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MODELS OF MASS GROWTH FOR 3 NORTH AMERICAN COUGAR POPULATIONS

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Abstract: Previous studies of cougar (*Felis concolor*) physiology and population dynamics relied on growth curves of cougars obtained from diverse locations and under various rearing conditions. We were concerned about potential biases in studies that make but do not test the implicit assumption of homogeneity of growth characteristics among collection sites. Thus, we compared body masses of wild cougars from populations in Florida (*F. c. coryi*), Nevada (*F. c. kaibabensis*), and California (*F. c. californica*). We modeled mass as a nonlinear Richards function of age for each sex and population demographic group. Groups were consistent with respect to estimated birth mass and location of the inflection point of the growth curve. Adult mass was greater ($P < 0.001$) in males than females in all populations, and the size of the difference was similar among populations. Estimated adult masses of Florida and California cougars were not different ($P = 0.381$) from each other but were less ($P < 0.001$) than that of adult Nevada cougars. Growth rate varied by population but not by sex; Nevada cougars grew fastest to adult mass. Cougar mass is too variable to serve alone as an indicator of age beyond 24 months. Failure to control for population-specific influences on growth may bias inferences about growth.

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Inferences about productivity (Robinette et al. 1961), energetics (Ackerman et al. 1986), and growth (Zullinger et al. 1984) of cougars have been based on predictive curves of growth in mass. Further, Robinette et al. (1961) used a growth curve to back-estimate age of cougar kittens. These curves were estimated from data collected from captive-raised cougars and those from geographically separated areas (Robinette et al. 1961, de Carvalho 1968, Eaton and Velandier 1977). Currier (1979:21) found that mass differed between wild and captive cougars, and Kurtén (1973) and Iriarte et al. (1990) found significant relationships between mass and latitude over the range of the species. Thus, growth curves that do not control for rearing conditions and for geography can be biased.

We assessed demographic variability in growth characteristics of wild cougars from 3 widely separated populations and determined the likelihood that cougar growth follows a common trajectory. We also provide quantitative evidence that mass alone does not reliably indicate age in cougars.

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METHODS

Data Collection

We captured, radioinstrumented, and recaptured cougars in southwestern Florida during 1981-92 using tracking and handling methods described by Maehr et al. (1991) and McCown et al. (1990). Mass was measured to the nearest kg with a portable spring scale (Hansen, Inc., Shubuta, Miss.). For individuals born to radioinstrumented females, we defined parturition date as the onset of denning, signaled by a sharp decline in the mother's movements (Maehr et al. 1989a), or as the 95-day gestation following mating (Maehr et al. 1991). Mating encounters were determined via telemetry by locating a solitary adult of each sex together ≥ 1 day. These encounters occurred infrequently (Maehr et al. 1991) and usually resulted in pregnancy. Age was recorded as the time in months between birth and capture date. For solitary adults and subadults, age at first capture was estimated by tooth wear and pelage condition (Shaw 1983). We defined age classes following Maehr et al. (1991): dependent kitten (0-18 months old), subadult (18-36 months old), and adult (>36

months old). Although we documented female reproduction at 18 months (Maehr et al. 1989b), age at first reproduction is generally accepted as ≥ 36 months (Anderson 1983:31). Maehr et al. (1991) described the subtropical study area.

Wild cougars from Nevada caught during 1972–82 were aged from several criteria including body mass (D. L. Ashman et al., Nev. Dep. Wildl., Carson City, unpubl. rep.). Hopkins (1989) estimated California cougar age from several criteria, none of which he identified explicitly as body mass. We used the interval midpoint wherever the Nevada report or Hopkins (1989) provided an age range for an individual.

