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Is There a Positive Relationship Between Body Size and Fecundity in Lesser Snow Geese?

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Lack (1967) proposed that egg production in nidifugous waterfowl is ultimately limited by availability of nutrient resources (fat, protein, minerals) during the egg-laying period. In some species, there is considerable variation in the extent that egg production depends upon stored nutrient reserves and reserves acquired during laying (Krapu 1981, Alisauskas and Ankney 1985, Drobney and Fredrickson 1985, Rohwer 1986, Ankney et al. 1991, Arnold and Rohwer 1991, Drobney 1991). In Arctic-nesting geese the relationship between endogenous nutrient reserves and egg production probably is less complex. It has been traditionally believed that little food is available during the prelaying and laying period (Ryder 1970, Raveling 1979), and that geese subsist exclusively on stored nutrient reserves for maintenance and egg production (Ryder 1970, Ankney and MacInnes 1978). The potential impact of feeding by the geese during the prelaying and laying periods at some colonies on this traditional view is considered later in this paper.

Ryder (1970) suggested the amount of nutrient reserves that could be stored by Arctic-nesting geese might be limited in part by the structural size of the bird; the larger the bird, the greater the absolute mass of nutrients that could be carried to the breeding ground and used for egg production. Ankney and MacInnes (1978) and Alisauskas (1988) have shown significant positive correlations between structural size and nutrient reserves in Lesser Snow Geese (*Chen caerulescens caerulescens*). Although this led to predictions of a significant direct association between structural size and clutch size, results of such analyses have been contradictory. Ankney and MacInnes (1978) found that Lesser Snow Geese with longer culmens (used as a univariate index of structural size) had greater absolute levels of reserves and laid larger clutches in two consecutive years.

In contrast, Davies et al. (1988) found no significant relationship for Lesser Snow Geese between a multivariate index of structural size and clutch size using data from La Pérouse Bay pooled over several years. They suggested the difference between their results and those of Ankney and MacInnes (1978) may have been due to a lack of control for covariation of age and structural size in their sample. Davies et al. (1988) showed that older females in the La Pérouse Bay sam-

ple were significantly larger than younger females, and argued the increase in mean structural size with age was due to an earlier age of first breeding for smaller birds. They suggested the smaller birds in the sample analyzed by Ankney and MacInnes (1978) were likely to be younger birds. Since younger Lesser Snow Geese lay significantly smaller clutches than older birds (Finney and Cooke 1978, Rockwell et al. 1983), the smaller clutch size for small birds detected by Ankney and MacInnes could have been because the smaller birds were also younger.

Alisauskas and Ankney (1990) recently disagreed with these conclusions on three methodological grounds. First, the inclusion of body mass measured during wing molt in the multivariate index of size might have confounded analyses by introducing a source of variation not directly relevant to the relationship of structural size and fecundity. Second, the original analyses of Davies et al. (1988) pooled data across years. If the relationship between structural size and fecundity is year specific, then such a pooled analysis would obscure relations between body size and annual fecundity. Finally, the exclusion of younger birds by Davies et al. (1988) would introduce a systematic bias in pooled data if age and age of first breeding covaried.

Cooke et al. (1990) showed that inclusion of body mass measured during wing molt in the multivariate size index did not affect the results of the analyses of Davies et al. (1988). However, a number of factors prompt further analysis of the relationship of structural size and fecundity in Lesser Snow Geese. First, responses by Cooke et al. (1990) to the other criticisms raised by Alisauskas and Ankney (1990) were based on logical expectations rather than empirical findings. We now have sufficient data to address directly the remaining methodological questions raised by Alisauskas and Ankney (1990). Second, recent analysis from data from La Pérouse Bay has shown a long-term decline in cohort-specific structural size of breeding adult females (Cooch et al. 1991; cohort = year of birth), which was not detected by Davies et al. (1988). Thus, an increasing proportion of young (≤ 5 years) birds in pooled data from La Pérouse Bay come from more recent cohorts that are significantly smaller structurally. If this long-term decline is controlled statistically by including cohort as a term, there is no significant difference overall in structural size among different adult age classes ($F = 1.05$, $df = 1$ and $2,691$, $P = 0.391$), and no direct evidence that

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smaller birds tend to start breeding at a younger age than do larger birds, contrary to suggestions by Davies et al. (1988).

