#118

Using nonlinear mixed effects models to estimate size–age relationships for black bears

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Abstract: Size–age relationships for three physical characteristics, body length, zygomatic width, and pad width, were modeled for black bears (*Ursus americanus*) captured in northeastern Minnesota, U.S.A. Because the curves representing size–age relationships were nonlinear, and because some of the data consist of repeated, longitudinal observations for multiple bears, nonlinear mixed effects model analyses were required. The results are presented as parameter estimates with standard errors and estimated population curves with 95% confidence intervals. Variance estimates obtained using mixed-effects models are compared with erroneous estimates obtained using ordinary least-squares techniques. Comparisons are made between male and female Minnesota bears with respect to parameter estimates and estimated population curves. In addition, the results for Minnesota bears are compared with results from similar studies on bears in other regions.

Résumé : Les relations taille–âge de trois caractéristiques physiques, longueur du corps, largeur de la tête au niveau de l'arc zygomatique, largeur de la paume, ont servi à la création d'un modèle chez des Ours noirs (*Ursus americanus*) capturés dans le nord-est du Minnesota, É.-U. Comme les courbes représentant les relations taille–âge ne sont pas linéaires et parce que certaines des données sont des observations longitudinales répétées de plusieurs ours, nous avons dû utiliser des analyses de modèles non linéaires d'effets mixtes. Les résultats sont présentés sous forme d'estimations des variables démographiques avec erreurs types et de courbes d'estimation des populations avec intervalles de confiance de 95%. Les estimations de la variance obtenues à partir des modèles d'effets mixtes ont été comparées aux estimations erronées obtenues par la technique usuelle des moindres carrés. Les mâles et les femelles de la population du Minnesota sont comparés entre eux des points de vue de l'estimation des variables et de l'estimation des courbes de la population. De plus, les résultats obtenus chez les ours du Minnesota sont comparés à ceux obtenus au cours d'autres études en d'autres régions.
[Traduit par la Rédaction]

Introduction

Quantitatively describing an animal species' characteristic size–age relationships, both for individuals and populations, is an important component of population studies (Fitzhugh 1976). Estimates of size–age curves, together with reliable precision estimates, help in the assessment of differences among populations (Kingsley et al. 1988; Yoccoz et al. 1993), changes in populations over time (Kingsley 1979), and differences between the sexes within a population (Sauer 1975; Alt 1980). Animal growth and size–age relationships are often analyzed using longitudinal data consisting of repeated observations over time on each one of many animals (Fitzhugh 1976; Kaufmann 1981; Zullinger et al. 1984). Statistical procedures that accommodate the nature of these data must be used if unbiased parameter estimates and reliable precision estimates are to be obtained. A long-standing difficulty in many growth and size–age studies is that appropriate methods have not been available for dealing with repeated and serially correlated observations for multiple individuals (Fitzhugh 1976; Yoccoz et al. 1993). Recent advances in nonlinear mixed effects modeling have the potential to substantially alleviate this difficulty. To assess the performance of nonlinear mixed effects modeling procedures in this context, we estimated size–age relationships for northeastern Minnesota black bears (*Ursus americanus*), compared the results with estimates from other geographic regions, and compared variance estimates with those that would have been obtained erroneously with ordinary least squares.

Methods

Data collection

Data were collected from bears captured in the Superior National Forest in northeastern Minnesota, U.S.A. (Rogers 1987). Vegetation in the study area contains components of both the boreal and temperate deciduous forests and is typical of the northern Great Lakes region (Maycock and Curtis 1960). The climate is cool-temperate, and during the data-collection period the frost-free growing season averaged 118 days. The ground was generally snow-covered from mid-November through mid-April, and bears were typically in dens from mid-October until mid-April (Rogers 1987).

