Research Article

A Reexamination of Age-Related Variation in Body Weight and Morphometry of Maryland Nutria

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Abstract

*Age-related variation in morphometry has been documented for many species. Knowledge of growth patterns can be useful for modeling energetics, detecting physiological influences on populations, and predicting age. These benefits have shown value in understanding population dynamics of invasive species, particularly in developing efficient control and eradication programs. However, development and evaluation of descriptive and predictive models is a critical initial step in this process. Accordingly, we used data from necropsies of 1,544 nutria (*Myocastor coypus*) collected in Maryland, USA, to evaluate the accuracy of previously published models for prediction of nutria age from body weight. Published models underestimated body weights of our animals, especially for ages <3. We used cross-validation procedures to develop and evaluate models for describing nutria growth patterns and for predicting nutria age. We derived models from a randomly selected model-building data set (n = 192–193 M, 217–222 F) and evaluated them with the remaining animals (n = 487–488 M, 642–647 F). We used nonlinear regression to develop Gompertz growth-curve models relating morphometric variables to age. Predicted values of morphometric variables fell within the 95% confidence limits of their true values for most age classes. We also developed predictive models for estimating nutria age from morphometry, using linear regression of log-transformed age on morphometric variables. The evaluation data set corresponded with 95% prediction intervals from the new models. Predictive models for body weight and length provided greater accuracy and less bias than models for foot length and axillary girth. Our growth models accurately described age-related variation in nutria morphometry, and our predictive models provided accurate estimates of ages from morphometry that will be useful for live-captured individuals. Our models offer better accuracy and precision than previously published models, providing a capacity for modeling energetics and growth patterns of Maryland nutria as well as an empirical basis for determining population age structure from live-captured animals.* (JOURNAL OF WILDLIFE MANAGEMENT 70(4):1132–1141; 2006)

Key words

Age prediction, body weight, eye lens, Gompertz equation, growth model, morphometry, Myocastor coypus*, nutria.*

Nutria were introduced on the lower Eastern Shore of Maryland, USA, around 1940 (Willner et al. 1979). Initially viewed as a valuable fur resource, the species is now considered an undesirable invader of sensitive coastal marsh habitats. The Maryland population has expanded from the initial introduction site at Blackwater National Wildlife Refuge (NWR) to include most of the Atlantic Coastal Plain, USA (Bounds and Mollett 2000), but it is largely isolated from other lower-density populations that inhabit the Atlantic Coast and Mississippi Delta, USA. Because of the severe and lasting effects of nutria on Chesapeake Bay marshes, a long-term program of coordinated research and population control was initiated in 2000, including studies of nutria reproduction, physiology, population ecology, and movement patterns (Bounds et al. 2003).

Quantifying growth patterns can contribute to management efforts for invasive species by providing a foundation for energetic studies and detection of nutritional or physiological influences on populations. Data used to derive descriptive growth models also may be useful in developing models for predicting age from morphometry. These predictive models can be valuable tools in reconstructing population age structure, providing a foundation for understanding demographic consequences of population control. For example, age predictions for live-captured or harvested animals can be used in conjunction with estimates of reproductive and survival parameters to derive retrospective population censuses, which are key components of biologically based population control (Gosling et al. 1981, Gosling and Baker 1987, Doncaster and Micol 1989, Guichón et al. 2003). Similarly, descriptive growth models would provide a useful baseline against which to assess physiological changes in the Maryland nutria population.

Dixon et al. (1979) developed growth models for Maryland nutria from body weights obtained while live-trapping the Blackwater NWR population for mark–recapture population estimation. For each recaptured animal ($n = 163$), Dixon et al. (1979) measured changes in body weight during intervals between capture events. Resulting data were used to generate 2 models (1 for males, 1 for females) of the form:

$$W_t = (W_{\max} - W_0)(1 - e^{-bt}) + W_0 \qquad (1)$$

where W_t is body weight at time t, $W_{\max}$ is asymptotic body weight, W_0 is body weight at $t = 0$, b is growth rate, and e is the base of natural logarithms. The models subsequently were used as predictors of nutria age from body weight (Willner et al. 1980:345) after being evaluated with data from nutria aged by tooth development and wear (Aliev 1965). To predict ages, Willner et al. (1980) rearranged the equations developed by

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Dixon et al. (1979), retaining the original parameter estimates. Predicting age in this manner, however, results in biased estimates of the former independent variable (i.e., inverse prediction of age; Seber 1977). Generating new parameter estimates by regressing the independent variable (age) on the dependent variable (body weight) is unbiased and, therefore, preferable (Draper and Smith 1998, Laundré and Hernández 2002).

A drawback to the Dixon et al. (1979) models is that they were derived from animals for which age had not been empirically determined. Growth rate parameters (b) are measures of growth for intervals between weight measurements. These time periods should be positively correlated with, but not necessarily a direct measure of, age. In validating the models, Willner et al. (1980) assigned nutria ($n = 133$ F, 233 M) to 1 of 5 discrete age classes (0.5, 1, 2, 3, or 4 yr) based on tooth wear and compared mean predicted ages with mean observed ages. This approach is limited by age-related change in nutria body weight, which reaches an asymptote at about 2 years (Willner et al. 1980). Therefore, this classification essentially consisted of 3 groups (0.5, 1, or 2+ yr), providing a relatively insensitive test of b as a predictor of growth rate. Improved forms of model derivation and evaluation that provide better measures of agreement between observed and predicted values would enhance confidence in predictive models (Mayer and Butler 1993, Power 1993, Johnson 2001).