This finding has at least two implications. First, Alisauskas and Ankney's (1990) argument that excluding younger birds introduced a systematic bias in the analysis by Davies et al. (1988) was based upon their assumption of a significant covariation of age of first breeding and structural size, as reported by Davies et al. (1988). However, as demonstrated above, such a relationship does not exist. Second, unless it is presumed that there was a similar decline in structural size of Lesser Snow Geese in the sample analyzed by Ankney and MacInnes (1978), there is no reason to assume that the smaller birds in their sample also were younger. Therefore, there is no direct evidence to support the conclusions of Davies et al. (1988) that the apparent correlation of body size and clutch size reported by Ankney and MacInnes (1978) was in fact due to a confounding correlation of age and structural size.

In addition, egg production is a function not only of the number of eggs produced, but also of the size of the eggs. Neither the original analyses of Davies et al. (1988) or recent discussions by Alisauskas and Ankney (1990) and Cooke et al. (1990) considered covariation of both egg size and clutch size with structural size of the adult. As noted by Lessells et al. (1990), a significant negative correlation between egg size and clutch size in Lesser Snow Geese is predicted if the size of the body reserves limits egg production. If body size limits the amount of nutrient reserves available for egg production, then potential trade offs between clutch size and egg size, at the phenotypic level, may be constrained by structural size of the bird. Lessells et al. (1990) did not specifically control for structural size of the adult in their analysis of evidence for trade offs between egg mass and clutch size in Lesser Snow Geese.

Thus, we re-examine the relationship between structural size and several different measures of fecundity in Lesser Snow Geese when the effects of both age and cohort are controlled for statistically, using data collected from the colony of Lesser Snow Geese nesting at La Pérouse Bay, Manitoba, 1976–1990. We also consider the more general issue of structural size as a proximate limit to egg production, particularly in birds which rely predominantly on stored reserves, and assess the degree to which structural size may influence possible trade offs between clutch size and egg size.

In our analyses, we attempted to detect any relationship between structural size and measures of fecundity that are influenced by levels of prelaying nutrient reserves. First, we assessed variation in clutch size (defined as number of eggs found in nest at time of hatch) and laying date (back-dated from date of hatch; Hamann and Cooke 1987). Female Lesser Snow Geese with greater levels of prelaying nutrient re-

serves initiate nesting earlier and lay more eggs than birds with lower levels of prelaying nutrient reserves (Hamann and Cooke 1989), although the causal relationship between the two is undefined. We also assessed covariation of structural size with both mean egg mass and total clutch mass. For most analyses, we restricted the data to clutches for which fresh egg mass (in grams on day of laying) was known for every egg found in the nest on daily nest checks during the laying period. General descriptions of field methods are given in Cooke et al. (1985).

We derived a single measure of structural size for each female by extracting the first principal component (PC1; PROC PRINCOMP; SAS Institute 1989) of the correlation matrix of culmen, head, and tarsus lengths for different subsets of the data (measurements described in Davies et al. 1988). We used mean measurements made for each individual in different years to minimize measurement error. This approach is valid since Lesser Snow Geese do not grow significantly beyond the first year (Davies et al. 1988). Component loadings for all three measurements varied depending upon the data set, but always were positive and of generally equal magnitude. PC1 generally explained approximately 62% of the total character variance, which is similar to the 68% reported by Davies et al. (1988) for PC1 including body mass.

Clutch size, laying date, mean egg mass and total clutch mass covary significantly with age in Lesser Snow Geese until age five years, and are independent thereafter (Rockwell et al. 1983, Hamann and Cooke 1987; D. B. Lank, unpubl. data). Thus, the relationship of structural size with any of these factors will be confounded by the covariation of structural size with age for birds two to five years of age only. Therefore, we analyzed the relationship of covariation of each factor with structural size for younger (2–5 years) and older (>5 years) birds separately. We used pooled analyses to increase our ability to detect a significant overall relationship of structural size with both laying date and clutch size, and intrayear analyses to test for year-specificity of any relationships.

