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PTILOCHRONOLOGY: INDUCED FEATHER GROWTH IN NORTHERN CARDINALS VARIES WITH AGE, SEX, AMBIENT TEMPERATURE, AND DAY LENGTH

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ABSTRACT.—Growth bars indicate 24-h periods of feather growth. Ptilochronology uses the width of growth bars on an induced feather to monitor avian nutritional condition, the wider the growth bars the better the condition. Because such an interpretation could be confounded if extraneous variables remained uncontrolled, we investigated whether seasonality, temperature, photoperiod, and a bird's age and sex influenced the daily growth of an induced feather. Width of growth bars, and the total length and mass of both an induced feather and the original feather grown from the same follicle during the preceding pre-basic molt varied significantly with the age and sex of Northern Cardinals (*Cardinalis cardinalis*). These same characteristics of induced feathers also varied significantly with season. Despite strong collinearity between ambient temperature and photoperiod, the former appeared to be the more important predictor of feather growth. These results indicate that variation in feather growth due to age, sex, and season of the year must be accounted for in the design of experiments using ptilochronology to examine avian nutritional condition. *Revised 11 Jan. 1991, accepted 13 March 1991.*

The technique termed ptilochronology uses the width of daily growth bars on an induced feather as an index of a bird's nutritional condition (Grubb 1989). Because the plumage coat is important in protection, thermoregulation, and locomotion (Murphy et al. 1988), feather regeneration should proceed as rapidly as possible subject to certain constraints. Such constraints could be exogenous (e.g., food scarcity), endogenous (e.g., allocation of assimilated resources to reproduction), or both. Reduction of feather growth might then be considered a 'compensatory mechanism' (sensu King and Murphy 1985) counterbalancing such constraints. Thus, the reduced growth of an induced feather might indicate a reduction in nutritional condition too minor to cause the net catabolism of body tissues and resulting mass loss that King and Murphy (1985) considered to be the definitive indicators of "nutritional stress."

Ptilochronology depends on two principles, both of which now have empirical support: (1) one growth bar equals 24 hours' growth of the feather (Michener and Michener 1938), and (2) a deficient diet causes a

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reduction in growth bar width (Grubb, in press). However, the interpretation that a reduction in growth bar width indicates a lowering of nutritional condition could be confounded if other factors also influence the rate of feather growth. Recently, Zuberbier and Grubb (unpubl. data) have shown that the rate of daily feather growth in captive White-breasted Nuthatches (*Sitta carolinensis*) on ad libitum food was unaffected by various wind velocities in combination with ambient temperatures well below the thermal neutral zone. Thus, reduction of daily feather growth in birds wintering in cold climates can be more confidently ascribed to a reduction in nutritional condition uncomplicated by any "wind-chill" phenomenon acting at the level of the follicle.

We examined daily growth of induced rectrices of Northern Cardinals (*Cardinalis cardinalis*) in relation to the birds' age and sex, and to the ambient temperatures and daylengths in which the rectrices were regenerated. This sedentary species inhabits old-field communities and the brushy margins of woodlands (Dow 1969a, b). While omnivorous, cardinals maintain a higher percentage of plant food in their diet during winter (88%) than during summer (39%), with spring and autumn intermediate (Martin et al. 1951).

METHODS

At two banding stations (39°00′N, 84°02′W and 39°00′N, 84°03′W) near Cincinnati, Ohio, AJW pulled the outermost right (R6) rectrix from Northern Cardinals during the latter months of 1968, all of 1969, and the early months of 1970. Birds were sexed by plumage color. Age was determined by color of body plumage and bill, retained juvenile primaries and/or secondaries, color and shape of rectrix tips (Scott 1967), skull ossification, or by a combination of these characteristics (Wiseman 1977). AJW then collected the regenerated feather weeks or months later, sometimes retrapping a bird several times and obtaining a sequence of induced R6 rectrices. To reduce the potential impact of uncontrolled variables, we confine this analysis to the first induced R6 rectrix of 186 individual cardinals first caught during 1969. All of these birds had access to supplementary food in the form of sunflower seeds and mixed small grains throughout the year.