Given the limited empirical basis for the models of Dixon et al. (1979), we anticipated that they might not accurately predict nutria age. Eye-lens weight is a reliable predictor of nutria age (Gosling et al. 1980) but is not viable for studies requiring live release of animals and is labor-intensive when large samples of animals are involved. Predictors that can be quickly and reliably applied to live-captured and released animals are desirable for reconstructing the age distribution and demographic history of populations (Gosling et al. 1981). Given this need, Bounds et al. (2003) identified age-estimation techniques for live animals as one of the principal research priorities for North American nutria.

Management of nutria populations in the United States and Great Britain has involved development of simulation models that predict population and habitat responses to climatic variation, harvest, and habitat change (Gosling et al. 1983, Carter et al. 1999). These models can be sensitive to changes in demographic parameters, suggesting that errors in estimation of age could compromise the accuracy of model output, particularly where these errors introduce substantial variation in estimated production of young per female. These errors may be further magnified under conditions that delay the onset of puberty in nutria, such as birth during autumn (Newson 1966, Evans 1970) and under nutritional constraints (Atwood 1950).

Control and eradication programs often consist of intensive trapping of a discrete area, followed by less-intensive trapping aimed at removing individuals missed during intensive trapping. Animals trapped under these circumstances could be resident animals that were missed during the intensive trapping phase or animals that immigrated to the trapped area subsequent to intensive trapping. Distinguishing resident from immigrant animals is nearly impossible in an unmarked population, but obtaining accurate ages of these animals could indicate whether they were likely born before or after the cessation of intensive trapping. Given that nutria are relatively sedentary animals for which long-distance movements are not typical (Warkentin 1968, Linscombe et al. 1981, Ras 1999, S. L. Daugherty et al., University of Maryland Eastern Shore, unpublished data), estimated birth dates that succeed intensive trapping would indicate whether a reproductively viable segment of the population was not eliminated (Guichón et al. 2003). This approach is analogous to retrospective population censuses, which can provide a key scientific basis for successful eradication efforts (Gosling et al. 1981, Gosling and Baker 1987).

We focused on growth patterns of Maryland, USA, nutria, and our 3 principal goals were 1) to evaluate the predictive models of Dixon et al. (1979) using an extensive data set from the nutria population currently occupying the same study area, 2) to develop descriptive models for growth patterns of body weight and skeletal measurements (collectively morphometric data), and 3) to generate and evaluate predictive models for rapid estimation of age from morphometric variables.

Study Areas

The Chesapeake Nutria Partnership (hereafter, the Partnership) was a cooperative venture comprising 27 federal, state, and private organizations that share a common goal: identifying effective and efficient population-control techniques for nutria in the Chesapeake Bay and adjacent watersheds. Partnership activities have occurred primarily in Dorchester County, which contained the greatest abundance of nutria in Maryland, USA. Dorchester County was characterized by extensive brackish marsh that was rapidly being converted to open water by foraging nutria. We conducted field work in 3 study areas: Blackwater NWR (7,000 ha), Fishing Bay Wildlife Management Area (11,500 ha), and Tudor Farms (2,800 ha; Fig. 1). These 3 areas contained the most heavily damaged marsh in Maryland, USA (Bounds and Mollett 2000) and supported the state's greatest nutria density (Willner et al. 1979).

Methods

Capture Methods

The Partnership initiated a research program in January 2001 that included monthly trapping of the nutria population on each study area to address 2 principal goals: 1) mark and recapture animals for estimation of demographic parameters and movement rates, and 2) euthanize a portion of the captured animals and conduct detailed necropsies for evaluation of health and reproductive factors. To meet the objectives of concurrent reproductive studies, we collected 10 nutria of each sex monthly from each of 2 trapping sites in each study area.

We conducted trapping from January 2001–March 2002 with unbaited, single-door box traps and padded-jaw foothold traps set on nutria runs and riverbank locations where they climb out. We checked traps daily, and we promptly removed animals and transported them by boat or vehicle to the project headquarters at Blackwater NWR. Normally, we conducted euthanasia by gunshot