In analyses pooling data across years, we first removed variation in size due to differences among cohorts by obtaining residuals from a MANOVA (PROC GLM; SAS 1989) of culmen, head and tarsus lengths. We then created an index of structural size that was free from cohort effects by extracting the first principal component from the correlation matrix of these residuals. We included year (to account for chronological differences in the response variable), as well as female age as factors in the analysis of this pooled data set, and tested for overall covariation of clutch size with the fecundity variables. Nonsignificant interaction terms were sequentially eliminated, beginning with the highest-order interactions, until all remaining terms in the model were either main effects or included within an interaction for which the estimated significance had a probability (P) of 0.15

TABLE 1. Variation in clutch size, laying date, mean egg mass, and total clutch mass of young (≤ 5 years) Lesser Snow Geese as a function of age and structural size (pooled across years 1976–1986). Sample sizes for clutch size and laying date were 270, and those for egg and clutch mass were 39.

Term	df	F (range) ^a	
Clutch size			
Year (Y)	9	2.28*	(1.85–2.72)
Age (S)	3	7.14***	(6.85–10.04)
Size ^b	1	0.19	(0.13–0.46)
Y \times S	9	1.53	(1.42–1.91)
Laying date			
Year	9	256.53***	(233.7–278.1)
Age	3	17.18***	(15.3–22.3)
Size	1	0.24	(0.03–0.35)
Y \times S	9	1.61	(1.24–1.81)
Egg mass			
Year	9	0.69	(0.48–0.73)
Age	3	0.39	(0.33–0.44)
Size	1	2.50	(1.45–2.62)
Clutch mass			
Year	9	0.70	(0.58–1.02)
Age	3	0.54	(0.48–0.66)
Size	1	0.16	(0.00–0.34)

^a Median *F*-statistic for 10 different subsets of randomly selected individuals calculated using partial (Type III) sums of squares (PROC GLM; SAS Institute 1989). Nonsignificant interaction terms not included in final model. *, $P < 0.05$; ***, $P < 0.005$. Range of *F*-values included for 10 different subsets of randomly selected individuals.

^b First principal component of correlation matrix of residuals of MANOVA of culmen, head, and tarsus lengths across cohort.

or less. We selected a single breeding record for each individual bird at random to eliminate statistical problems caused by the presence of multiple records for individuals in the data set. To confirm that the results were not dependent upon the particular birds included in the randomly selected data set, we repeated the analyses several times. We report the median and range of values of the *F*-statistic estimated for each term observed in analyses of 10 different subsets of randomly chosen individuals. In no case did the general results for a given analysis change due to a particular randomized data set. For younger birds, age (in years) was included as a classification variable in all analyses to statistically control for the covariation of age with structural size. For older birds, age was not included as a factor in pooled analyses, since the measured of fecundity are all independent of age among older birds. Thus, we were able to increase significantly our sample size in analyses of older birds by including any bird older than five years.

For within-year analyses, variation among younger birds due to cohort differences was statistically removed as described above to eliminate possible confounding of age and size (age = cohort in intrayear analyses). For older birds, no adjustment for cohort

TABLE 2. Variation in clutch size, laying date, mean egg mass, and total clutch mass of old (> 5 years) Lesser Snow Geese as a function of structural size (pooled across years 1976–1990).^a Sample sizes for clutch size and laying date were 818, and those for egg and clutch mass were 148.

Term	df	F (range)	
Clutch size			
Year	9	3.26***	(2.52–4.22)
Size ^c	1	0.79	(0.40–1.21)
Laying date			
Year	9	599.13***	(559.7–690.1)
Size	1	1.71	(0.3–3.7)
Egg mass			
Year	9	1.11	(0.72–1.56)
Size	1	0.47	(0.06–0.78)
Clutch mass			
Year	9	0.58	(0.40–0.71)
Size	1	0.43	(0.35–0.55)

^a Footnotes in Table 1 also apply to this analysis.

differences was made, since both clutch size and laying date are independent of age among older birds, and age was not included as a variable. For both age groups, significances of intrayear analyses were determined *a posteriori* using a sequential Bonferroni adjustment with tablewide significance ($\alpha = 0.05$) to control the overall probability of declaring differences to be significant by random chance (Rice 1989).

To assess the possible role of structural size in possible trade offs of egg mass and clutch size for birds, we used partial regression analysis (PROC GLM; SAS Institute 1989) for both intrayear and pooled analyses. As with other analyses, age was included as a variable along with structural size in analyses of young birds. For older birds, age was not included as a factor (see above).