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Fig. 1. Distributions of male (*a*) and female bears (*b*) by age.
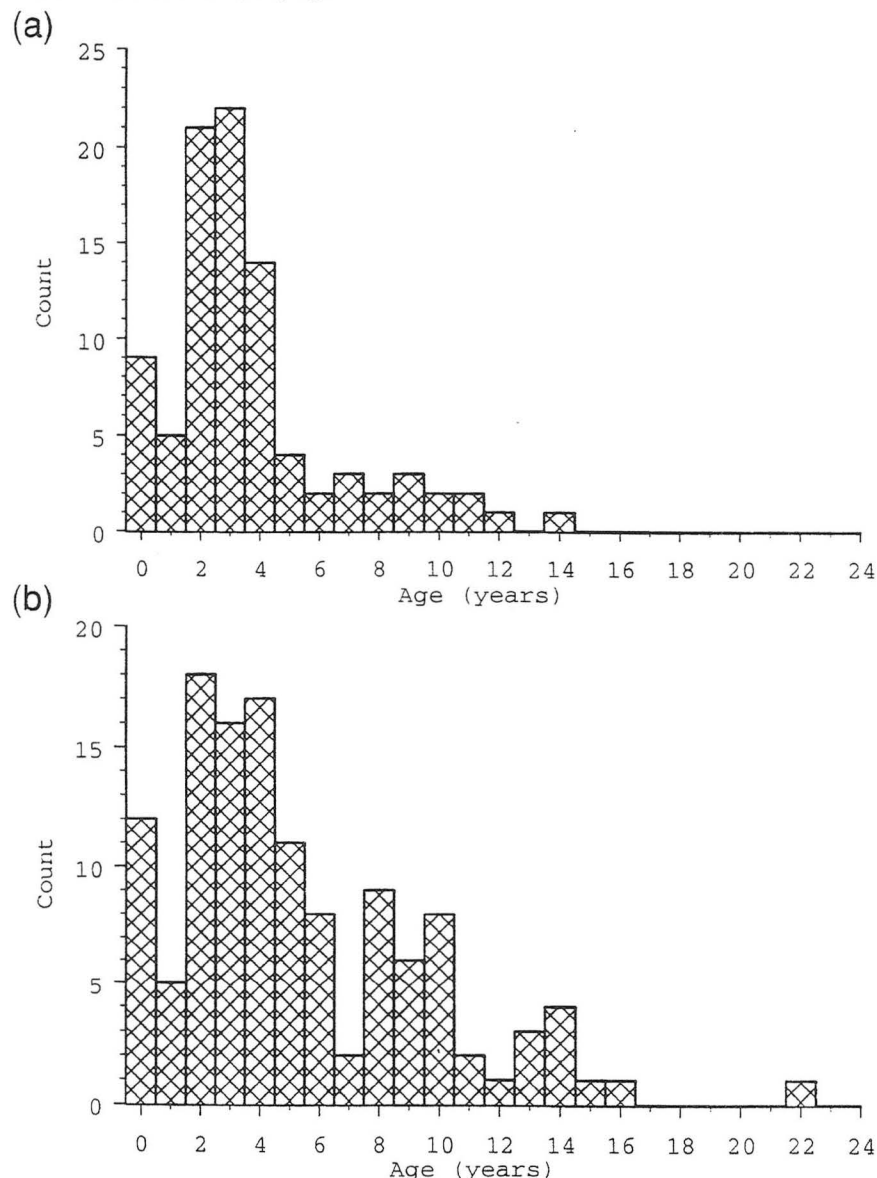
Bears were captured in foot snares, culvert live traps, or dens and were immobilized with drugs for examination and measurement (Rogers 1987). At the time of capture, each bear was sexed and weighed, and body length, zygomatic width, and pad width were measured. Body length was measured along the contour of the back from the tip of the nosepad to the tip of the bone in the tail, taking care to position the muzzle, head, back, and tail in as straight a line as possible. Zygomatic width, including skin and fat, was measured with calipers at the zygomatic arches of the skull. The forefoot pad was measured across its greatest width, taking care to flatten the pad to approximate its shape when bearing weight. Maximum pad width was measured between the hairlines at the edges of the calloused pad. Age was determined by counting cementum annuli in longitudinal sections from a first upper premolar (Stoneburg and Jonkel 1966; Willey 1974; Rogers 1978). Bears were ear-tagged and some were radio-collared to facilitate serial measurements.

The size–age analyses are based on up to 88 observations from as many as 68 male bears ranging in age from less than 1 year to 14 years and on up to 120 observations from as many as 69 female bears ranging in age from less than 1 year to 22 years (Fig. 1). No more than seven observations were available for any bear, and only a single observation for many bears (Fig. 2). Owing to some missing and unusable observations, the same numbers of bears and observations were not available for the analyses of all variables (Table 1).

Data analyses

Selection of an appropriate analytical technique requires that the nature of the study and the data-collection strategy first be identified. In a discussion of the characteristics that distinguish experiments and observational studies, Wold (1956) set down three criteria for experiments: (1) replications are made under similar conditions; (2) replications are mutually independent; and (3) uncontrolled variation in the replications is subjected to randomization.

On the basis of these criteria, both Wold (1956) and McKinlay (1985) characterize cross-sectional and longitudinal studies as experiments, while arguing that observational studies violate at least one criterion.

Cross-sectional studies are typically based on mutually independent observations obtained from different subjects. Observations within replications are collected in the same short time interval, are