As the original and induced rectrices were collected from each bird, they were taped by the rachis to an index card on which were recorded the collection dates of the feathers plus the bird's band number, age and sex. The feathers remained in storage until they were measured by TCG in 1989. During the intervening score of years, several feathers were partially consumed by feather lice. Therefore, while two of the three measures of feather growth we employed for analysis, growth bar width (Grubb 1989) and total feather length, were available for the entire sample, feather mass was obtained (to the nearest 0.1 mg on an analytical balance) for only the 177 pairs of original and induced feathers that had no apparent damage.

We inferred from our unpublished observations of other passerine species that regeneration of the 10 growth bars from which we computed mean daily growth of an induced feather (Grubb 1989) had occurred at about the middle of the 30-day period after the original feather had been pulled. Therefore, to assess the effects of day length and ambient temperature on feather growth, we first determined mean daylength (minutes between sunrise and sunset) at 40° N (Hoffman 1988) and mean daily maximum, minimum and average temperature (°C) at the Abbe Observatory near Cincinnati (39°09′N, 84°31′W; Anon. 1969) for the 30-day period after each pull date.

Statistical analyses.—We used three-way multivariate analysis of covariance (MANACOVA) to examine whether each of the three measures of induced feather growth in Northern Cardinals was related to age, sex or season (Jan–Apr, May–Aug, Sept–Dec), and whether interaction effects existed among these factors. In this design, the dependent variables were daily growth (mean growth bar width), total length and mass of the induced RC rectrix. The corresponding covariates were daily growth, total length and mass of the original R6 rectrix. We used the MANACOVA procedure because the daily growth, total length and mass of the induced rectrix were related roughly linearly to the daily growth, total length and mass of the original rectrix. Therefore, differences found in any of the three dependent variables between adults and juveniles, between males and females, or among seasons could be partly attributable to differences in the daily growth, total length or mass of the original rectrix. The MANACOVA should have removed this possible source of bias.

The results of the MANACOVA revealed significant covariate effects for all three dependent variables. Therefore, to assess whether the three measures of the growth of original R6 rectrices (daily growth, total length, and mass) might have been age- or sex-specific, we performed two-way analyses of variance on those measures.

To investigate whether photoperiod or air temperature might have been responsible for the seasonal patterns in rectrix regeneration, we first performed stepwise regressions of daily growth (DG_i), total length (TL_i), and mass (M_i) of the induced feather for each of the age-sex classes on several variables, mean day length and mean minimum, maximum and average temperatures, during the 30-day post-pluck period. We also performed the same analyses on the corresponding measures of growth of the original R6 rectrix (DG_o, TL_o, and M_o). The alpha-to-enter and alpha-to-remove were both set at 0.15. This procedure was used only to select a subset model for prediction purposes (see Wilkinson 1989 for rationale). We then used multiple regression analysis to estimate partial regression coefficients for each of the predictors (factors) selected to the subset model by the stepwise procedure. For the results of stepwise and parametric multiple regression analyses to be meaningful, a three-dimensional surface fitted to the relationship among three variables should form a tilted plane with relatively little global flex. Surface plots produced by distance-weighted least-squares smoothing (Wilkinson 1988) revealed pronounced nonplanar relationships among temperature, day length and all three measures of growth for cardinals of all four age-sex classes. In general, feather regeneration tended to be enhanced at high temperatures irrespective of day length, and on short days when temperature was relatively high. Therefore, all of the analyses described above were performed on ranks. This method is usually less powerful than parametric methods, but it circumvents the problem of nonplanar relationships among the variables and its results parallel those of parametric methods (Conover 1980).