Data Analysis

Data from recaptures of Florida cougars were removed to eliminate a source of error autocorrelation. We plotted mass against age, by cohort (a sample of cougars of the same sex from 1 study location). Because mass increased smoothly with age to an asymptote, we assumed that the flexible Richards curve (Richards 1959) would provide a reasonable model of cougar mass growth. We used a more intrinsically stable formulation of the curve as suggested by Brisbin et al. (1986a) and Leberg et al. (1989):

$$M(t) = \{A^{1-m} - [A^{1-m} - B^{1-m}] \cdot \exp[-2t(m + 1)/T]\}^{1/(1-m)}$$

The symbol $M(t)$ represents mass at age t . Parameters A and B represent asymptotic or adult mass and birth mass, respectively. T represents the time required to complete the “major part of growth” (Richards 1959:298). In the text, we loosely use the term growth rate in conjunction with T . Parameter m controls the curve shape: greater values of m place location of the curve’s inflection point closer to the age at attainment of adult mass. Specific values of m result in simpler forms of the model including the non-sigmoidal von Bertalanffy or monomolecular ($m = 0.0$), the sigmoidal von Bertalanffy ($m = 0.67$), the Gompertz ($m \rightarrow 1.0$), and the logistic ($m = 2.0$) models. These simplifications of the Richards model have been used to describe mammalian growth (Zullinger et al. 1984). By estimating m from empirical data, it is not necessary to assume a specific curve shape a priori or compare several fixed-shape curves (e.g., Zullinger et al. 1984). We used nonlinear regression (Seber and Wild 1989) to fit the curve to mass data.

Data plots also revealed that mass variability increased proportionally with mass itself. Be-

cause such variance heterogeneity reduces the precision of parameter estimates, we stabilized mass variability by log-transforming both mass and the growth curve:

$$\log_e M(t_i) = (1 - m)^{-1} \log_e \{A^{1-m} - [A^{1-m} - B^{1-m}] \cdot \exp[-2t_i(m + 1)/T]\} + \epsilon_i$$

The component ϵ_i represents error in predicting \log_e mass for animal i . Predicted curves and confidence bands were back-transformed for presentation. Model parameter estimates were not affected by the transformation and thus required no back-transformation.

To model differences in growth curves due to gender and geography, we allowed curve parameters to vary by sex, by population, or by both demographic effects. Letting θ represent any of the 4 Richards curve parameters, we determined which state of variability best described the behavior of θ : (1) constant with respect to sex and population, (2) varying by sex, (3) varying by population, or varying by both sex and population with (4) sex constant among populations (additivity) or (5) sex varying among populations (interactivity). These variability states are analogous to effects in a factorial ANOVA for θ . Therefore, we expressed each $\theta_{F,S}$ (θ for population P and sex S) as an ANOVA-like sum of population and sex effects β_{ij} , an approach used in computer packages for linear models (e.g., SAS GLM, SYSTAT MGLH):

$$\begin{aligned} \theta_{\text{Fla},F} &= \beta_{00} \\ \theta_{\text{Fla},M} &= \beta_{00} + \beta_{01} \\ \theta_{\text{Nev},F} &= \beta_{00} + \beta_{10} \\ \theta_{\text{Nev},M} &= \beta_{00} + \beta_{01} + \beta_{10} + \beta_{11} \\ \theta_{\text{Cal},F} &= \beta_{00} + \beta_{20} \\ \theta_{\text{Cal},M} &= \beta_{00} + \beta_{01} + \beta_{20} + \beta_{21} \end{aligned}$$

Six non-zero estimates for β_{ij} represented the highest state of variability for θ , i.e., interactivity. Eliminating the fourth column of β terms implied additivity of population and sex effects with respect to θ . Similarly, population-only and sex-only effects were modeled by eliminating columns 2 and 4 and columns 3 and 4, respectively. Elimination of columns 2–4 provided the model of no variability by sex or population.

Five states of variability for each of 4 growth curve parameters induced 625 demographic configurations of the growth curve. The size k of a model configuration was the total number of β_{ij} for all 4 curve parameters. In the smallest model configuration ($k = 4$), cohorts were ig-

nored and a single Richards curve was fit to all the data; Richards curves fit separately to data from each cohort composed the largest configuration ($k = 24$). Models of intermediate size implied that growth curves among cohorts were similar in some aspects and different in others.