Fig. 2. Distributions of male (*a*) and female bears (*b*) by number of observations per bear.
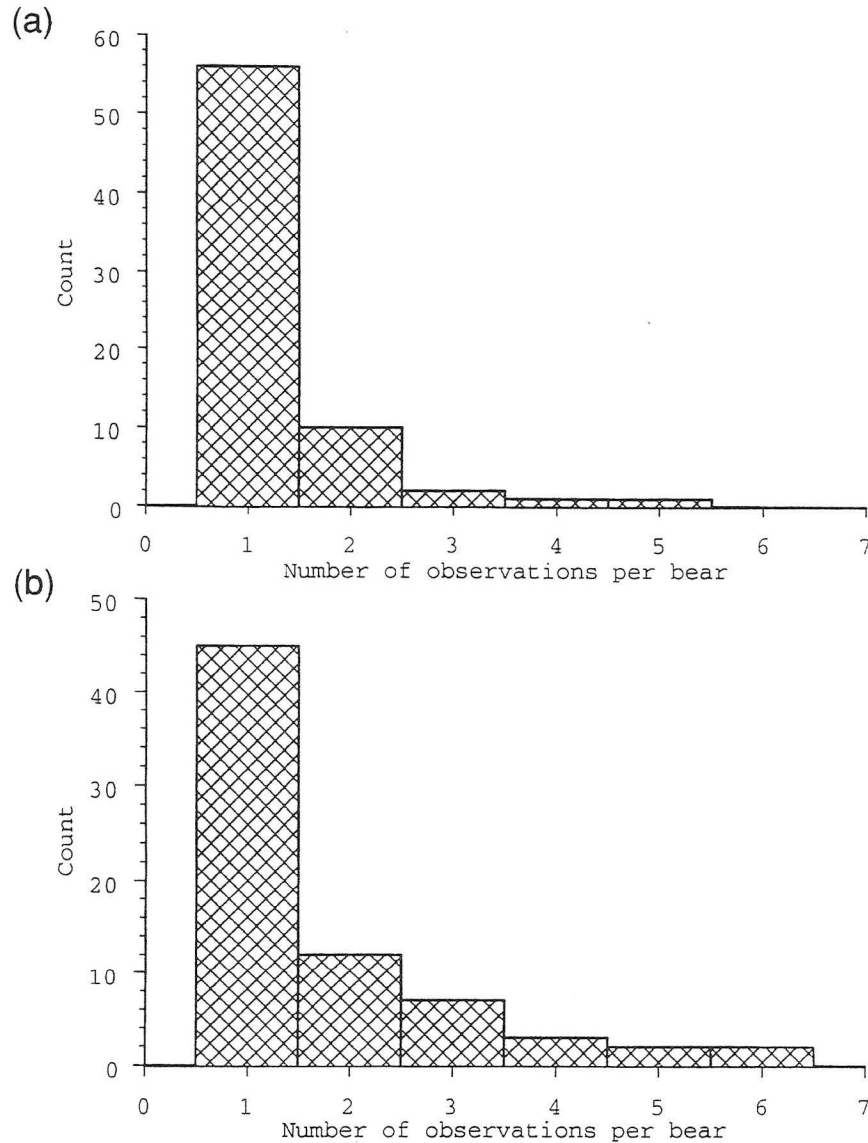
**Table 1.** Mixed effects models estimates for $E(Y) = \beta_1[1 - \beta_2 e^{-\beta_3(t-1)}]$.

Variable	Sex	n_{obs}	n_{bears}	$\mathrm{Var}(b_{i1})$	σ^2_{res}	$\hat{\beta}_1 \pm SE(\hat{\beta}_1)$	$\hat{\beta}_2 \pm SE(\hat{\beta}_2)$	$\hat{\beta}_3 \pm SE(\hat{\beta}_3)$
Body length	Male	73	64	90.44	0.65	169.65±2.02	0.43±0.01	0.38±0.02
	Female	91	62	32.51	5.42	141.37±1.20	0.36±0.01	0.54±0.03
Zygomatic width	Male	85	64	1.68	0.46	22.63±0.94	0.50±0.02	0.20±0.03
	Female	99	63	0.59	0.17	16.01±0.19	0.29±0.03	0.44±0.04
Pad width	Male	88	68	0.27	0.53	12.43±0.37	0.38±0.03	0.38±0.02
	Female	120	69	0.23	0.04	9.37±0.08	0.21±0.01	0.70±0.10

mutually independent, and are made under similar conditions to minimize or provide measures of uncontrolled variation. Although cross-sectional data preclude any analysis of individual subjects, statistical analyses need not accommodate within-subject variation or correlation.

Longitudinal studies are typically based on multiple observations from multiple subjects and feature serial correlation and both within and among subject sources of variation. These studies focus on the analysis of individual subjects and the development of population relationships based on the aggregation of individual relationships. Although population analyses for longitudinal studies are more complex than for cross-sectional studies, some of the difficulties can be alleviated with balanced, regularly spaced designs and models that are linear in the parameters.

Fig. 3. Zygomatic width versus age profiles for female bears.
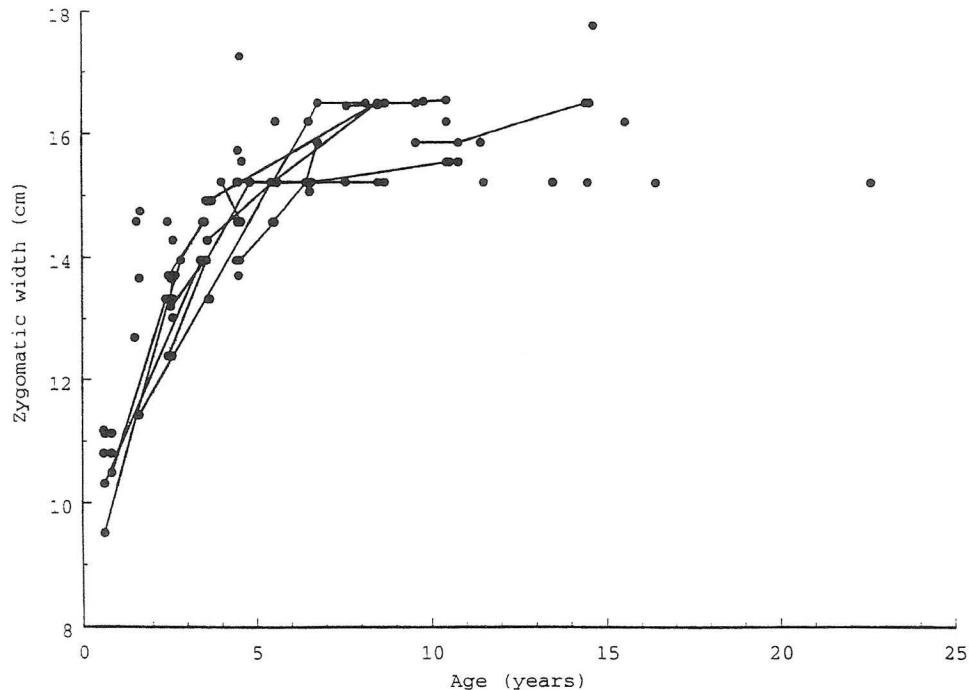
Wold (1956) defines observational data as those in which at least one of his criteria is violated, while McKinlay (1985) uses "observational" to denote investigations described negatively as "not experiments." Because in many investigations of size–age relationships in wildlife populations the observations must be obtained as they become available, they typically violate one or more of Wold's criteria for experiments. Such is the case for our study, where there is no opportunity for randomization, experimental replication, or control for external factors. In addition, the observations were obtained without regard to time of year, age, size, annual environmental conditions, or the design features that simplify analyses. Finally, the data contain multiple observations for some subjects, as in a longitudinal study, but only single observations for the remaining subjects, as in a cross-sectional study. Thus, our investigation is an observational study and particular caution is necessary to assure that analytical techniques accommodate the features of the data.