RESULTS

The most striking result of the three-way MANACOVA (Table 1) was the significant effect of season for all three measures of rectrix regeneration (Fig. 1), with cardinals tending to regenerate their R6 rectrix most slowly and to the smallest total length and mass during the winter months. The sexes differed significantly in the mean daily growth rate of the induced rectrix. Although statistically significant, the difference between the means for males ($\bar{x}$ ± SD: 3.33 ± 0.33 mm/day) and females (3.35 ± 0.38 mm/

TABLE 1

RESULTS OF THREE-WAY MANACOVA FOR THREE MEASURES OF THE REGENERATION OF INDUCED R6 RECTRICES (DAILY GROWTH, TOTAL LENGTH, AND MASS) IN NORTHERN CARDINALS[a]

Measure of rectrix growth	Factor	df	*F*	*P*
Daily growth (N = 186)	Age	1, 173	0.443	0.506
	Sex	1, 173	4.014	0.047
	Season	2, 173	12.322	<0.001
	Age*sex	1, 173	0.000	0.991
	Age*season	2, 173	5.605	0.004
	Sex*season	2, 173	2.346	0.099
	Age*sex*season	2, 173	0.272	0.762
	DG_o	1, 173	7.455	<0.001
Total length (N = 186)	Age	1, 173	0.435	0.511
	Sex	1, 173	0.072	0.789
	Season	2, 173	14.978	<0.001
	Age*sex	1, 173	0.016	0.900
	Age*season	2, 173	2.052	0.131
	Sex*season	2, 173	3.104	0.047
	Age*sex*season	2, 173	0.301	0.740
	TL_o	1, 173	89.498	<0.001
Mass (N = 177)	Age	1, 173	0.091	0.764
	Sex	1, 173	1.465	0.228
	Season	2, 173	18.177	<0.001
	Age*sex	1, 173	0.076	0.783
	Age*season	2, 173	2.130	0.122
	Sex*season	2, 173	0.939	0.393
	Age*sex*season	2, 173	0.276	0.759
	M_o	1, 173	27.692	<0.001

[a] The factors are age, sex and season (Jan–Apr, May–Aug, Sept–Dec), and the corresponding covariates are daily growth (DG_o), total length (TL_o) and mass (M_o) of the original R6 rectrices.

day), irrespective of age and season, was small (see Fig. 2). Two significant interaction effects also emerged. First, differences in the daily growth rate of the induced R6 rectrix in juveniles and adults varied across seasons (Fig. 3a). In particular, juveniles tended to regenerate their rectrix more slowly than adults during the May–August period. Second, differences in the total length of the induced R6 rectrix in males and females varied across seasons (Fig. 3b). While females grew a longer induced rectrix than did males during the May–August period, they grew a shorter one during the other times of year.

It seems probable that the significant covariate effects for all three measures of rectrix regeneration (Table 1) were largely the result of dif-