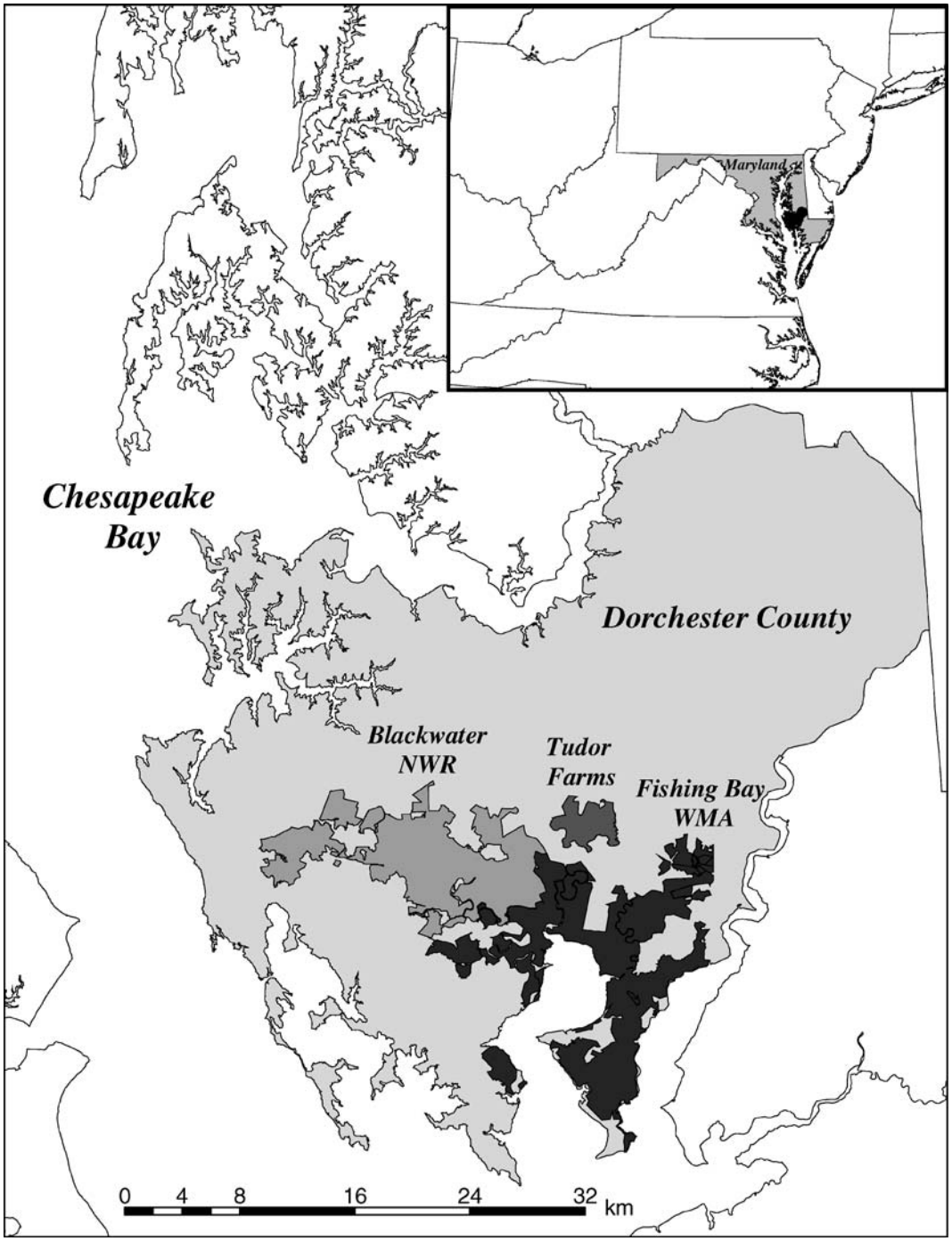

Figure 1. Study area map. Growth and age models were generated using necropsy data from 1,544 nutria trapped at Blackwater National Wildlife Refuge (NWR), Tudor Farms, and Fishing Bay Wildlife Management Area (WMA), Dorchester County, Maryland, USA.

and necropsy on the day of capture, but high capture rates occasionally required that animals be held overnight and processed the following morning. We conducted field and laboratory procedures in accordance with guidelines of an Animal Use Protocol approved by the Institutional Animal Care and Use Committee of the University of Maryland Eastern Shore (IACUC 12-13-01–008). We performed euthanasia as described by the American Veterinary Medical Association Panel on Euthanasia (AVMA 2001).

Necropsies

We conducted detailed necropsies of 1,544 nutria (680 M, 864 F), during which we measured the following physical features: 1) body weight (g; WEIGHT) to the nearest 100 g, using a spring scale, 2) body length (cm; LENGTH), the longest dimension from the tip of the nose to the base of the tail, 3) axillary girth (cm; GIRTH), the circumference around the animal's thorax immediately behind the front legs, and 4) right hind-foot length (cm; FOOT), from the base of the tubercalcis to the distal end of the longest digit.

Table 1. Sample sizes used in model-building and evaluation data sets for derivation of the Gompertz growth models and linear regression models for using morphometric variables to predict age of nutria collected in Dorchester County, Maryland, USA, during Jan 2001–Mar 2002. Age classes are based on estimates derived from eye-lens weight (AGE_{eye}).

	Males		Females	
Age class	Model building	Evaluation	Model building	Evaluation
0	8	0	9	0
3	10	46	10	52
6	10	62[b]	10[d]	72
9	10	60	10	52
12	10	36	10	12
15	10	27	10[d]	23
18	10	31	10	25
21	10	31	10	26[h]
24	10	25	10	28
27	10	33	10[d]	47[i]
30	10	35[c]	10[e]	54[j]
33	10	39	10	50
36	10	26	10	65
39	10	19	10	53
42	9[a]	7	10	31
45	10	6	10[d]	27
48	10	4	10	13[k]
51	8	0	10	9
54	9	0	10	3
57	4	0	10	0
60	2	0	5[f]	0
63	1	0	4[g]	0
66	1	0	4	0
69	0	0	5	0

[a] $n = 10$ for WEIGHT.
[b] $n = 61$ for FOOT.
[c] $n = 34$ for GIRTH.
[d] $n = 9$ for WEIGHT.
[e] $n = 9$ for GIRTH.
[f] $n = 4$ for WEIGHT.
[g] $n = 3$ for FOOT.
[h] $n = 25$ for WEIGHT.
[i] $n = 46$ for WEIGHT.
[j] $n = 52$ for WEIGHT.
[k] $n = 12$ for WEIGHT.

Sample sizes varied slightly among morphometric variables due to missing data points (Table 1).

We enucleated both eyes during necropsy, and we fixed them in 10% formalin. Intact eyes remained in formalin for at least 1 month to allow hardening of lenses (Gosling et al. 1980). We removed lenses, rinsed them with distilled water, separated them from other tissues, and dried them at 80°C for 24 hours. We weighed dry lenses separately on an analytic balance to the nearest 0.01 mg. We used the mean weight of the 2 lenses to estimate age, following the Gosling et al. (1980) equation, as transformed by Bounds et al. (2003):

$$AGE_{eye} = 10^{0.511+0.013\times LW} - 4.34 \qquad (2)$$

where AGE_{eye} is the estimate of age (months), and LW is mean eye-lens weight (mg). We treated AGE_{eye} as the actual age for each animal because it represented the best-possible estimate of age for wild animals for which birth date is not precisely known.