Caution must also be exercised when comparing the results from observational studies with those from other studies. When an appropriate statistical technique is correctly applied for each type of study, unbiased estimates of model parameters and population curves are obtained, as well as valid variance estimates. Using these estimates, crude, but valid, statistical comparisons of population curves can be made, and when the same models are used, valid statistical comparisons of model parameters can also be made. However, despite the statistical validity of these comparisons, the biological validity may be questionable because of differences in replication and randomization strategies, control of external factors, and the effects of nonlinearity when observations from individuals are aggregated to produce population estimates.

For our study, care was taken to accommodate numerous characteristics of the data, of which three are crucial to the selection of an analytical technique: (1) multiple observations were obtained for some bears; (2) size–age curves for individual bears deviated from population size–age curves; and (3) mathematical models of size–age relationships for both individuals and the population were nonlinear in the parameters (Fig. 3). First, because multiple measurements were obtained for some bears, the observations are characterized as repeated-measures data. In addition, because the multiple observa-

tions for individuals could not be randomized with respect to age, they are further characterized as longitudinal data. Thus, even though our investigation is considered an observational study, the analytical technique must accommodate longitudinal data. Second, under the assumption that the captured bears represent a random sample from the population of interest, two sources of variation must be accommodated in the analyses: (1) the deviations of observations from individual size–age curves and (2) the deviations of individual size–age curves from population size–age curves. Failure to accommodate the two sources of variation separately may result in unreliable estimates of parameters, population curves, residual variation, covariance structures, and confidence intervals. Finally, the nonlinear form of the size–age models requires iterative techniques that compound the difficulty of accommodating multiple sources of variation.

In recent years, procedures have been developed for estimating the parameters of nonlinear population models using longitudinal data for multiple individuals (Davidian and Giltinan 1995; Littell et al. 1996; Vonesh and Chinchilli 1998). Models associated with these techniques are known as nonlinear mixed effects models because they contain both fixed effects population parameters and random effects representing the deviations of the parameters for individuals from the population parameters. In addition, these techniques accommodate unbalanced, irregularly spaced observations and serial correlation among residuals for the same subject.

A simple example illustrates the dangers inherent in failure to use mixed effects models analyses when required by the data. We used nonlinear ordinary least squares (OLS) and mixed-effects models (MEM) analyses to estimate population curves for zygomatic width versus age based on data for four female bears. The OLS analysis incorrectly assumed that the observations were independent and estimated a population curve that characterized only the observations. The MEM analysis correctly estimated a population curve that characterized the population of individual curves (Fig. 4a). In addition, the OLS approximate 95% confidence interval is too narrow because of the erroneous assumption of independent observations; the MEM confidence interval is much wider because it acknowledges that the observations represent only four individuals (Fig. 4b). Thus, failure to deal with the longitudinal nature of the data for multiple individu-