A superior model configuration provided precise parameter estimates (small k), yet, closely fit the data (small residual sum of squares, SS_R). Given sample size n , the Akaike (1973, 1974) information criterion (AIC) is a compromise of both quantities:

$$AIC = n(1 + \log_e 2\pi) + n \log_e(SS_R/n) + 2k.$$

Models with small AIC provide a good description of the data with a minimum of parameters. Models with AIC values that differ by <1 are essentially similar in merit (Sakamoto et al. 1986: 84–85). In simulation studies (Bozdogan 1987, Hurvich and Tsai 1989), the AIC favored models with large k more often than expected. Model selection criteria that place a greater penalty on increasing model size than does AIC were proposed by Schwarz (1978):

$$SC = n(1 + \log_e 2\pi) + n \log_e(SS_R/n) + k \log_e n$$

and Sawa (1978):

$$BIC = n(1 + \log_e 2\pi) + n \log_e(SS_R/n) + 2n(k + 2) (\hat{\sigma}^2/SS_R) - 2(n\hat{\sigma}^2/SS_R)^2,$$

where $\hat{\sigma}^2$ is an independent estimate of residual variance. Because replicate values of mass at each age rarely occurred, we estimated residual variance using mean squared error from the largest model ($k = 24$), i.e.,

$$\hat{\sigma}^2 = SS_R/(n - k).$$

As with AIC, one chooses models having low values of SC or BIC. Other model selection criteria (Borowiak 1989:90) or iterative resampling schemes (Borowiak 1989:137–163) may have been more appropriate for these data, but we believed that the more sophisticated approaches would have provided results consistent with those of the simple criteria above and thus would not have justified the great effort entailed. Szymczak and Rexstad (1991) provided a recent example in a wildlife setting of choosing a parsimonious model through AIC.

We calculated AIC, SC, and BIC for each model configuration and investigated those models possessing the 3 smallest values of each criterion. Because model selection criteria rarely

agree on the “best” model, we subjectively chose a final model from this group. In making our choice, we relied on hypothesis tests among competing models (F -test of reduction in SS_R , Seber and Wild 1989:197–199), potential weaknesses of the data, and our own observations of cougar growth dynamics.

We used the iterative NONLIN procedure of the SYSTAT software (Wilkinson 1990) to fit models. We directly searched over the parameter space (option SIMPLEX) to find parameter estimates minimizing SS_R for a given model, a method fairly robust to poorly-chosen starting values. For $k \leq 12$, we considered the estimates to have converged when all estimates in successive iterations l and $l + 1$ did not differ by >0.00005 in absolute magnitude, i.e.,

$$|\hat{\theta}_{(l+1)} - \hat{\theta}_{(l)}|/|\hat{\theta}_{(l)}| < 0.00005.$$

To achieve faster convergence in larger models ($k > 12$), we increased the criterion to 0.0001. We checked the fit of each model by plotting residual values of \log_e mass against predicted \log_e mass. We used the Wald statistic (Seber and Wild 1989:197–199) to compare among levels of parameters that varied by cohort and to construct 95% prediction limits for mass (Seber and Wild 1989:193). Tests and prediction limits based on Wald statistics are approximate (Seber and Wild 1989:193, 199).

RESULTS

We captured 48 Florida cougars (30 M, 18 F) and recaptured 10 on 17 occasions. None were younger than 4 months (range = 4–120 months), and 20 kittens were of known age (range = 4–10 months). Range of estimated age for 74 Nevada cougars (46 M, 28 F) was 2–120 months. The age range (4–102 months) in Hopkins (1989) was comparable to that in the other samples, but substantial age gaps existed among the 9 male (none >24 and <60 months) and 15 female (none >12 and <48 months) California cougars.

Mass of females from Florida decreased with age after 60 months (Fig. 1). Otherwise, mass data from every cohort revealed no consistent pattern of departure from the Richards curve. Fit of the curve to each group of data was good ($R^2 > 0.928$, Table 1). Adult mass (A) was estimated with very high precision ($CV \leq 6\%$) for all cohorts. Growth period (T) was estimated with good precision ($CV \leq 17\%$) for all cohorts except for Florida and California females. In