Statistical Analyses

Evaluation of existing models.—We assigned each animal to a 3-month age class, using t_i to represent the interval beginning at age i. For each age class and sex, we determined mean body weight and an associated 95% confidence interval. We then used the models of Dixon et al. (1979; Equation 1) to derive predicted body weights for the range of ages represented in our sample of necropsied animals. We evaluated these growth curves graphically, examining each age class to determine whether the predicted value fell within the 95% confidence interval of mean body weight for our animals.

Derivation of growth models.—We derived new models describing nutria growth patterns in relation to morphometric variables using cross-validation procedures, which simulated replication of a study by splitting the data into model-building and evaluation data sets (Myers 1990, Neter et al. 1990, Johnson 2001). We randomly selected a model-building data set that was as evenly distributed across the 3-month age classes as possible so that each age class had approximately equal influence on parameter estimates. We were restricted from maximizing the number of animals in the model-building data set because of the small sample sizes in age class 0 and in the oldest age classes (Table 1). We selected a sample size of 10 per age class as a reasonable compromise, judging that the importance of accurately estimating growth-rate parameters justified a slight underrepresentation in age class 0. We judged limited sample sizes ($n < 10$) to be of relatively little practical importance because these age classes occurred well into the asymptotic portion of the growth curves.

We used Gompertz growth equations to model the relations between age and morphometric variables for the model-building data sets. Gompertz equations are of the form:

$$W_t = A \times \exp(-e^{-b(t-k)}) \qquad (3)$$

where W_t is the value of the response variable for age t, A is the asymptotic value of W, e is the base of natural logarithms, k is the value of the dependent variable at the point of maximum growth rate, and b is the growth-rate parameter. Because Gompertz curves have been effectively used to model growth patterns for a variety of species (Reed et al. 1999, Huin and Prince 2000, Lammers et al. 2001), we expected that they would also be useful for describing nutria growth dynamics. We used nonlinear regression (PROC NLIN, SAS Institute Inc. 1990) to estimate the Gompertz model parameters (A, k, and b) for each of the 4 response variables we measured (WEIGHT, LENGTH, GIRTH, and FOOT). Although nutria are not strongly dimorphic, maximum weights tend to be greater in males (Bounds et al. 2003). As some of the variables we measured were likely to be influenced by pregnancy (e.g., WEIGHT, GIRTH), we analyzed data separately for the sexes without controlling for the effect of pregnancy. We selected starting values for iterative parameter estimation in PROC NLIN by examining a scatter plot of each response variable against AGE_{eye}. We evaluated our models graphically by plotting curves from Equation 3 and examining their correspondence with 95% confidence limits for mean morphometric variables within age classes from evaluation data sets (Myers 1990, Neter et al. 1990, Johnson 2001). When data splitting is used for

model evaluation, final parameter estimates should be based on the entire data set to make use of all of the available information (Myers 1990). Therefore, although we used split data sets to develop initial parameter estimates and evaluate the functional form of the resulting models, we reported parameter estimates that were derived from the entire data set.

Derivation of predictive age models.—We derived univariate models for predicting nutria age from morphometric variables using linear regression, with the 4 morphometric measurements as independent variables and AGE_{eye} as the dependent variable (Draper and Smith 1998, Laundré and Hernández 2002). The asymptotic form of growth curves places a limitation on ability to predict the age of animals that have reached growth maturity. Consequently, we eliminated observations at or above the asymptote, and we retained data within the logarithmic portion of the growth curve for use in predictive models (Laundré and Hernández 2002). The asymptote of a growth curve represents the mean size of a morphometric character at the completion of growth, but age at growth maturity, is mathematically undefined. Therefore, we substituted $W_t = 0.99 \times A$ in Equation 3 and solved for t. We eliminated observations for which $AGE_{eye} > t$, and we used simple linear regression to generate predictive models of the form:

$$\log_e(AGE_{eye}) = x \times \log_e(W_t) + b \qquad (4)$$

where AGE_{eye} is age derived from the eye-lens weight, and W_t indicates one of the variables (WEIGHT, LENGTH, GIRTH, or FOOT), which we used to estimate age. We assessed accuracy of our models using standard graphical diagnostics for residuals, including plots against predicted values and normal probability plots, to evaluate model fit (Draper and Smith 1998).

Results

Evaluation of Existing Models

The growth models of Dixon et al. (1979) predicted body weights that were within the 95% confidence limits of our measured weights for age-class 0 in females and age classes 0–9 in males (Fig. 2). Above these age classes, the Dixon et al. (1979) models substantially underestimated the range of observed values for body weight (Fig. 2). Discrepancy between the models and our data was most pronounced for age classes 12–36; for that period, the models underestimated mean weight of our animals by 520–1,090 g for females and 520–980 g for males (Fig. 2). Predictions from the Dixon et al. (1979) models were within the 95% confidence limits for body weight of age classes ≥45 for females and ≥39 for males; that was about 8 and 6 age classes after our animals had attained asymptotic weight (Fig. 2).

Descriptive Growth Models

We derived Gompertz growth models relating the 4 morphometric variables to AGE_{eye} for both male and female nutria. Explained variation (r^2) was consistently higher for males than for females (Table 2), and it was highest for LENGTH in both males and females. The asymptotic value (A) of WEIGHT was 14.5% higher for males than for females, and the remaining 3 asymptotes also were higher for males but to a lesser degree (4.1%, 8.8%, and 5.3% for LENGTH, GIRTH, and FOOT, respectively; Table 2). In contrast, growth rate parameters (b) for all 4 variables were higher for females than for males (Table 2).