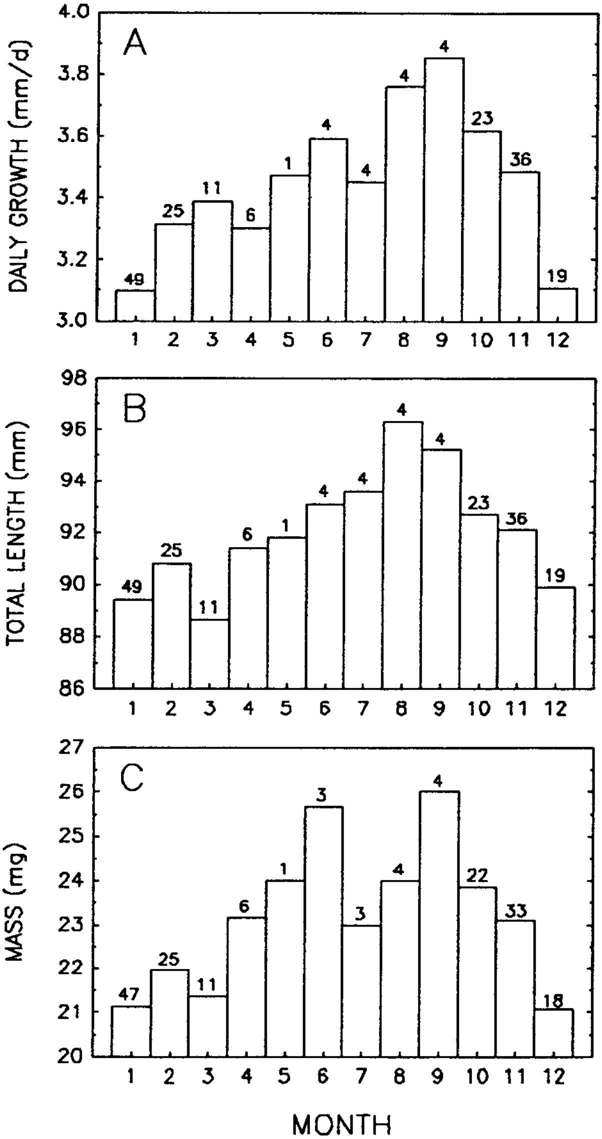

FIG. 1. Regeneration of R6 rectrices in Northern Cardinals throughout the year (Jan–Dec); the width of daily growth bars on the induced rectrix (A), and the total length (B) and mass (C) of the induced rectrix. The bars indicate the means, and the numerals represent the sample sizes.

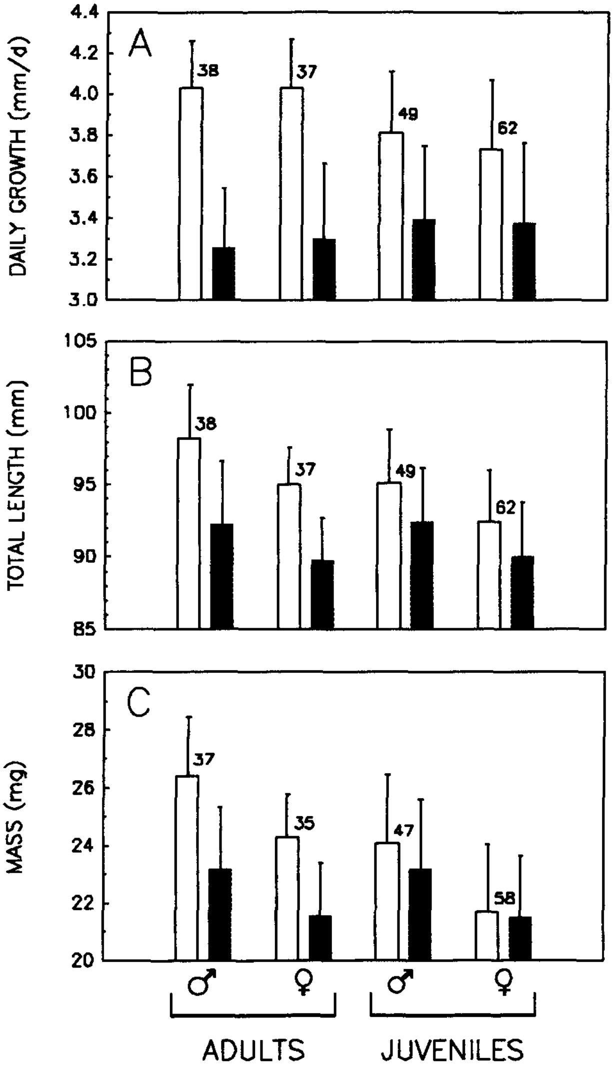

FIG. 2. Growth of original (open bars) and induced (filled bars) R6 rectrices in Northern Cardinals of different age-sex classes; the width of daily growth bars of the original and induced retrices (A), the total length (B) and mass (C) of the original and induced rectrices. The bars represent the means and the vertical lines indicate one SD. The numerals correspond to the number of cardinals of a given age-sex class from which both an original and an induced rectrix were taken.