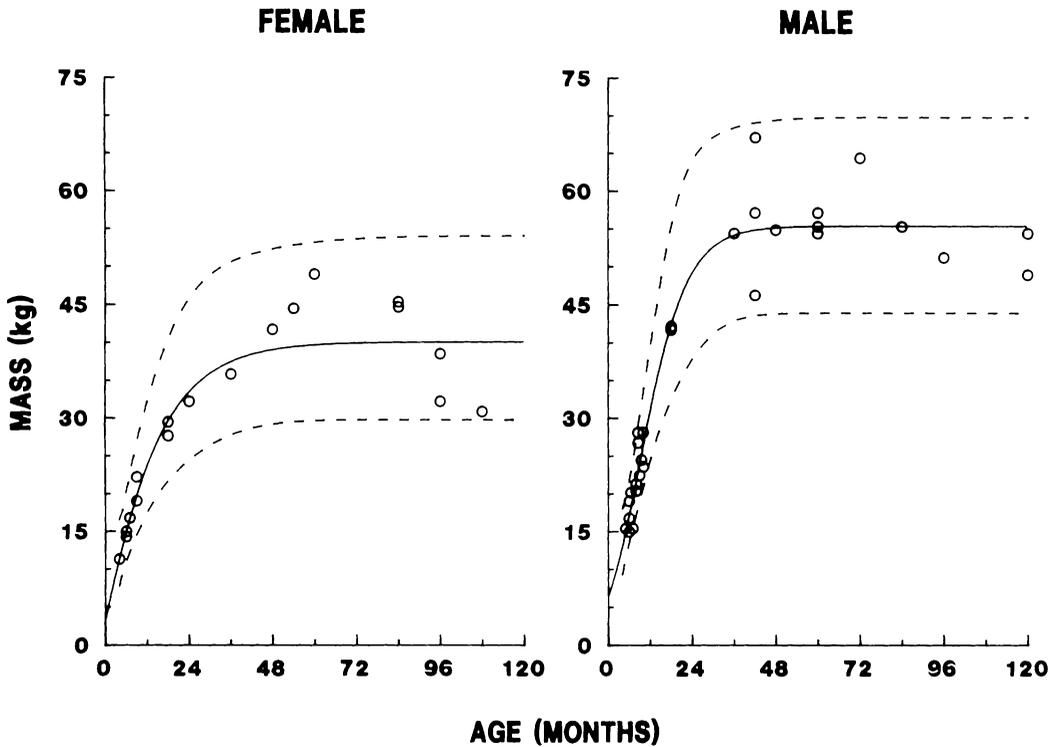


Fig. 1. Mass fit to age by a 4-parameter Richards curve (solid line), by sex, for 48 Florida cougars captured in southwestern Florida, 1981-92. Approximate 95% prediction limits are displayed (dashed lines) on either side of the prediction line.

general, the curve shape parameter (m) and birth mass (B) were estimated with poor precision. Growth models allowing no cohort differences ($SS_R = 6.77, k = 4$) or sex-only differences ($SS_R = 3.66, k = 8$) in parameters were rejected ($P < 0.001$) in favor of models fit individually to cohorts.

The models providing the smallest values of AIC and SC both allowed additive sex and population variability for A but permitted no variation in m or B with respect to cohort (Table

2). In the SC-selected model, A was greater for males than for females in any population, and Nevada cougars grew to greater mass than did cougars from other populations (Table 3). The models differed in how T was assumed to vary. The SC-selected model permitted T to vary only by population. In this model, T was least for the Nevada population and was indistinguishable between the Florida and the California populations (Table 3). However, the AIC-selected model proposed that T varied interactively by

Table 1. Sample size, mean squared error ($\hat{\sigma}^2$), corrected (for the mean) R^2 , and point ($\hat{\theta}$) and interval (ASE) estimates of parameters from Richards growth curves fit to log_e mass data from 3 wild cougar populations.

Population	Sex	n	$\hat{\sigma}^2$	R^2	Parameter estimates ^a							
					A (kg)		T (months)		m		B (kg)	
					$\hat{\theta}$	ASE	$\hat{\theta}$	ASE	$\hat{\theta}$	ASE	$\hat{\theta}$	ASE
Florida	F	18	0.0167	0.933	40.1	1.9	31.2	16.1	0.21	1.08	3.3	7.3
	M	30	0.0117	0.960	55.4	1.7	34.6	4.7	1.44	1.18	6.4	3.3
Nevada	F	28	0.0123	0.928	44.6	1.6	31.0	5.4	1.96	1.71	8.7	2.6
	M	46	0.0106	0.969	63.3	1.7	27.3	2.1	1.60	0.51	7.1	1.1
California	F	15	0.0086	0.966	37.4	1.1	27.7	40.4	3.62	25.42	7.0	7.6
	M	9	0.0082	0.967	55.6	3.4	40.7	5.7	0.14	0.26	0.0	0.0
	Pooled	146	0.0116	0.958								

^a A = adult mass, T = growth period, m = curve shape parameter, B = birth mass.