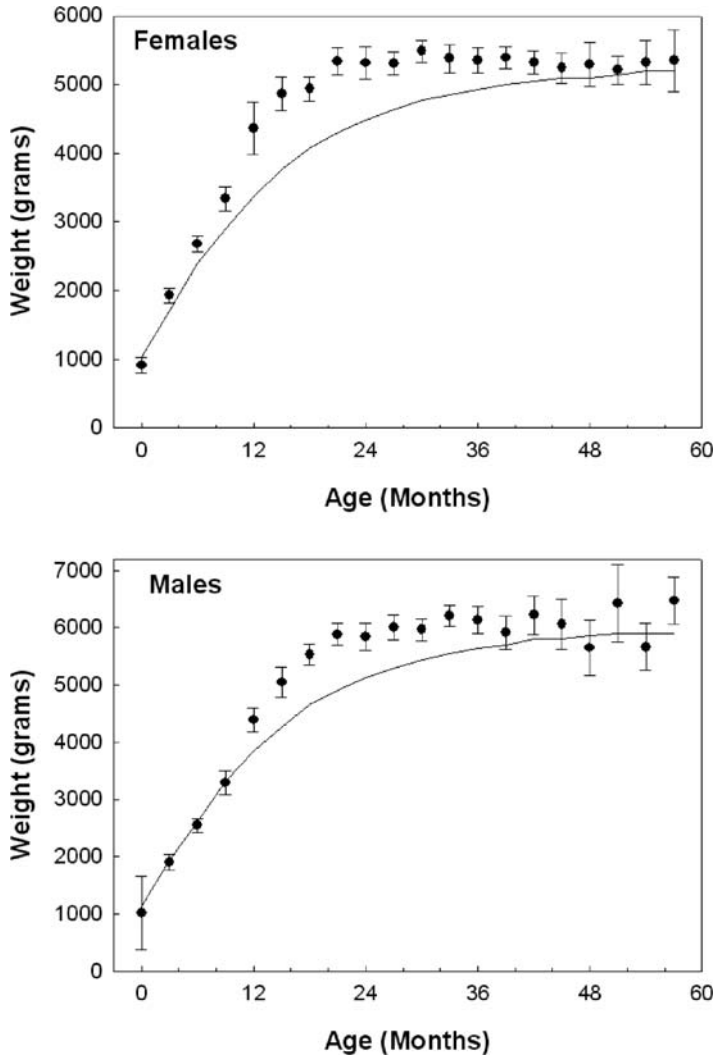

Figure 2. Relationship between mean body weight (g; ±95% CI) and AGE_{eye} of male ($n = 679$) and female ($n = 849$) nutria collected in Dorchester County, Maryland, USA, during 2001–2002. Points and confidence intervals represent measured values of age and weight, and the line represents the relationship between age and weight predicted by Dixon et al. (1979) for nutria collected in the same location.

Our estimated ages of growth completion suggested that FOOT growth was completed at the earliest age and WEIGHT growth at the latest age for both sexes (Table 3). Whereas age of growth completion was identical between the sexes for FOOT, it was 4.0, 2.4, and 8.2 months earlier for females for WEIGHT, LENGTH, and GIRTH, respectively (Table 3).

The Gompertz models provided good graphical correspondence with the range of data in evaluation data sets for each variable. In particular, our WEIGHT model (Fig. 3A) provided a substantially better fit than did the Dixon et al. (1979) models (Fig. 2), particularly for age classes 12–33. LENGTH for the evaluation data set exhibited little variation within age classes, and 95% confidence intervals included the Gompertz model prediction for most age classes (Fig. 3B). There was considerably more variation

Table 2. Parameter estimates and standard errors for Gompertz equations describing growth of morphometric measurements of nutria in relation to AGE_{eye}, where W_t is the value of the response variable, $t = AGE_{eye}$, and $W_t = A \times \exp(-e^{-b(t-k)})$. We derived parameter estimates from the entire data set (680 M, 864 F) of nutria collected in Dorchester County, Maryland, USA, during Jan 2001–Mar 2002.

	A		*b*		*k*				
Response variable	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	***n***	***F****	r^2
Males									
WEIGHT	6,163.2	46.89	0.152	0.0064	6.429	0.157	193	12,422	0.84
LENGTH	57.328	0.208	0.138	0.0055	−1.211	0.295	192	65,894	0.84
GIRTH	41.434	0.243	0.131	0.0079	−1.222	0.455	192	27,070	0.70
FOOT	12.802	0.034	0.182	0.008	−2.079	0.338	193	93,866	0.78
Females									
WEIGHT	5,382.2	36.13	0.178	0.001	5.382	0.191	217	11,137	0.72
LENGTH	55.026	0.151	0.157	0.0067	−1.130	0.313	222	77,182	0.79
GIRTH	38.083	0.167	0.154	0.011	−1.742	0.566	221	31,001	0.56
FOOT	12.161	0.024	0.195	0.0093	−2.622	0.387	221	127,674	0.70

* $P < 0.001$ for all models.

in GIRTH, both within and among age classes, particularly for females (Fig. 3C). However, direction and extent of this variation did not suggest any bias for the Gompertz model. FOOT exhibited a pattern across age classes that was similar to that of LENGTH, with each age class being characterized by a relatively small range of values that were well represented by the Gompertz model (Fig. 3D).