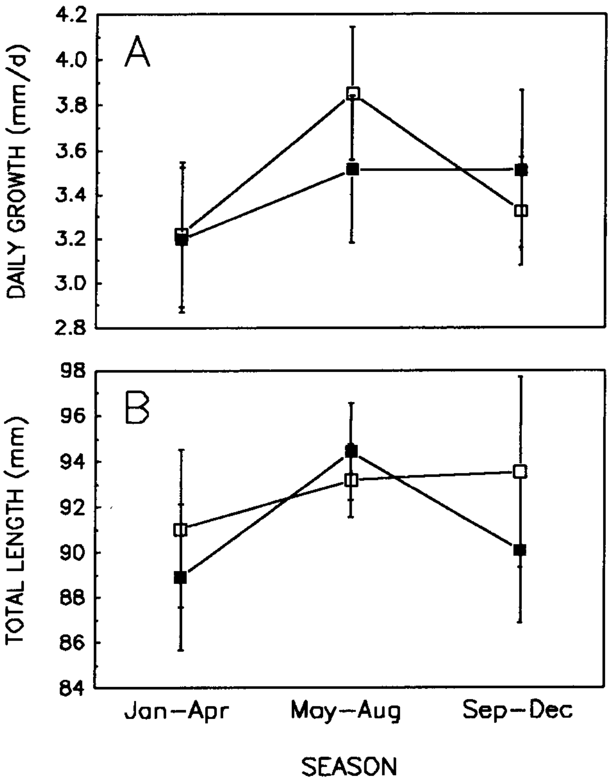

FIG. 3. (A) Mean width of daily growth bars on induced R6 rectrices grown by adult (open squares) and juvenile Northern Cardinals (filled squares) during different seasons (Jan–Apr, May–Aug, Sept–Dec). (B) Mean total length of induced R6 rectrices grown by male (open squares) and female cardinals (filled squares) during different seasons. Vertical lines indicate ±SD.

ferences among the age-sex classes of cardinals. Fig. 2 shows the measures of growth of the original and induced R6 rectrices for the four age-sex classes. Two-way analysis of variance (Table 2) indicated that adults grew their original rectrix faster and to a greater total length and mass than did juveniles. In addition, males tended to grow a longer and heavier induced rectrix than did females.

Multiple regression analysis (Table 3) showed that at least one measure of air temperature was a significant predictor of all three measures of rectrix regeneration in cardinals of all four age-sex classes. Although a negative partial correlation emerged between M_i and T_{max} in juvenile females, the positive sign of the 12 remaining partial regression coefficients

TABLE 2

RESULTS OF TWO-WAY ANALYSIS OF VARIANCE FOR THREE MEASURES OF THE GROWTH OF ORIGINAL R6 RECTRICES IN NORTHERN CARDINALS

Measure of rectrix growth	Factor	df	*F*	*P*
Daily growth (N = 186)	Age	1, 182	34.765	<0.01
	Sex	1, 182	0.703	0.403
	Age•sex	1, 182	0.818	0.367
Total length (N = 186)	Age	1, 182	30.685	<0.001
	Sex	1, 182	32.135	<0.001
	Age•sex	1, 182	0.305	0.582
Mass (N = 177)	Age	1, 173	55.249	<0.001
	Sex	1, 173	46.612	<0.001
	Age•sex	1, 173	0.259	0.611

indicates that the cardinals regenerated their R6 rectrix at a faster daily rate and to a greater total length and mass at higher temperatures. In addition, day length was a significant predictor of all three measures of rectrix regeneration in juvenile males and a significant predictor of DG_i in juvenile females. Juvenile cardinals had enhanced rectrix regeneration during *shorter* days.

DISCUSSION

Our results suggest that several factors other than a bird's nutritional condition may influence the rate at which a feather is regenerated (Table 1). Aside from differences that might have been expected due to age- and sex-specific variation in such factors as body size, social dominance, and foraging efficiency (e.g., males may have had an advantage over females during winter; see Fig. 3b), there was a pronounced seasonal pattern in feather growth. All four age/sex categories displayed an annual cycle with more rapid growth in summer than in winter.