Although both clutch size and laying date are discrete variables, we treated both as continuous variables, allowing use of commonly available linear procedures. Use of linear models allowed a more complete testing of various interactions of main effects than is currently possible with polychotomous regression techniques. Variation in both mean egg mass and total clutch mass is continuously distributed. We used SAS (SAS Institute 1989) for all analyses.

Among 270 younger (2–5 years) Lesser Snow Geese, there was no overall effect of structural size on either clutch size or laying date after controlling for cohort, year and age (Table 1). No significant ($P \leq 0.05$) interactions of any of the variables were detected. However, the interaction of year and size was included in the final model because it was marginally significant ($P \leq 0.15$) for certain subsets of randomly selected individuals. There was a highly significant effect of age on both clutch size and laying date, controlling

TABLE 3. Annual variation in relationships of clutch size and laying date with structural size among young (2–5 years) Lesser Snow Geese, 1976–1986.

Year	Term	df	n	Clutch size		Laying date	
				F ^a	P	F	P
1976	Age	3	17	0.46	0.718	1.72	0.217
	Size ^b	1		0.67	0.429	0.63	0.443
1977	Age	3	25	0.28	0.840	1.04	0.396
	Size	1		1.57	0.224	7.36	0.013
1979	Age	3	28	1.78	0.180	7.12	0.002*
	Size	1		0.91	0.349	1.98	0.173
1980	Age	3	66	3.96	0.012	7.73	<0.001*
	Size	1		0.06	0.802	0.95	0.333
1981	Age	3	30	1.44	0.254	1.42	0.259
	Size	1		0.71	0.407	0.23	0.637
1982	Age	3	34	5.37	0.005*	2.83	0.056
	Size	1		0.02	0.877	0.00	0.956
1983	Age	3	33	0.52	0.675	0.47	0.706
	Size	1		5.55	0.026	3.89	0.059
1984	Age	3	62	2.29	0.088	3.83	0.014
	Size	1		0.07	0.792	0.47	0.497
1985	Age	3	13	0.81	0.524	0.74	0.559
	Size	1		3.61	0.094	0.68	0.433
1986	Age	3	14	0.30	0.827	0.31	0.818
	Size	1		2.99	0.118	0.00	0.955

^a F-statistic calculated using partial (Type III) sums of squares. *, $P < 0.05$ at tablewide level.

^b First principal component of correlation matrix of residuals of MANOVA of culmen, head, and tarsus lengths across cohort.

for year, size, and the interaction of year and size. Thus, the significant increase in clutch size and advancement of laying date with age from two to five years is not an artifact of covariation of age and structural size in our sample. Among young birds, there was no significant relationship of structural size with mean egg mass or with total clutch mass, although the small sample size of birds for which both egg and clutch mass data were available significantly reduced the statistical power of this analysis (Table 1). Among 962 older birds (≥ 5 years), there was also no overall effect of structural size on clutch size or laying date (Table 2). There also was no detectable covariation of either mean egg mass or total clutch mass with structural size among 148 older birds for which data were available (Table 2). There is little evidence in our data for a relationship of structural size to any of the individual measures of egg production.

Despite highly significant differences among years in chronology of breeding and condition of birds upon arrival (Davies and Cooke 1983, Cooch et al. 1989), we also found no evidence in any year of a significant statistical relationship between structural size and either clutch size or laying date among young birds in 10 different years (Table 3), or among older birds in any of 15 years (Table 4); our samples for younger birds were small in some years. We had insufficient data to test for intrayear covariation of mean egg mass and total clutch mass with structural size among younger birds. However, in nine years for which data from older birds were available, there was no significant relationship of structural size to either variable

at the tablewide significance (Table 4). Thus, there is little support in our data for the suggestion of Alisauskas and Ankney (1990) that any relationship between structural size and individual measure of egg production at La Pérouse Bay is year specific.