Predictive Age Models

Each of the 4 morphometric variables was a significant ($P < 0.001$) predictor of AGE_{eye}, with an explained variation being >72% for males and >59% for females (Table 4). Explained variation was greatest for the WEIGHT and LENGTH models and least for the GIRTH and FOOT models for both sexes (Table 4). Nearly all of the data points from our evaluation data sets fell within 95% prediction limits derived from the model-building data sets (Fig. 4). Similarly, conventional residual diagnostics did not reveal any substantial departures from expected patterns.

Discussion

Evaluation of Existing Models

The models derived by Dixon et al. (1979) consistently underestimated weight of our animals. Discrepancies between the models and our data were most pronounced as weight was rapidly increasing and approaching its asymptote (AGE_{eye} = 1–3 yr). Although these discrepancies are minor as a percentage of total body weight, they illustrate a shortcoming of inverse-prediction methods (Seber 1977). Relatively small errors in estimation of weight from age using sigmoid growth curves can translate into substantial errors if models are rearranged for prediction of age from weight. The majority of our animals were <3 years old (80% of males and 65% of females), suggesting that biased estimates of age from body weight would be common in our data set under those models.

Table 3. Estimated age (months) at which morphometric measurements attain 99% of the asymptotic value predicted by Gompertz growth models for male and female nutria collected in Dorchester County, Maryland, USA, during Jan 2001–Mar 2002.

Morphometric variable	**Males**	**Females**
WEIGHT	34.3	30.3
LENGTH	29.5	27.1
GIRTH	34.5	26.3
FOOT	22.2	22.2

Errors of that nature will have their greatest consequences where body weights are used to estimate time since attainment of a biologically important life-history event, such as puberty. For example, Laurie (1946) reported that nutria in Great Britain attained puberty at ~5 months of age and at a body weight of 1.8–2.2 kg. Predicted ages for a 2.0-kg female nutria using Dixon et al. (1979) and our WEIGHT model are nearly identical (5.9 and 6.0 months, respectively), suggesting that the 2 models would be equivalent in their ability to predict reproductive maturity for females of this size. However, the Dixon et al. (1979) model and our WEIGHT model predict ages of 25.7 and 16.9 months, respectively, for a 4.5-kg female nutria. Assuming a 2-week interval from parturition to conception (Gosling 1980) and a gestation period of 130–134 days (Newson 1966, Gosling 1974, Willner et al. 1979, Gosling and Skinner 1984), this difference in predicted age is adequate for 2 complete reproductive cycles. Age prediction errors of this magnitude could lead to inaccurate estimates of previous reproductive activity, which would be further magnified when compounded through multiple generations in a retrospective population census (Gosling et al. 1981, Gosling and Baker 1987).

An alternative and simpler explanation for model discrepancy is that the Dixon et al. (1979) models were not accurate because of a lack of empirical age data for the animals used to derive them. The validation of the Dixon et al. (1979) models presented by Willner et al. (1980) had little potential to illustrate model inaccuracy because it was based on tooth wear (Aliev 1965), an aging technique that is subjective, insensitive to changes in age <1 year, and potentially influenced by food quality (Kinler et al. 1987). In contrast, our models are based on a technique that has been shown to accurately predict the age of nutria to within 1 month (Gosling et al. 1980).

Our analysis was predicated on the assumption that AGE_{eye} is an unbiased estimate of true age. Strictly speaking, we only evaluated

