK, R. A., AND T. C. GRUBB JR. 1995. Parent petrels shunt all experimentally increased reproductive costs to their offspring. *Animal Behaviour* 49:999-1008.
- MICHENER, H., AND J. R. MICHENER. 1938. Bars in flight feathers. *Condor* 11:149-160.
- MURPHY, M. E. 1992. Ptilochronology: accuracy and reliability of the technique. *Auk* 109:676-680.
- MURPHY, M. E., AND J. R. KING. 1991. Ptilochronology: a critical evaluation of assumptions and utility. *Auk* 108:695-704.
- NILSSEN, J.-A., H. KÄLLANDER, AND O. PERSSON. 1993. A prudent hoarder: effects of long-term hoarding in the European nuthatch, *Sitta europaea*. *Behavioral Ecology* 14:369-373.
- OGDEN, L. J. E., AND B. J. M. STUTCHBURY. 1996. Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. *Condor* 98:736-744.
- PEHRSSON, O. 1987. Effects of body condition on molting Mallards. *Condor* 89:329-339.
- PIPER, W. H. 1990. Exposure to predators and access to food in wintering White-throated Sparrows (*Zonotrichia albicollis*). *Behaviour* 112:284-298.
- PIPER, W. H., AND R. H. WILEY. 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-throated Sparrows (*Zonotrichia albicollis*). *Behavioral Ecology and Sociobiology* 26:201-208.
- PIPER, W. H., AND R. H. WILEY. 1991. Effects of laparotomies on wintering White-throated Sparrows and the usefulness of wing chord as a criterion for sexing. *Journal of Field Ornithology* 62:40-45.
- PYLE, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.
- RIDDLE, O. 1908. The genesis of fault bars in feathers and the cause of alteration of light and dark fundamental bars. *Biological Bulletin* 3:289-294.
- SAS INSTITUTE INC. 1995. JMP statistics and graphics guide. Version 3.2. SAS Institute Inc., Cary, NC.
- SCHNEIDER, K. J. 1984. Dominance, predation, and optimal foraging in White-throated Sparrow flocks. *Ecology* 65:1820-1827.
- SENAR, J. C., F. URIBE, J. DOMÉNECH, AND L. M. CARRASCAL. 1998. Successive removal of individual rectrices does not influence the subsequent growth of the replacement feathers in the Great Tit *Parus major*. *Ibis* 140:522-530.
- WAITE, T. A. 1990. Effects of caching supplemental food on induced feather regeneration in wintering Gray Jays *Perisoreus canadensis*: a ptilochronology study. *Ornis Scandinavica* 21:122-128.
- WHITE, D. W., AND E. D. KENNEDY. 1992. Growth of induced feathers in photostimulated American Tree Sparrows. *Condor* 94:543-545.
- WHITE, D. W., E. D. KENNEDY, AND P. C. STOFFER. 1991. Feather regrowth in female European Starlings rearing broods of different sizes. *Auk* 108:889-895.
- ZUBERBIER, G. M., AND T. C. GRUBB JR. 1992. Ptilochronology: wind and cold temperatures fail to slow induced feather growth in captive White-breasted Nuthatches *Sitta carolinensis* maintained on *ad libitum* food. *Ornis Scandinavica* 23:139-142.