Fig. 4. Results from mixed-effects models (MEM) versus ordinary least squares (OLS) models. (*a*) Population curves. (*b*) Approximate 95% confidence intervals.
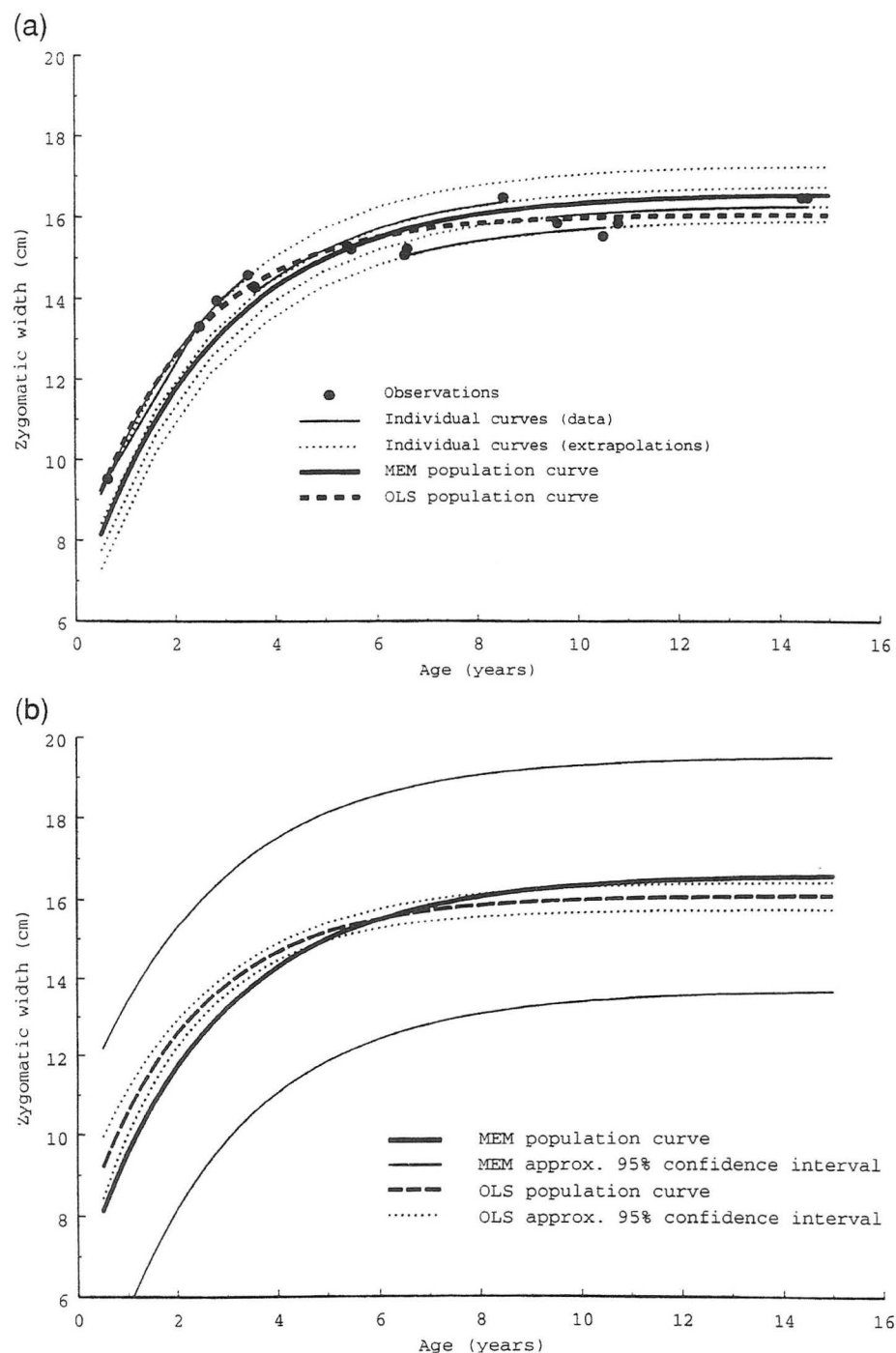
als may result in inadequate estimates of population curves and erroneous confidence intervals.

The general form of the mixed effects model for this application may be expressed as

[1] $Y_{ij} = f(t_{ij}; \boldsymbol{\beta} + \boldsymbol{b}_i) + \epsilon_{ij}$

where

t_{ij} is the age of the ith bear at its jth observation

Y_{ij} is the dependent variable corresponding to t_{ij}

$\boldsymbol{\beta} = (\beta_1, \beta_2, ..., \beta_p)$ is a vector of fixed-effects population parameters of length p

$\boldsymbol{b}_i = (b_{i1}, b_{i2}, ..., b_{ir})$ is a vector of random effects of length r, $r \leq p$; $\boldsymbol{b}_i$ represents the deviations of the parameters for the ith individual bear from the population parameters and is assumed to be distributed $N(0, \boldsymbol{V})$

f is a mathematical function expressing the relationship among $\boldsymbol{\beta}$, $\boldsymbol{b}_i$, and t

ϵ_{ij} is a residual representing the deviation of Y_{ij} from the corresponding model expectation for that individual; ϵ_{ij} is assumed to be distributed $N(0, \sigma^2 \Lambda_i)$, where Λ_i is the matrix of correlations among residuals for the ith bear; residuals for different bears are assumed to be independent

Model parameters were estimated and corresponding statistics were calculated using the nonlinear mixed effects models macro in the Statistical Analysis System (SAS) software (Littell et al. 1996).

An appropriate mathematical form for the function f was determined by comparing likelihood statistics for a variety of two- and three-parameter models. For each mathematical form, the appropriate number of random effects to be included and the appropriate residual correlation structure were determined using likelihood-ratio tests of significance. For all analyses, the number of observations was required to exceed the total number of parameters, which is calculated as

$$n_{tot} = p + r\, n_{bears}$$

where p is the number of fixed effects population parameters, r is the number of random effects per bear, and n_{bears} is the number of bears. Thus, it was not possible to include random effects for all fixed effects population parameters for the complete data sets because of the large numbers of bears with only one or two observations. However, tests of combinations of random effects were conducted on the largest data sets that would support the analyses.

The statistical expectation of the model selected to describe the black bear size–age relationships for both individuals and populations has the general mathematical form

[2] $\qquad E(Y) = \beta_1(1 - \beta_2\, e^{-\beta_3 t})$

where Y, t, and β are as defined for [1]. This model is often referred to as the monomolecular model (Yang et al. 1978) and can be derived from the von Bertalanffy model (1957), provided a theoretical constraint on a parameter is relaxed. The parameters of [2] can be interpreted in a manner similar to those for the von Bertalanffy model: β_1 is asymptotic size; $1 - \beta_2$ is birth size as a proportion of asymptotic size; and β_3 is a growth rate constant. Because birth date is difficult to estimate accurately and because few observations for the first few months were available, model [2] was revised as follows:

[3a] $\qquad E(Y) = \beta_1[1 - \beta_2\, e^{-\beta_3(t-1)}]$

where Y, t, β_1, and β_3 are as defined for [2], but $1 - \beta_2$ is now size at 1 year of age as a proportion of asymptotic size.