Our study appears to be the first to relate temperature and daylength to nonmolt feather regeneration, but several workers have examined the influence of temperature and photoperiod during the pre-basic molt. In general, the onset of molt occurs earlier in birds exposed to longer photoperiods (e.g., Blackmore 1969, Chilgren 1978), but Chilgren found that at 20°C, molting captive White-crowned Sparrows (*Zonotrichia leucophrys*) grew out a primary feather at statistically indistinguishable daily rates under 8:16 and 4:20 L:D regimes. He concluded that growth rates of individual feathers during the molting season do not seem to vary with photoperiod as long as some presently undefined maximum length of daylight is available.

TABLE 3

RESULTS OF MULTIPLE REGRESSION OF DAILY GROWTH (DG_i), TOTAL LENGTH TL_i) AND MASS (M_i) OF INDUCED R6 RECTRICES IN NORTHERN CARDINALS OF FOUR AGE-SEX CLASSES ON THOSE PREDICTORS (FACTORS) SELECTED BY A PRIOR STEPWISE REGRESSION PROCEDURE[a]

Age-sex class	Measure of rectrix regeneration	Factor	Partial rank regression coefficient	*P*	Multiple R^2	N	df
Adult males	DG_i	T_{max}	0.339	0.039	0.114	38	1, 36
	TL_i	TL_o	0.836	<0.001	0.654	38	2, 35
		T_{max}	0.408	<0.001			
	M_i	M_o	0.729	<0.001	0.608	37	3, 33
		T_{min}	0.625	<0.001			
		Day length	−0.180	0.144			
Adult females	DG_i	T_{mean}	0.483	0.003	0.259	37	2, 34
		DG_o	0.294	0.058			
	TL_i	TL_o	0.355	0.004	0.574	37	2, 34
		T_{mean}	0.599	<0.001			
	M_i	T_{min}	0.632	<0.001	0.509	35	2, 32
		M_o	0.314	0.018			
Juvenile males	DG_i	T_{min}	0.885	<0.001	0.360	49	2, 46
		Day length	−0.600	0.001			
	TL_i	TL_o	0.385	0.002	0.394	49	3, 45
		Day length	−0.562	0.002			
		T_{min}	0.708	<0.001			
	M_i	M_o	0.210	0.103	0.332	47	3, 43
		Day length	−0.544	0.015			
		T_{max}	0.879	<0.001			
Juvenile females	DG_i	DG_o	0.269	0.009	0.458	62	3, 58
		Day length	−0.325	0.033			
		T_{min}	0.892	<0.001			
	TL_i	TL_o	0.639	<0.001	0.611	62	2, 59
		T_{min}	0.560	<0.001			
	M_i	M_o	0.415	<0.001	0.552	58	3, 54
		T_{max}	−0.847	0.043			
		T_{min}	1.446	0.001			

[a] See methods for details. All analyses were performed on ranks.

Our results suggest that ambient temperature was a more important predictor of feather growth rate than was photoperiod, particularly in adult cardinals (Table 3). The negative correlations between photoperiod and feather growth in juveniles suggest that they were less well nourished than adults (Fig. 3a) during the long summer days soon after fledging. Later on, they were presumably better at finding food and so actually were in better nutritional condition during the shorter days of autumn. However, because of strong collinearity between day length and temperature, one must be cautious in assessing the relative importance of these two variables in explaining variation in any of the measures of rectrix regeneration. Similarly, inferences based on which of the three temperature variables entered the model for any particular measure of growth should be made cautiously.

If Chilgren (1978) was correct in stating, "Growth rates of individual feathers appear to be unalterable under conditions of adequate nutrition and some brief, but undefined photopheriod," why did our cardinals regenerate a longer, heavier rectrix faster in warmer weather? Perhaps their nutrition may not have been equally "adequate" throughout the year. Existence metabolism is much higher in winter than in summer for resident temperate-zone birds (e.g., Munzinger 1974). Furthermore, during the winter, such birds must deal with a diminishing food supply. Thus, less net energy may be available for feather growth in the colder, leaner months of the year. Support for this idea comes from a study of White-breasted Nuthatches regenerating induced rectrices in controlled temperatures of −15, −5, or +5°C (Zuberbier and Grubb, unpubl. data). Under conditions of ad libitum food, feathers grown over this 20°C range of temperatures did not differ in daily growth. This explanation based on differential nutritional condition is somewhat confounded, however, because throughout the year the cardinals we studied could have had access to supplementary food at the trapping sites. Unfortunately, the extent to which individual birds used this supplementary food is unknown. Had there been no extra food, the influence of ambient temperature on feather growth might have been even more substantial.