Table 2. Three optimum models of growth of log_e mass for 3 wild cougar populations according to each of 3 model selection criteria.

Type	Criterion	Value	Growth model ^a							Tests between competing models	
			Configuration ^b					SS _R	Hypothesis ^c		P
			A	T	m	B	k				
AIC	1	-232.0	a	i	c	c	12	1.480	H ₀ : T(P), H _A : T(i)	0.041	
	2	-231.6	a	i	S	c	13	1.464	H ₀ : m(c), H _A : m(S)	0.235	
	3	-230.8	a	i	c	S	13	1.472	H ₀ : B(c), H _A : B(S)	0.407	
SC	1	-202.2	a	P	c	c	9	1.574			
	2	-199.2	a	P	S	c	10	1.553	H ₀ : m(c), H _A : m(S)	0.177	
	3	-198.6	a	P	c	S	10	1.559	H ₀ : B(c), H _A : B(S)	0.253	
BIC	1	-226.6	same model as AIC #1 above								
	2	-225.7	same model as SC #1 above								
	3	-225.6	same model as AIC #2 above								

^a Models differ in how 4 Richards curve parameters estimated for each population-sex cohort vary with respect to cohort (model configuration).

^b The letter under each of the Richards curve parameters A, T, m, or B represents 1 of 5 variability states for the parameter: (c)onstant with respect to sex and population, varying by (S)ex only or by (P)opulation only, or varying by both effects either (a)dditively or (i)nteractively.

^c Each test compares the given model (H_A in the hypothesis) to another model (H₀) obtained by restricting the variability state of 1 parameter. For example, population-only variability in T, symbolized by T(P), is a restriction of population-sex interactivity in T, T(i). Rejection of H₀ indicates that the given model provides a better fit to the data than the simpler model hypothesized under H₀.

cohort (Table 2): T differed by sex for cougars from California (P = 0.006) but not for cougars from other populations (P > 0.720). The null hypothesis that the SC-selected model provided as good a fit as the AIC-selected model was rejected (P = 0.041, Table 2).

Apart from disagreement in variability of T, the sequence of models within either the AIC or SC criterion was identical. The second and third-ranked models allowed m and B, respectively, to vary by sex, although no tests of such hypotheses were significant (P > 0.177, Table 2). In sex-dependent models for m, the inflection

point for females occurred at an earlier stage of growth than for males. In models allowing B to vary by sex, females had greater estimated birth mass than did males.

Models selected by the BIC criterion coincided with those chosen by AIC and SC. In descending order of preference, these models were the first-ranked model of AIC, the first-ranked model of SC, and the second-ranked model of AIC (Table 2).

DISCUSSION

Considerable demographic variability exists in cougar growth. Our data conclusively demonstrate that ignorance of the sample composition from which growth models are estimated may invalidate inferences on those physiological processes based on growth of cougars.

Our best model of each criterion indicated that adult mass and growth rate of cougars varied by population; whereas birth mass and curve shape were consistent among populations. Furthermore, adult mass of males was greater than that of females, but the mass difference was equal in all populations.

We selected the top-ranked model of the SC criterion as the best model for these data. Despite evidence that differences in growth rate due to sex were inconsistent among populations, we rejected the model favored by AIC. The contrast in growth rate between sexes was evident only in the California population for which data were sparse over ages 12–48 months. The “shoulder” of the growth curve occurs in this

Table 3. Parameter estimates and asymptotic standard errors (ASE) for a sex and population-dependent Richards growth model^a of mass of 3 populations of wild cougars.