Among 148 older birds for which data were available, there was a significant negative correlation overall between egg size and clutch size when controlled for variation in year and structural size; the median correlation (r) from 10 samples of randomly selected individuals was -0.169 ($P \leq 0.05$) with a range of -0.081 to -0.263 . Within year, the relationship was tablewide significant in only 1 of 10 years, although the relationship was in the right direction in 6 of 9 years (Table 5). Increasing the sample size by using data from clutches where fresh egg mass was available for a variable proportion of the eggs in a clutch (from one egg to entire clutch) raised the number of negative relationships to seven of nine, but did not affect the statistical significance of the relationship in any year, despite the increased statistical power.

Despite the overall significant negative relationship of egg mass with clutch size, the slope of the relationship was low; the median slope (b) from 10 samples of randomly selected individuals was -1.35 g/egg, with a range of -0.629 to -2.06 . The median values of the correlation and slope are very similar in magnitude to those reported by Lessells et al. (1990) in an analysis of trade offs at the phenotypic level among individuals with repeated measures (range of $r = -0.021$ to -0.160 ; maximum b of -2 g/egg). The similarity of our results with those of Lessells et al.

TABLE 4. Annual variation in relationships between clutch size, laying date, mean egg mass, and total clutch mass with structural size in old (>5 years) Lesser Snow Geese, 1976-1990.^a

Year	n	Clutch size		Laying date		n	Egg mass		Clutch mass	
		F	P	F	P		F	P	F	P
1976	52	1.39	0.245	0.29	0.593	—	—	—	—	—
1977	86	2.44	0.122	0.03	0.852	—	—	—	—	—
1978	15	0.06	0.814	0.41	0.531	—	—	—	—	—
1979	55	1.22	0.274	1.01	0.319	—	—	—	—	—
1980	118	1.15	0.286	0.01	0.930	24	0.09	0.762	1.70	0.206
1981	123	2.92	0.090	0.37	0.546	33	1.81	0.188	0.68	0.414
1982	137	1.24	0.268	1.27	0.262	40	1.34	0.255	4.21	0.047
1983	173	0.07	0.785	1.21	0.273	28	0.55	0.467	0.01	0.961
1984	214	0.04	0.838	0.31	0.578	31	1.81	0.189	0.69	0.413
1985	79	1.50	0.224	0.76	0.387	46	0.03	0.863	0.03	0.873
1986	130	0.25	0.620	0.84	0.361	24	0.02	0.901	0.08	0.774
1987	84	0.05	0.822	0.46	0.501	13	0.69	0.425	0.06	0.815
1988	110	0.01	0.938	1.22	0.271	24	5.44	0.029	2.50	0.128
1989	56	0.26	0.615	0.18	0.669	—	—	—	—	—
1990	62	1.09	0.300	0.00	0.959	—	—	—	—	—

^a Structural size indexed by PCI of culmen, head, and tarsus lengths across cohort. Dashes indicate that statistics not estimated due to small sample size ($n \leq 10$).

(1990) is perhaps not surprising since there is some degree of overlap in the respective data sets.

While the relatively small sample sizes reduced the statistical power of some of our analyses, particularly of younger birds, we failed to find any compelling evidence to support the hypothesis that any measure of fecundity in Lesser Snow Geese at La Pérouse Bay is affected by variation in structural size. Furthermore, although there is some evidence of a statistically significant phenotypic trade off of clutch size and egg size among older birds of a given structural size in our data, the magnitude of the trade off is significantly lower than expected if there is direct trade off between clutch size and egg size under the endogenous-nutrient-limitation hypothesis, given average egg mass (124 g) and clutch size (4) in this species (Lessells et al. 1990). Given the likelihood that such a small decrease in egg size expected for an increase in clutch size by one egg (approximately a 1% decrease) has little effect on gosling growth and survival (Newell 1988), we concur with Lessells et al. (1990) in concluding that there is no biologically significant trade off at the phenotypic level between clutch size and egg size in this species, even when controlling for a potential limit to levels of endogenous reserves.

Our failure to detect any significant correlation of structural size with mean egg size differs from recent observations for Barnacle Geese (*Branta leucopsis*) nesting on Gotland, Sweden, where larger birds were found to lay larger eggs (Larsson and Forslund 1992). In our analyses, we first adjusted structural size of females for the systematic increase with age. If we did not adjust structural size for age differences, we also detected significant positive correlations of structural size and mean egg mass in most years. The lack

of a correlation of egg size with structural size when we first adjusted structural size for age differences indicates that, in our data, mean egg size increases with age and not structural size. While systematic covariation of structural size with age among Barnacle Geese on Gotland has not been demonstrated directly, published data from that population is suggestive (Larsson and Forslund 1991; table 2). Thus, it is possible that the correlation of structural size and egg size in Barnacle Geese obtained by Larsson and Fors-

TABLE 5. Annual variation in the correlation of mean egg mass and clutch size for old (>5 years) Lesser Snow Geese, controlling for year and structural size, 1980-1988.

