

ESTIMATING AGE OF YOUNG BIRDS WITH A MULTIVARIATE MEASURE OF BODY SIZE

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ABSTRACT.—We analyzed the relationship between age and body size of 65 Great Black-backed Gull chicks (*Larus marinus*) between 0 and 56 days of age ($n = 209$ sets of measurements) using birds from southern New Brunswick in 1989. The logistic model provided the best fit to the body size and age data; it was used to make linear transformations of body-size variables (culmen, tarsus, and wing cord). The first principal component (PC1) from the correlation matrix of transformed morphological variables also was used as a measure of body size. We estimated linear-regression models of univariate body-size measures and of PC1 versus age, and a multiple-linear-regression model of all body size measures versus age. Accuracy of the predictors was evaluated from a verification sample of chick measurements that were, initially, withheld from the analysis. All predictors had negligible bias in age estimation, but PC1 and multiple-linear-regression models estimated age more precisely than did univariate predictors. The increased accuracy of the multivariate models resulted from the reduced effect of outliers on age estimation. Received 16 October 1990, accepted 13 January 1992.

THE ABILITY to age chicks accurately can add valuable information to many studies of young birds, but it is often difficult and time consuming to obtain a large sample of known-age young. Chicks grow rapidly and, thus, predictive models for age can be derived from the relationship between body size and age for a sample of known-age young. Several predictive models are usually developed, each based on single measures of body size, and the one that produces the most precise estimates of age is used (e.g. Lyons and Mosher 1983, Bortolotti 1984, Coleman and Fraser 1989). However, recent studies have indicated that single measures of body size (e.g. wing and tarsus) are not reliable predictors of overall body size of adult birds (Rising and Somers 1989, Freedman and Jackson 1990). Hence, a model that describes overall size of young chicks at a given age, not just of a particular structure, should improve the accuracy of age prediction.

Multivariate analysis can be a powerful analytical tool, but the nonlinear nature of growth relationships excludes this type of the analysis in all but special cases. For example, multiple linear regression was used by Elowe and Payne (1979) for aging chicks, but the usefulness of this model was restricted to the portion of the

nestling period for which growth is linear. Mineau et al. (1982) used a multivariate model to estimate age by taking a linear combination of the nonlinear regressions of each structure. This results in an accurate but difficult model to estimate.

Simple transformations of variables (log, arcsine, etc.) are commonly used to reduce heteroscedasticity and produce linearity. Transformations of growth variables to a linear form are possible if the nonlinear model that describes the relationship between age and body size is known (Johnson 1975, Dapson 1980). When the appropriate nonlinear model is estimated, the linear form of the model can be derived. Once this transformation is obtained, the adjusted variables can be subjected to any of the general linear models (provided the assumptions of the models are met).

At least two techniques using multiple variables are appropriate for predicting age from body size. The first, multiple linear regression of age on body size variables is the simplest, but the validity of this type of model often is suspect when applied to observational data (see Discussion). The second, principal-component analysis, is more complicated. The first principal component (PC1) of morphological measurements is a good predictor of overall body size in adult birds (Alisauskas and Ankney 1987, Rising and Somers 1989, Freedman and Jackson 1990). Thus, a predictive model based on age

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and a multivariate measure of body size (PC1) can be estimated using simple least-squares regression. The purpose of our study was to evaluate the accuracy of multivariate measures, as opposed to single-variable measures of body size, in estimating the age of chicks of Great Black-backed Gulls (*Larus marinus*).

METHODS

Age and body-size data for gull chicks were collected on Flatpot Island, a small island in the Wolves Archipelago near the New Brunswick/Maine border (44°57'N, 66°44'W). Great Black-backed Gull nests were monitored weekly from 26 April through 25 July 1989 (nests were not visited during rainy or foggy days), except during hatching. All nests were marked individually with a numbered wooden stake, and all eggs in the nest were numbered with a permanent marker.