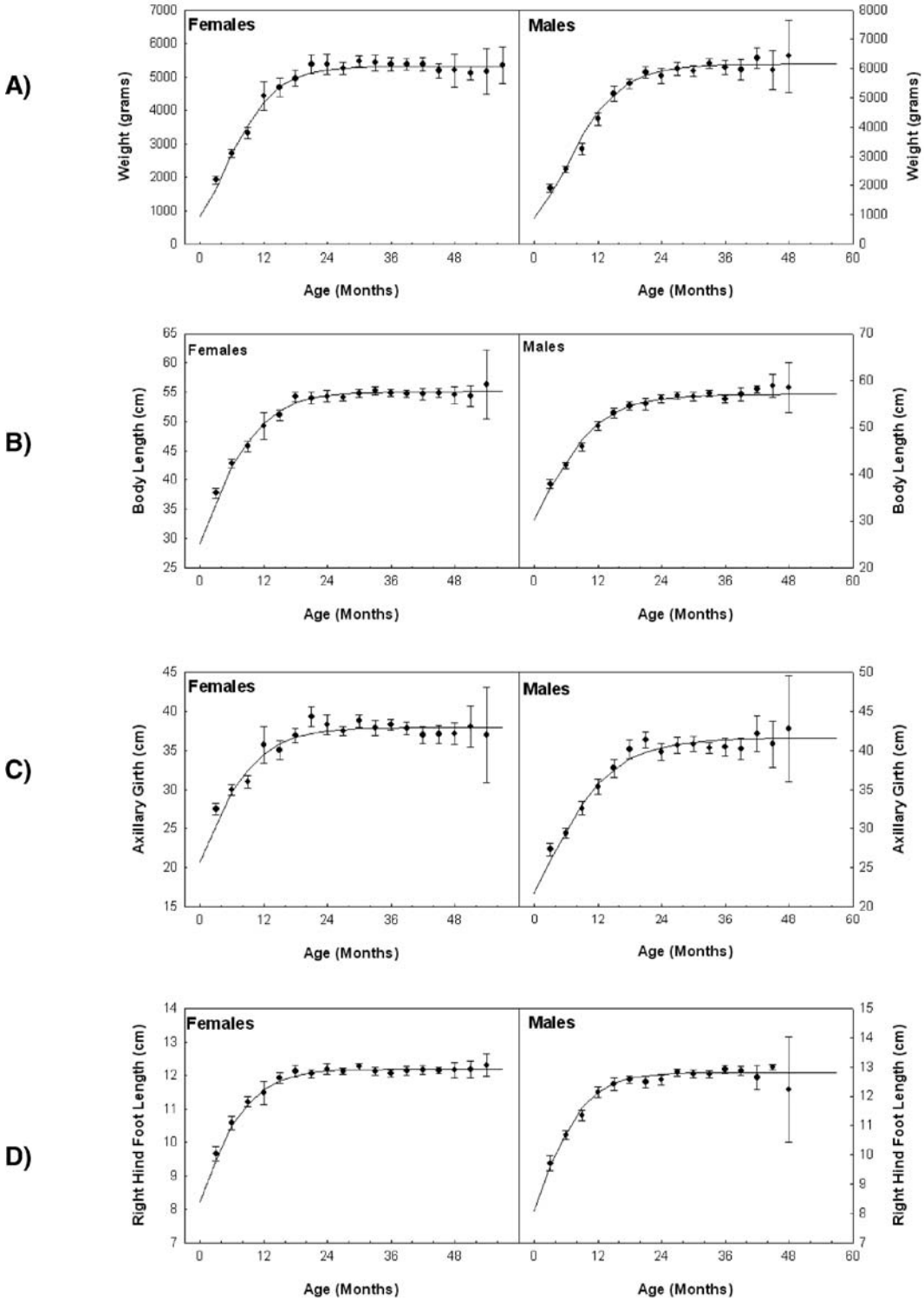

Figure 3. Growth curves for (A) body weight, (B) body length, (C) axillary girth, and (D) right hind-foot length of male and female nutria collected in Dorchester County, Maryland, USA. Curves were generated by applying Gompertz growth models to the randomly selected model-building data set. Mean of the dependent variable (±95% CI) is shown for animals in the evaluation data set in 3-month age classes.

the ability of the Dixon et al. (1979) models to accurately predict AGE_{eye}, which is itself an age estimate with associated variance rather than a true age measurement. However, we believe that AGE_{eye} is a good estimate of true age, as indicated by the high precision of the original predictive model for nutria (Gosling et al. 1980) and the general acceptance of eye-lens weight as an estimator of age for wild animals of unknown birth date (Connolly et al. 1969, Gourley and Jannet 1975, Thomas and Bellis 1980, Hardy et al. 1983, Rowe et al. 1985). Extensive modeling of population dynamics for the nutria population in Great Britain

Table 4. Parameter estimates and standard errors for using morphometric variables in logarithmic equations [$\ln(AGE) = x \times \ln(var) + b$; where *var* represents one of the morphometric variables] to estimate age of nutria collected in Dorchester County, Maryland, USA, during Jan 2001–Mar 2002.

	x		*b*				
var	**Estimate**	**SE**	**Estimate**	**SE**	***n***	***F****	r^2
Males							
WEIGHT	1.231	0.0240	0.952	0.0348	510	2,629	0.84
LENGTH	3.370	0.0714	−10.517	0.276	449	2,226	0.83
GIRTH	2.995	0.0823	−8.004	0.293	509	1,325	0.72
FOOT	3.679	0.119	−6.600	0.288	341	957	0.73
Females							
WEIGHT	1.279	0.0296	0.904	0.0395	431	1,867	0.81
LENGTH	3.144	0.0917	−9.644	0.351	379	1,176	0.76
GIRTH	2.777	0.106	−7.273	0.369	363	680	0.65
FOOT	3.496	0.164	−6.100	0.390	314	456	0.59

* $P < 0.001$ for all models.

was based on eye-lens weight as the sole aging criterion (Gosling et al. 1981).

Growth Models

Our models revealed several differences in growth patterns between the sexes that have not previously been described in the literature. For example, our parameter estimate for asymptotic body weight was 14.5% higher in males than in females, whereas asymptotes for the 3 skeletal measurements were 4–9% greater in males. However, all 4 parameters were characterized by faster growth rates in females than in males, leading to a more rapid attainment of physical maturity in females for these parameters. Rapid growth rates should provide a selective advantage for females because of the premium placed on resource allocation to reproduction. Other parameters, such as seasonal survival rates, are also known to vary between male and female nutria (Doncaster and Micol 1990, Gosling and Baker 1991), suggesting that population control efforts should account for physiological differences between the sexes to the extent possible.

Willner et al. (1980) concluded there was a decline in body weight for older (>2 yr) females, but this conclusion was based on 13 3-year-old and 2 4-year-old nutria. With a greater number of animals in age classes >24 months, our data suggested that mean body mass did not vary across age classes after asymptotes were reached (Fig. 3A). Consequently, we conclude that the decline in female body mass described by Willner et al. (1980) was a consequence of small sample sizes. Asymptotes were similarly well-defined for the 3 skeletal measurements we employed (Fig. 3B–D).

Age Prediction

Although few other data on dimorphism in nutria are available, we developed models separately for each sex to account for potential effects of pregnancy. We were able to determine the reproductive status of females during necropsies, but we did not include a pregnancy variable in our models. To be useful in predictive models, a pregnancy variable would have to be measurable in live animals. However, few first- and second-trimester pregnancies are evident on gross external examination. Although effects of pregnancy are probably limited to the third trimester, we obtained a higher level of precision for males than for females for each of the 4 variables we measured. Given our a priori suspicions regarding influence of pregnancy on age estimation, the relatively poor performance of the GIRTH model for females was not surprising. However, that result can not be exclusively attributed to pregnancy because the GIRTH model for males performed similarly. Further, the WEIGHT model for females, which should have had approximately equal sensitivity to pregnancy as the GIRTH model, performed very well.