The analyses for [3a] indicated that correlation among residuals for the same bears was small and usually nonsignificant; this correlation was ignored for the final analyses. For all three characteristics and for both sexes, the random effect corresponding to fixed effects population parameter β_1 was the only random effect that significantly ($\alpha = 0.05$) improved the quality of fit. This result held for complete data sets and for reduced data sets for which two or more random effects were included. Thus, the final mixed effects model used to describe black bear size–age relationships is given by

[3b] $\qquad Y_{ij} = (\beta_1 + b_{i1})\,[1 - \beta_2\, e^{-\beta_3(t_{ij}-1)}] + \epsilon_{ij}$

where Y, t, β, and b_i are as defined for [3a] and ϵ is a residual deviation assumed to be distributed $N(0,\sigma_{res}^2)$.

A 95% confidence interval for each estimated population curve was approximated as

[4] $\qquad \hat{Y}_k \pm 2\, SE(\hat{Y}_k)$

where

[5] $\qquad \hat{SE}(\hat{Y}_k) = Z_k(\hat{\beta},\hat{b}_i,t_k)'\, Cov\,(\hat{\beta})\, Z_k(\hat{\beta},\hat{b}_i,t_k)$

$Cov\,(\hat{\beta})$ is the estimate of the covariance matrix of the population parameter estimates, and $Z_k(\hat{\beta},\hat{b}_i,t_k)$ is the vector of first derivatives of f with respect to the population parameters evaluated at $\hat{\beta}$, $\hat{b}_i$, and t_k.

Results and discussion

Nonlinear mixed-effects modeling
The mixed effects modeling procedure adequately estimated

size–age curves for both individuals and populations. Larger numbers of observations for individual bears would produce greater precision because greater numbers of random effects could be included in the analyses and tests of significance would be more powerful.

Assessment of the variation for repeated, longitudinal observations is more difficult than for independent observations, where all the variation is summarized in the residual variance, $\hat{\sigma}_{res}^2$. For the former case, assessment of variation requires knowledge of both the residual variance, $\hat{\sigma}_{res}^2$, around individual curves and the variation among estimates of individual curves as expressed by $\hat{V}$. When OLS and MEM are correctly applied, $\hat{\sigma}_{res}^2$ is interpreted in the same manner for both procedures. The geometric interpretation of $\hat{V}$ for MEM analyses is fairly simple; it is the variation among the estimated curves. The analytical interpretation of $\hat{V}$, however, may be difficult to express in an intuitive manner for two reasons: (1) $\hat{V}$ is model-dependent and (2) the effects of $\hat{V}$ cannot be readily visualized without sampling from the distribution and graphing the curves that result. Both the geometric and analytical interpretations of $\hat{V}$ are simplified for [3b] because there is only one random effect and the parameter to which it corresponds has straightforward geometrical and biological interpretations. For [3b], $\hat{V}$ is interpreted as the variation in asymptotes of the curves for individual bears or equivalently as the variation in maximum sizes of the bears.

For data requiring only OLS procedures, there is no V to estimate, because all the observations are independent and each represents a different individual. However, when OLS procedures are incorrectly applied to data requiring MEM procedures, the single estimate of variation, herein labeled σ_{OLS}^2, represents a pooling of both residual variation and the variation among individual curves. In these cases, $\hat{\sigma}_{OLS}^2$ is frequently, but incorrectly, used as an estimate of $\hat{\sigma}_{res}^2$. Unless there is virtually no variation among individual curves, $\hat{\sigma}_{OLS}^2$ usually overestimates σ_{res}^2, as is apparent in comparisons of $\hat{\sigma}_{res-MEM}^2$ and $\hat{\sigma}_{OLS}^2$ for our data sets: (1) for male body length, $\hat{\sigma}_{res-MEM}^2 = 0.65$, while $\hat{\sigma}_{OLS}^2 = 57.02$; (2) for female body length, $\hat{\sigma}_{res-MEM}^2 = 5.42$, while $\hat{\sigma}_{OLS}^2 = 28.24$; (3) for male zygomatic width, $\hat{\sigma}_{res-MEM}^2 = 0.46$, while $\hat{\sigma}_{OLS}^2 = 1.24$; (4) for female zygomatic width, $\hat{\sigma}_{res-MEM}^2 = 0.17$, while $\hat{\sigma}_{OLS}^2 = 0.54$; (5) for male pad width, $\hat{\sigma}_{res-MEM}^2 = 0.26$, while $\hat{\sigma}_{OLS}^2 = 0.56$; and (6) for female pad width, $\hat{\sigma}_{res-MEM}^2 = 0.04$, while $\hat{\sigma}_{OLS}^2 = 0.26$.

Although reliable confidence intervals require separate and accurate estimates for both sources of variation, the widths of OLS and MEM confidence intervals were similar for our data sets. We partially attribute this result to the fact that many of our data were independent because most bears had only a single observation.