Nests were monitored daily when eggs were hatching. During this period, progression of the hatch was monitored, and we noted whether eggs were: (1) starred, one to five star-shaped cracks in egg surface; (2) pipped, hole in egg surface; (3) or hatched. If an egg was pipped or hatching, the bill tip of the chick was marked with a colored permanent marker (for later identification as a known-age chick). Hatch dates were determined by direct observation, or were estimated for chicks whose egg was observed starred or pipped one to four days before first capture by adding the mean time between that stage and hatch of known-age chicks (rounded to the nearest day). On the day of hatch, chicks were given an arbitrary age 0, marked (web clipped with unique combinations), and measured. Chicks were also measured during each subsequent visit.

Three structural size variables were measured: (1) culmen (CUL), measured from tip of upper mandible to inside edge of nostril; (2) wing chord (WING), with the wing flattened and flexed at the wrist, measured from tip of wrist to distal end of phalanges or end of outer primary (after outer primary had erupted); and (3) tarsus (TAR), measured with leg flexed from the pit at junction of tibiotarsus and tarsometatarsus to distal end of the tibiotarsus. Measurements of CUL and TAR were taken with calipers to the nearest 0.1 mm, WING was measured with calipers up to 200 mm and, thereafter, measured with a ruler to the nearest 1.0 mm.

The equations for the three mathematical models were as follows: logistic,

$$Y = A/(1 + de^{-kX}); \quad (1)$$

Gompertz,

$$Y = Ae^{-de^{-kX}}; \quad (2)$$

and von Bertalanffy,

$$Y = A(1 - de^{-kX})^3. \quad (3)$$

In these equations, Y represents size, A is the asymptote, k is the growth-rate constant, X is age, and d is a fitted constant. The equations relate body size to age; equation parameters were estimated for each of the three measurements using nonlinear least-squares regression (program NONLIN in SYSTAT; Wilkinson 1988). A low residual sum of squares and an unbiased estimate of asymptotic size (the size of adult Great Black-backed Gulls collected from the Wolves Archipelago; Gilliland unpubl. data) were chosen as criteria for selecting the model. Once the model was chosen, the linear form of the model was derived (see Results for a description of the transformation). The asymptotes for the variables CUL, TAR, and WING estimated from the nonlinear regressions were used to transform the variables into the linear form (linear transformations of the original variables represented as CUL_L, TAR_L, and WING_L). We then performed a principal-components analysis of the correlation matrix of CUL_L, TAR_L, and WING_L (FACTOR program in SYSTAT; Wilkinson 1988), and used the scores on the first principal-component axis (PC1) as a measure of body size (Alisauskas and Ankney 1987).

Least-squares regression lines were derived (MGLH program in SYSTAT; Wilkinson 1988) for relationships of age on body size, and a multiple-linear-regression line was derived for measures of age on body size. Performance of the age predictors was assessed from comparisons of estimated with actual age for 30 randomly selected observations that were not used in the development of the predictive equations. Differences between estimated and observed ages were compared (PC1 scores were calculated for the verification observations by multiplying the transposed eigenvector from the principal-components analysis by each bird's vector of z-scores). This procedure was repeated 10 times, resulting in a sample of 300 observations being withheld from the development of predictive equations. The accuracy of the age predictors was determined using the average performance in predicting actual age over the 10 runs; the overall mean difference between the actual and estimated ages was used as a measure of bias, and the standard deviation used as a measure of precision.

RESULTS

Hatch dates were known for 22 chicks and estimated for 43 chicks from 34 nests. A total of 209 complete sets of measurements (sample sizes of variables differ due to incomplete information for some birds) was taken from these chicks between age 0 and age 56 (fledging). Sample sizes decreased over the nestling period (Fig. 1) due to mortality and because some chicks had not fledged when the study was terminated.

TABLE 1. Estimated parameters of three nonlinear growth models relating body size (Y) to age of Great Black-backed Gull chicks.