Adams (1956) defined 3 age classes for Louisiana, USA, nutria equivalent to our age classes 0, 3, and 6 and distinguished among them based on hind-foot lengths (≤11.0 cm, 11.3–12.5 cm, and ≥12.8 cm). Those values are substantially higher than the foot lengths of our animals, which were nearly identical for males and females (8.0, 9.7, and 10.7 cm for age classes 0, 3, and 6, respectively). Similarly, Ras (1999) documented animals with hind foot length <12.5 cm that were known to be >5 months old and concluded that the age criteria proposed by Adams (1956) were problematic for Maryland, USA, nutria. Although our models did not suggest that FOOT was either a better or worse predictor of age than the other variables, they did confirm the Ras (1999) conclusions.

Management Implications

Nutria control or eradication programs that target reproductively viable population remnants are most likely to achieve their objectives. Our models provide a capacity for rapid, reliable age estimation of Maryland, USA, nutria, which would support that need and would provide a stronger basis for population models (Carter et al. 1999). Our models improve upon several previously published aging techniques for nutria by providing a more accurate method for predicting ages from body weights or morphological measurements. We recommend use of these models to monitor age distribution of harvested nutria to enhance efficiency of control or eradication efforts. Because the degree to which they apply to other nutria populations is unknown, we recommend evaluation of our models using known-age animals before they are used in other regions.

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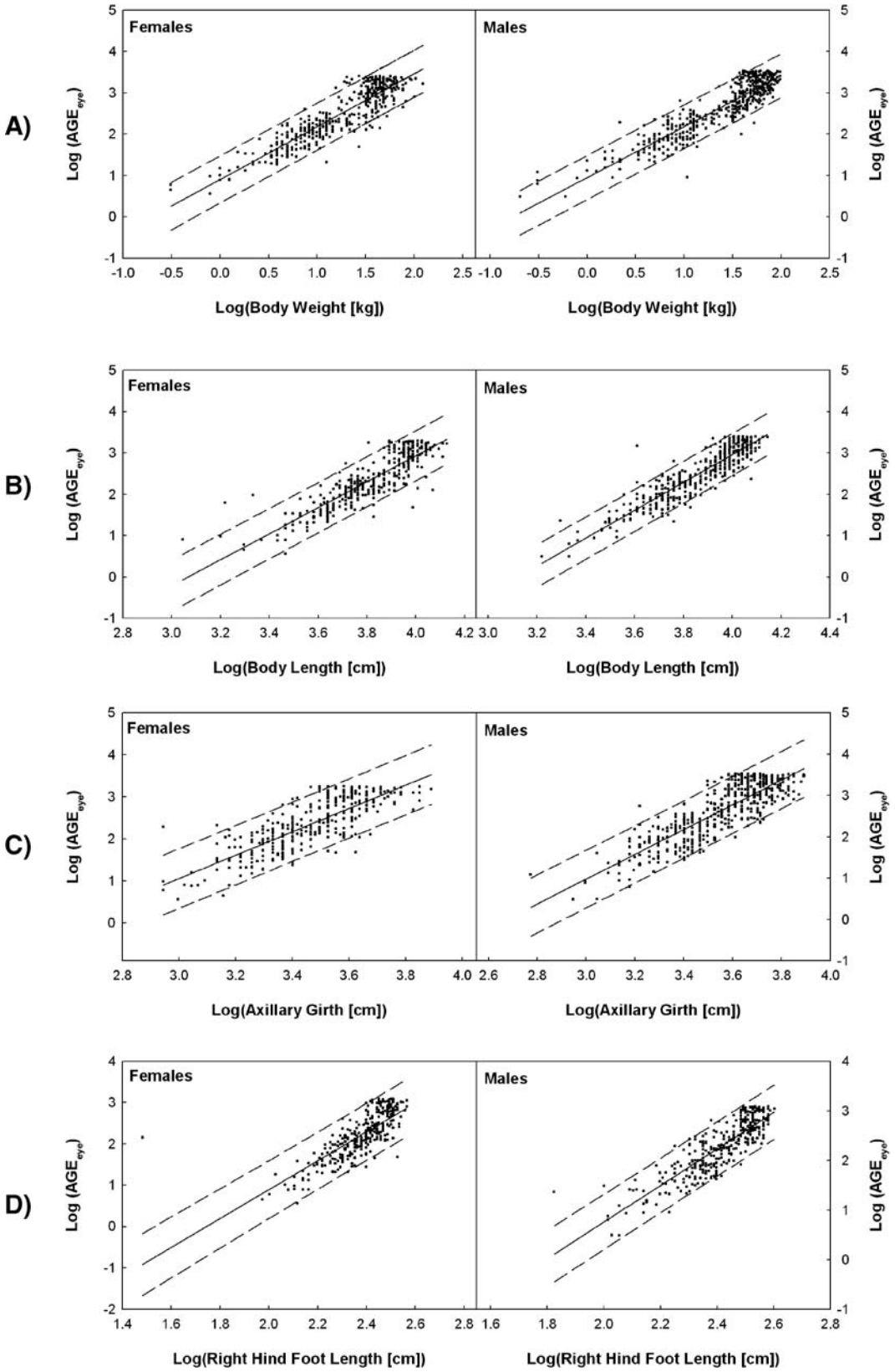

Figure 4. Predictive models relating AGE_{eye} to (A) body weight, (B) body length, (C) axillary girth, and (D) right hind-foot length of male and female nutria collected in Dorchester County, Maryland, USA. Regression equations were generated using the randomly selected model-building data set. Points represent AGE_{eye} in relation to each morphometric variable for the animals in the evaluation data set. Dotted lines represent 95% prediction intervals.

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