Growth and sexual dimorphism in growth
Comparisons between male and female Minnesota black bears are based on the estimated population parameter estimates (Table 1), evaluation of the model using these parameter estimates, the estimated population curves, and likelihood-ratio tests of significance. For all three characteristics, the estimated population curve for males differed significantly ($\alpha = 0.01$) from the curve for females, and each parameter estimate for the male population curve differed significantly ($\alpha = 0.01$) from the corresponding parameter estimate for the

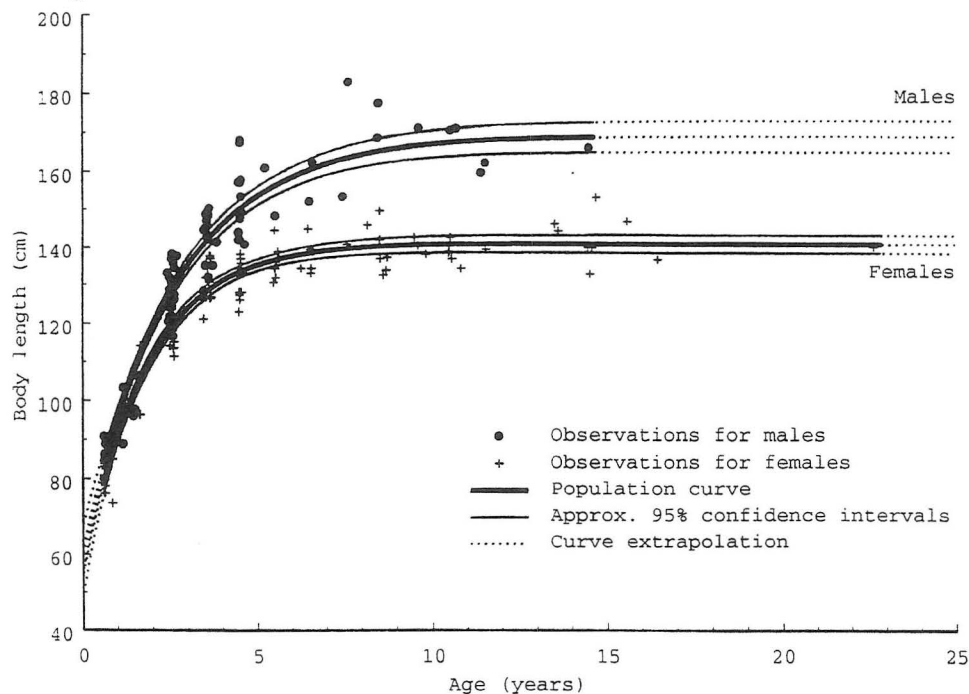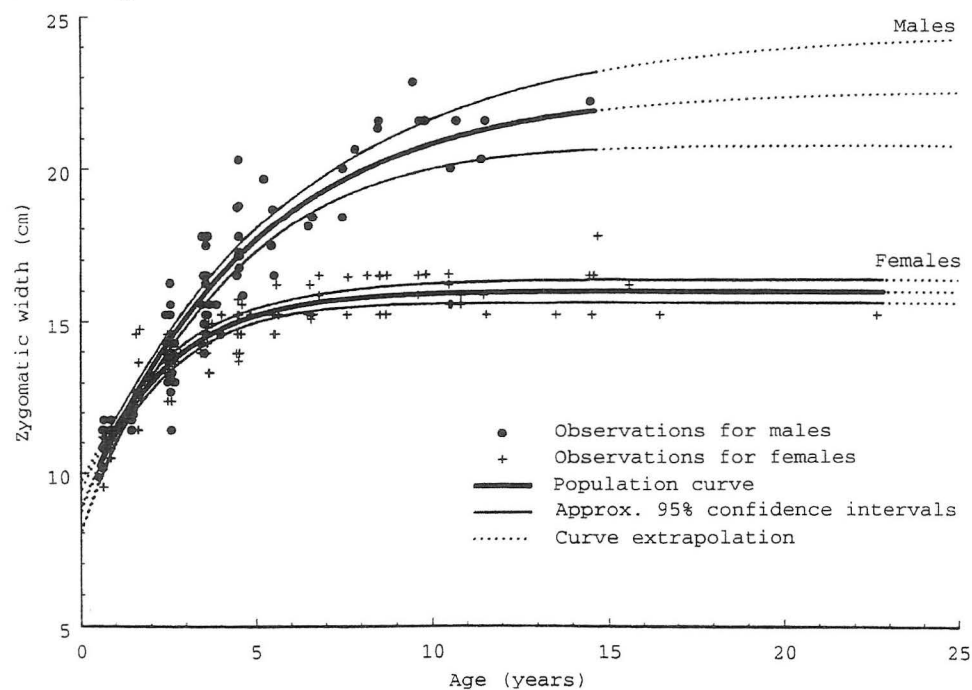**Fig. 5.** Body length versus age.

**Fig. 6.** Zygomatic width versus age.

female population curve. These results produce three features that distinguish the male and female population size–age curves: (1) male bears were larger at all ages; (2) female bears approached asymptotic size at greater rates than did male bears; and (3) growth continued at a greater age for male bears.