Model	Residual sum of squares	Fitted constant (d)	Growth-rate constant (k)	Asymptote (A)	n
Culmen					
Logistic	313.3	2.590	0.055	39.9	214
Gompertz	335.5	1.439	0.032	46.1	214
von Bertalanffy	325.5	0.401	0.024	50.9	214
Size at maturity ^a	—	—	—	40.3	28
Tarsus					
Logistic	2,658.6	2.265	0.088	84.4	219
Gompertz	2,856.1	1.259	0.059	89.2	219
von Bertalanffy	3,001.2	0.351	0.050	91.3	219
Size at maturity	—	—	—	80.0	28
Wing chord					
Logistic	63,268.9	25.120	0.098	466.0	217
Gompertz	78,965.6	4.008	0.038	715.3	217
von Bertalanffy	82,437.9	0.795	0.017	1,365.0	217
Size at maturity	—	—	—	494.3	28

^a Mean size of maturity estimated for 28 adults collected at the Wolves.

Of the three sigmoidal models tested, the logistic curve provided the best overall fit as it had the lowest residual sums of squares for TAR, CUL, and WING (Table 1). Although the differences among the residual sums of squares for the different models were small, the estimated asymptotes of the Gompertz and von Bertalanffy models greatly exceeded the observed mean size of adult birds (Table 1). Unbiased estimates of asymptotes were necessary for the linear transformations (Ricklefs 1967), and also are critical when primary interest is in growth rates, since A and k are highly correlated (Johnson 1975).

Linear transformations of the original vari-

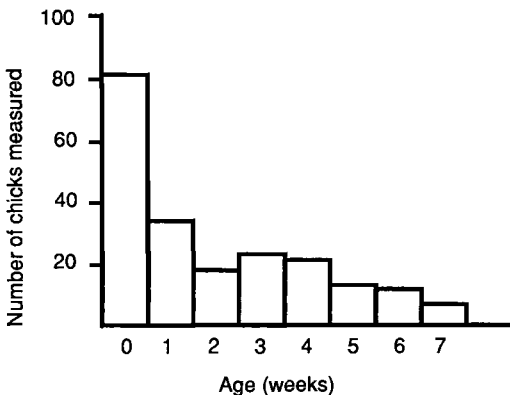


Fig. 1. Age distribution of Great Black-backed Gull chick measurements ($n = 209$).

ables to obtain CUL_{*t*}, TAR_{*t*}, and WING_{*t*}, were made using a linear form of the logistic model:

$$\ln[(A - Y)/Y] = b - aX, \quad (4)$$

where A is the asymptote, Y is a body size measure, X is age, and b and a are regression coefficients listed in Table 2. The linear transformation of the variables was made by substituting the fitted asymptote (Table 1) and simplifying the left-hand side of the equation. The resulting variables were linear and negatively correlated with age (Table 2, Fig. 2). The first principal component described positive covariation in CUL_{*t*}, TAR_{*t*}, and WING_{*t*}, with all variables loading equally (0.994, 0.990, and 0.991, respectively). The corresponding eigenvector was 0.337, 0.335, and 0.336, and PC1 accounted for 98% the total original variance.

The average difference between the estimated and actual ages for chicks in the verification

TABLE 2. Relationships ($Y = a + bX$) between body size and age of Great Black-backed Gull chicks as determined by regression analysis ($n = 209$).

Body size (Y) ^a	$Y = a + bX$			
	a	SE ^b	b	r^2
Culmen	17.41	3.00	-17.31	0.96
Tarsus	9.68	4.14	-10.21	0.93
Wing chord	32.12	2.85	-10.23	0.96
PC1	16.19	2.54	-14.77	0.97

^a Linear form of body measures.

^b Standard error of estimate.