The evidence from studies of molt concerning the influence of temperature on feather growth is sparse and conflicting. Warmer temperatures advanced the molt in White-crowned Sparrows (Chilgren 1978), but delayed it in Chaffinches (*Fringilla coelebs*) (Gavrilov and Dolnik 1974; cited by Chilgren 1978). Low temperature (5°C) reduced the overall duration of molt in White-crowned Sparrows (Chilgren 1978), but we have found no information on whether ambient temperature affects the daily growth of individual feathers during the molt.

In conclusion, these results limit the freedom with which ptilochronology can be used to study various aspects of avian behavior and ecology (Grubb 1989). Variation in feather growth due to age, sex, or season of the year must be accounted for in the design of experiments (e.g., Grubb 1989, Waite 1990, Grubb and Cimprich 1990).

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LITERATURE CITED

ANON. 1969. Local climatological data. Abbe Observatory, Cincinnati, Ohio. Superintendent of Documents, U.S. Government Printing Office, Washington, D.C.

BLACKMORE, F. H. 1969. The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 30: 433–444.

CHILGREN, J. D. 1978. Effects of photoperiod and temperature on postnuptial molt in captive White-crowned Sparrows. Condor 80:222–229.

CONOVER, W. J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley and Sons, New York, New York.

DOW, D. D. 1969a. Home range and habitat of the cardinal in peripheral and central populations. Can. J. Zool. 47:103–114.

———. 1969b. Habitat utilization by cardinals in central and peripheral populations. Can. J. Zool. 47:409–417.

GAVRILOV, V. M. AND V. R. DOLNIK. 1974. Bioenergetika i reguliaciia poslebracnoj i postiuvennoj linek u ziablikov (*Fringilla coelebs coelebs*). Academiya Nauk SSSR 55: 14--61.

GRUBB, T. C., JR. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. Auk 106:314–320.

———. 1991. A deficient diet narrows growth bars on induced feathers. Auk, In press.

——— AND D. A. CIMPRICH. 1990. Supplementary food improves the nutritional condition of wintering woodland birds: evidence from ptilochronology. Ornis Scand. 21:277–281.

HOFFMAN, M. S. 1988. The world almanac. Scripps Howard, New York, New York.

KING, J. R. AND M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? Amer. Zool. 25:955–964.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants: a guide to wildlife food habits. Dover, New York, New York.

MICHENER, H. AND J. R. MICHENER. 1938. Bars in flight feathers. Condor 40:149–160.

MUNZINGER, J. S. 1974. A comparative study of the energetics of the Black-capped and Carolina Chickadees, *Parus atricapillus* and *Parus carolinensis*. Ph.D. diss., The Ohio State Univ., Columbus, Ohio.

MURPHY, M. E., J. R. KING, AND J. LU. 1988. Malnutrition during the postnuptial molt of White-crowned Sparrows: feather growth and quality. Can. J. Zool. 66:1403–1413.

SCOTT, D. M. 1967. Postjuvenal molt and determination of age of the cardinal. Bird-Banding 38:37–51.

WAITE, T. A. 1990. Effects of caching supplemental food on induced feather regeneration in wintering Gray Jays (*Perisoreus canadensis*): a ptilochronology study. Ornis Scand. 21:122–128.

WILKINSON, L. 1988. Sygraph. Systat, Inc., Evanston, Illinois.

———. 1989. Systat: the system for statistics. Systat, Inc., Evanston, Illinois.

WISEMAN, A. J. 1977. Interrelation of variables in postjuvenal molt of cardinals. Bird-Banding 48:206–223.