The estimated population curves (Figs. 5–7) indicate that male Minnesota bears were larger than female Minnesota

bears at all ages. Sizes at 1 year of age were estimated as a proportion of asymptotic size by $1 - \hat{\beta}_2$ and in absolute terms by $\hat{\beta}_1(1 - \hat{\beta}_2)$. As a proportion of asymptotic size, males were significantly ($\alpha = 0.05$) smaller than females at 1 year of age for all three physical characteristics. However, with respect to absolute size at 1 year of age, males were significantly ($\alpha = 0.05$) larger than females with respect to body length but were not significantly ($\alpha = 0.05$) different with respect to zygo-

Fig. 7. Pad width versus age.
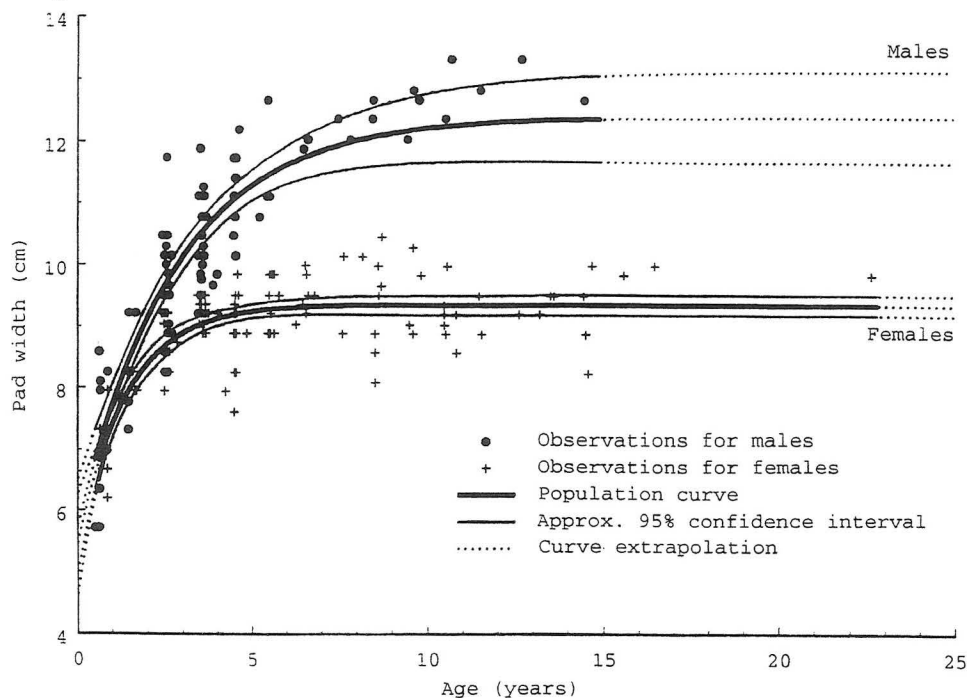
matic width or pad width. Population estimates of asymptotic size, $\hat{\beta}_1$, indicate that male Minnesota bears grew significantly ($\alpha = 0.05$) larger than females: 20% larger with respect to body length, 42% larger with respect to zygomatic width, and 33% larger with respect to pad width.

The nonlinear form of [3a] with respect to age indicates that growth rates for both male and female bears change with age. For each characteristic, estimates of β_3 were positive for both sexes but greater for females than for males. These results indicated that growth rates decreased as age increased for both sexes and that females approached asymptotic size more rapidly than did males. On average, female Minnesota bears reach reproductive maturity, the age at first reproduction, at 6.3 years (Rogers 1987). By this age, females had attained 97.9% of their asymptotic body length, 97.2% of their asymptotic zygomatic width, and 99.5% of their asymptotic pad width. Males did not attain these percentages until 9.0, 15.4, and 12.3 years of age, respectively. This result is consistent with the observation for brown bears in northwestern Canada and Alaska (Kingsley et al. 1988) that growth rates for males were less than those for females.

We compared age-specific population estimates for Minnesota bears with corresponding means reported for black bears in other regions: New York (Sauer 1975), Alaska (Rausch 1961), and Pennsylvania (Alt 1980). The age-specific population estimates for Minnesota bears were obtained by evaluating model [3a] using the population parameter estimates (Table 1). These comparisons should be viewed with some skepticism, because there is no assurance that the effects of external factors were similar. In addition, the comparisons were not statistical, because variance estimates were not always available. Nevertheless, for all three characteristics and for both sexes, Minnesota bears were similar to or larger than New York bears. Also, both male and female Minnesota bears were larger than Alaska bears with respect to zygomatic

width. However, Pennsylvania bears of both sexes had greater age-specific body lengths than Minnesota bears. Because Minnesota cubs were similar in body length to Pennsylvania cubs, the latter result confirms Alt's observation that "Pennsylvania bears appear to be growing more rapidly...than [bears] from other areas" (Alt 1980).

Conclusions

The nonlinear mixed effects modeling approach to estimating size–age relationships produced adequate estimates for both individual and population curves. The population curves characterized the population of individual curves rather than just the observations for the individuals sampled. Failure to apply nonlinear mixed effects modeling to data consisting of longitudinal, repeated-measures observations for multiple individuals may produce bias in the population estimates and erroneous confidence intervals for population parameters and curves.

Male Minnesota bears were larger at all ages than female bears, and continued to grow at a greater age than female bears. The greatest sex differences were for asymptotic zygomatic width, asymptotic pad width, and the age at which growth is completed. For the characteristics compared, Minnesota bears were larger than Alaska bears and similar to or larger than New York bears, but smaller than Pennsylvania bears.

The results of comparing Minnesota bears by sex and comparing Minnesota bears with bears from other regions were neither unique nor surprising; in fact, they were quite consistent with biological expectations. Although this consistency may be regarded as a mundane observation from a biological perspective, from a statistical perspective it ought to assure researchers unfamiliar with or skeptical of nonlinear mixed effects modeling techniques and encourage them to apply these techniques in appropriate circumstances.

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