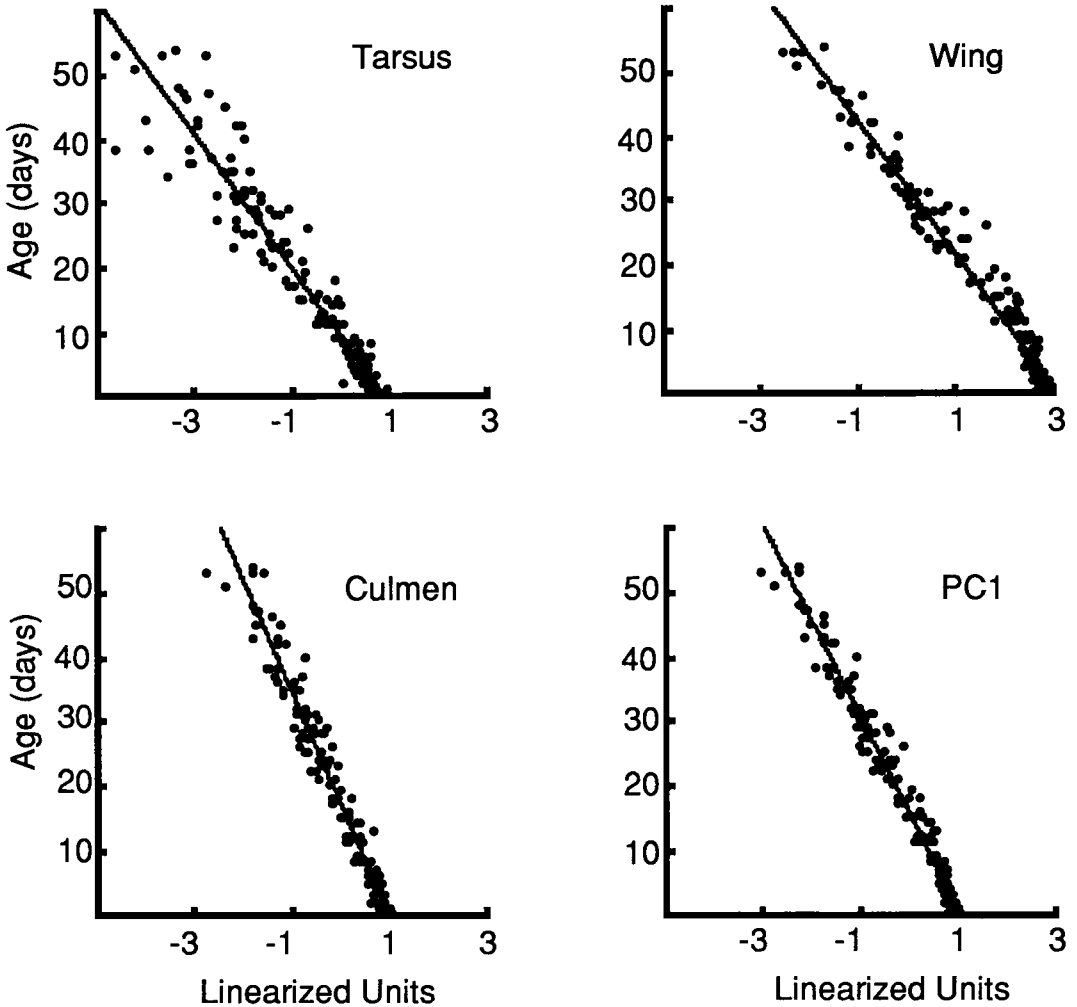


Fig. 2. Relationship between age and body size of Great Black-backed Gull chicks ($n = 209$).

sample was less than 0.5 days (Table 3). $WING_t$ overestimated age in the first five days, and underestimated age between the ages 5 and 20 (Figs. 2 and 3). CUL_t estimated age precisely over the nestling period (Fig. 2), but its overall performance was not as good as $WING_t$ (Tables 2 and 3). TAR_t gave the poorest estimate of age when used as an independent predictor (Table 3), and estimates became more variable after 35 days of age (Figs. 2 and 3) as tarsus approached asymptotic size.