Year	A. Complete clutch ^a			B. Partial clutch ^b		
	df	r ^c	P	df	r	P
1980	22	0.041	0.848	42	0.302	0.046
1981	31	-0.059	0.744	38	-0.103	0.524
1982	36	-0.448	0.003*	51	-0.393	0.004*
1983	26	-0.316	0.102	58	-0.200	0.125
1984	29	-0.400	0.026	50	-0.240	0.087
1985	46	0.015	0.922	60	0.077	0.554
1986	22	-0.121	0.574	41	-0.009	0.956
1987	10	0.050	0.876	13	-0.274	0.323
1988	21	-0.157	0.472	25	-0.277	0.161

^a Mean egg mass calculated for clutches where fresh-egg masses were available for all eggs in clutch.

^b Mean egg mass calculated for clutches where fresh-egg mass available for a variable proportion of clutch (one egg to entire clutch). Mean calculated using fresh egg masses only.

^c Partial correlation coefficient of mean egg mass and clutch size (counted at end of laying) controlling for structural size. *, $P < 0.05$ at tablewide level.

lund (1992) may in fact be due to confounding correlations of both structural size and egg size with age, as observed among Lesser Snow Geese at La Pérouse Bay.

We believe that there are at least two, not mutually exclusive, reasons why the hypothesis predicting a significant relationship between structural size and fecundity in this species was not supported. First, despite having lower proportional metabolic costs than smaller birds, larger birds require absolutely more reserves for metabolic maintenance than smaller birds (Kendeigh 1970, Calder 1984). Thus, larger birds will have more reserves available for egg production than smaller birds *only* if their relative rate of increase in total reserves with larger body size is greater than the rate of increase in total metabolic costs. Further, the residual amount of reserves remaining once metabolic costs have been subtracted would have to be sufficient to allow formation of at least one egg to make a detectable difference in number of eggs produced. Thus, although larger birds may arrive at La Pérouse Bay with absolutely more nutrient reserves, size-specific differences in the residual levels of reserves available for egg production after metabolic costs have been subtracted may not be sufficient to enable larger birds to produce more eggs. While data to test this hypothesis would be difficult to collect in wild populations, an important first step in studies of captive birds would be to examine relationships of: structural size; nutrient-reserve levels; acquisition and partitioning of fat and protein reserves between metabolic maintenance and egg production under different conditions.

A second explanation would be that larger Lesser Snow Geese at La Pérouse Bay in fact do not have absolutely more reserves available for egg production. Most geese apparently are carrying maximal nutrient reserves, limited by structural size, at departure from final staging areas (Alisauskas 1988); however, it is conceivable that this may not be true, or may not lead to having more reserves at the breeding site, for geese that breed under some circumstances. For example, there may be significant survival advantages to minimizing flight load by reducing the amount of nutrients carried from the final staging areas to extreme High Arctic colonies. At more southerly colonies, geese may bypass some staging areas by flying more directly to the breeding grounds than is possible for birds at more northern colonies (Alisauskas 1988), and may not have maximal nutrient reserves. In addition, there is proportionately less snow cover that disappears earlier in spring at La Pérouse Bay than observed at other colonies at higher latitudes, and food is available to the geese within the first few days of arrival. If geese breeding at these colonies arrive with less than maximal levels of nutrient reserves, then prelaying feeding (*sensu* Gauthier and Tardif 1991) may further confound the correlation between structural size and levels of reserves observed for most

birds during staging. One prediction of this hypothesis is that there may be a greater correlation between structural size and fecundity at midlatitude breeding sites (such as that studied by Ankney and MacInnes 1978), where birds are unable to bypass staging areas and prelaying feeding is uncommon, than at low latitudes. Testing this hypothesis will require comparative study of arrival conditions of prelaying feeding among different colonies at various latitudes.

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

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

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