The equation resulting from the multiple-linear-regression model was:

$$X = 25.59 - 7.85CUL_t - 5.69WING_t \quad (5)$$

with r^2 being 0.97 and the standard error of the estimate 2.55 days. The performance of PC1 and

the multiple-linear-regression models were similar (Table 3). The multiple-linear-regression model gave less biased estimates of age, but PC1 was slightly more precise in estimating

TABLE 3. Performance of age predictors in estimating actual age of chicks of verification sample. Statistics summarize differences between actual and estimated ages in days ($n = 300$).

Age predictor ^a	Mean error	SD	Range
Culmen	-0.341	2.89	22.9
Tarsus	-0.002	3.67	30.9
Wing	-0.361	2.93	17.7
PC1	-0.258	2.49	16.2
Culmen and wing ^b	-0.215	2.51	15.6

^a Linear form of body measures.

^b Multiple-regression model (see text).

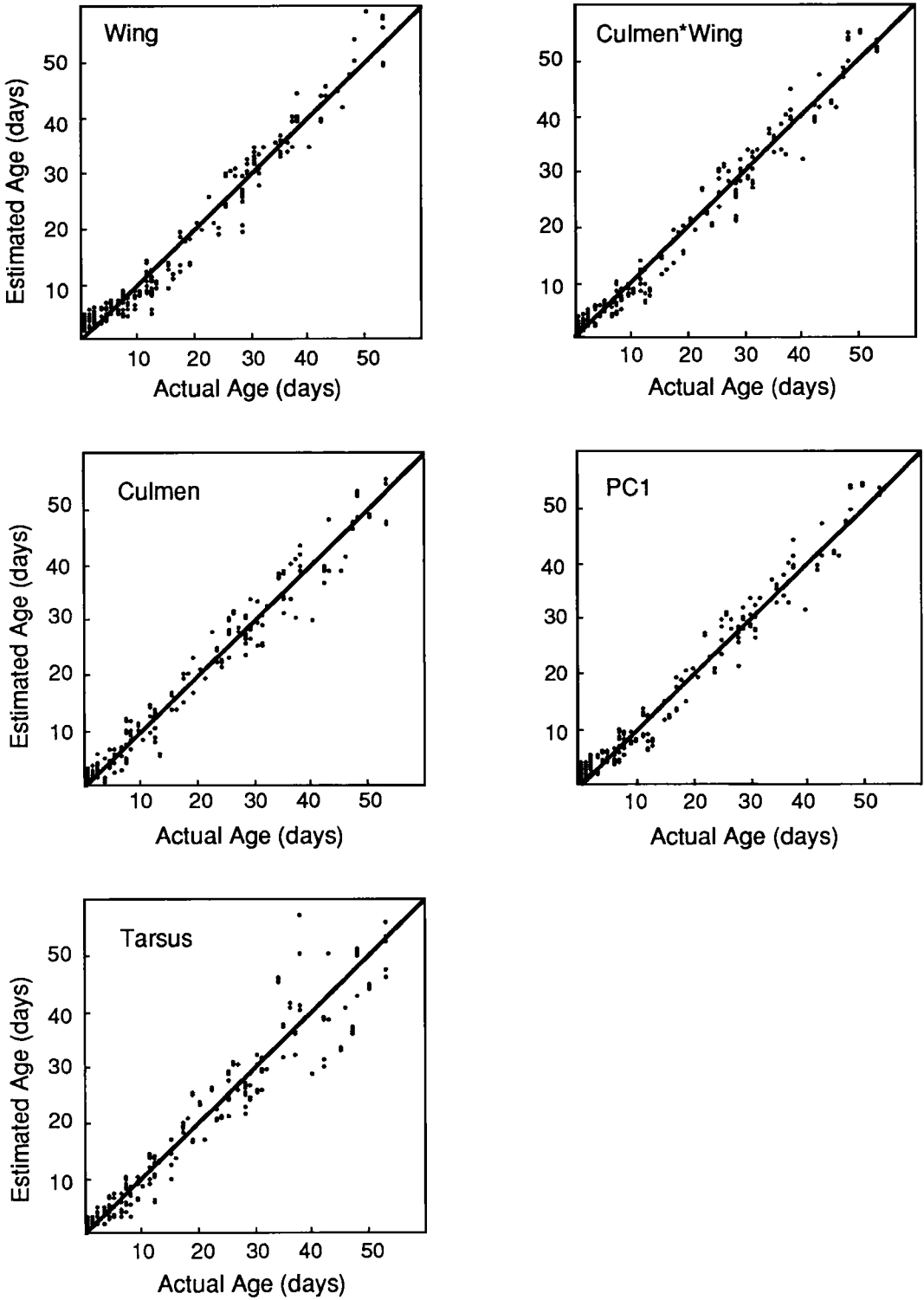


Fig. 3. Scatter plots for each predictive model of estimated age vs. known age for Great Black-backed Gull chicks in verification sample ($n = 300$; lines represent expected 1:1 relationship).

age (Table 3). However, PC1 estimated chick age the most accurately over the entire nestling period (see SE of estimate in Table 2).

DISCUSSION

Accurate predictors of age must be both unbiased and precise. All predictors tested had negligible bias in age estimation (<0.5 days), but their precision varied (Table 3). Not unexpectedly, age was predicted most precisely by predictors using multiple variables (Table 3).

The most accurate predication of age resulted from the regression of age on PC1 (Tables 2 and 3), with the multiple-linear-regression model performing similarly (Table 3). Generally, all models estimated age reasonably well in the early nestling period (Fig. 3). Partitioning the data into estimation and verification groups permitted testing the accuracy of predictors for the dependent variable. However, we caution against applying our equations and accuracy measures to other populations of Great Black-backed Gulls. The verification sample reflects the age distribution of birds in our data set (Fig. 1) and, because age was not estimated equally well across all ages (Fig. 3), measures of accuracy may not be reliable for other data sets. We recommend refitting and testing predictive models with a known-age sample (that is representative of the age distribution to be aged) before these aging techniques are applied to other populations.

A principal-components analysis is particularly well suited for growth studies, as PC1 almost always is an axis that operationally can be considered as size in a multidimensional space (defined by all morphological variables). For our data, PC1 had several advantages over any single measure of body size. For example, the fit of WING_t was poor over the first 20 days; however, PC1 was a good estimator during this period (Fig. 2). There are two possible explanations for this difference. First, one of the underlying assumptions of principal-components analysis is that relationships among the variables (measures of body size) are linear. Because the linear relationships among these variables were stronger than was the relationship between WING_t and age, PC1 may have had a stronger linear relationship with age than did the original variables. Second, because the closely covarying CUL_t and TAR_t were good age predictors during this interval (i.e. the first 20

days; Figs. 2 and 3) and both were important variables in defining the PC1 axis, they reduced the influence of WING_t in PC1 scores. Similarly, PC1 was less influenced by outliers than was any single predictor variable. Single-variable measures of body size (e.g. tarsus) estimate age best when they are growing fastest. However, because peak growth of each structure (culmen, wing, and tarsus) occurs at a different age, a multidimensional measure of body size, such as PC1, is likely to estimate age accurately over a longer period than will a measurement of any single structure.

Multiple-regression analysis is an alternative technique for describing relationships among several predictors. In this case, the performance of the multiple-linear-regression model is essentially the same as PC1 and, because multiple linear regression is relatively simple to use, this technique may be preferred. However, multiple linear regressions are restricted to predictive models and are not appropriate for studies of functional relationships. Both of these models (PC1 and multiple linear regression) benefited from the combined effect of more than one predictor, resulting in reduced effect of outliers on the precision of age estimates (see SD and range in Table 3).

In summary, we found that multivariable measures of body size were better predictors of age of Great Black-backed Gull chicks than were any of the original single-variable predictors. This was mainly due to increased precision and not a reduction in bias of the multivariate predictors in estimating age. PC1 was the best age predictor in our study, and it may be useful for aging other bird species.

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