Parameter	Population	Sex	Estimate ^b	ASE
A (kg)	Fla.	F	38.86 A	1.16
	Nev.	F	45.29 B	1.18
	Calif.	F	37.46 A	1.20
		M-F ^c	17.44	1.22
T (months)	Fla.		38.72 A	2.24
	Nev.		28.60 B	1.51
	Calif.		46.30 A	3.62
m			1.52	0.26
B (kg)			7.48	0.61

^a Mass growth model for members of population P and sex S:

$$M(t) = \{A_{P,S}^{1-m} - [A_{P,S}^{1-m} - B^{1-m}] \exp[-2t(m+1)/T_P]\}^{1/(1-m)}$$

where M(t) = mass (kg) at age t (months), A_{P,S} = adult mass (kg) for population P and sex S, m = curve shape parameter, B = birth mass (kg), and T_P = growth period (months) for population P.

^b Population-specific parameter estimates sharing the same letter were not different at the Bonferroni-protected 0.017 level.

^c Estimated difference in mass of adult males and females. For any population P, A_{P, Male} = A_{P, Female} + 17.44. Approximate SE for masses of adult males, by population, were 1.29 (Fla.), 1.30 (Nev.), and 1.58 (Cal.).

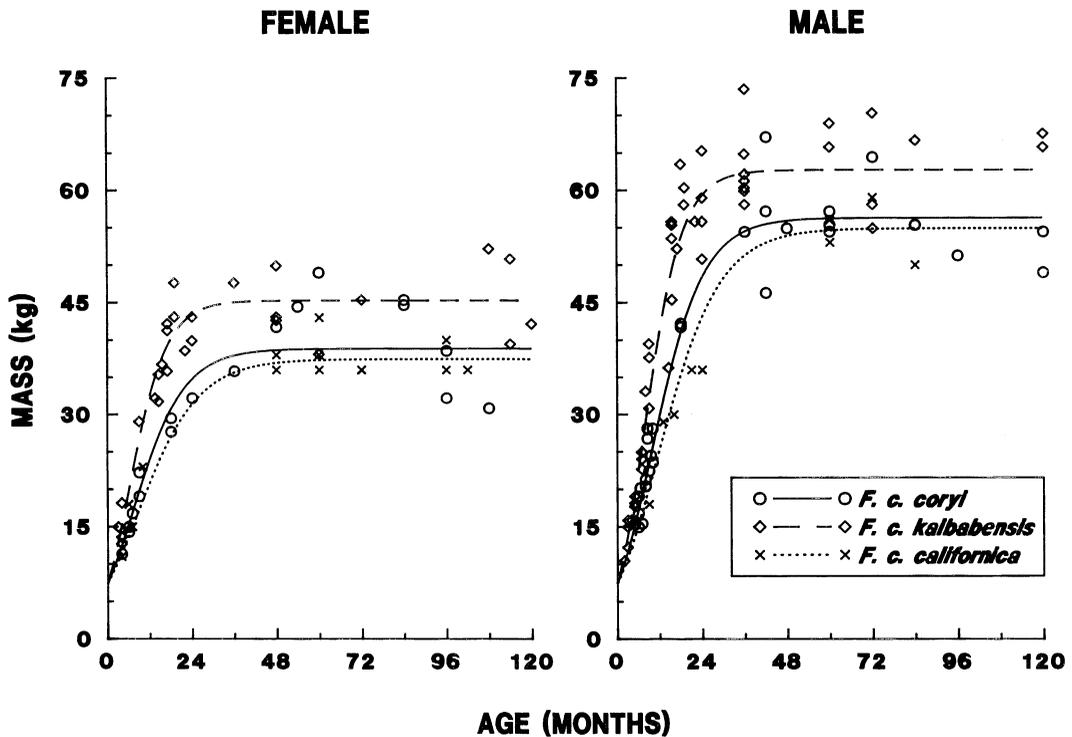


Fig. 2. Mass relative to age for wild cougar populations from Florida, Nevada, and California. Richards growth curves fit to these data forced curve shape and mass at birth to be independent of sex and population, allowed growth rate and adult mass to vary by population, and permitted a gender difference in adult mass.

range, and confidence in determining the placement of the shoulder is necessary for precise estimation of the duration of growth. Also, because sample size was smallest for this population, and because *P* for the test of interaction was not sufficiently small to transcend even a modest error in the approximation of *P*, we could not confidently conclude that the observed population × sex interaction in growth rate was real. We believe that the more parsimonious model selected by SC more likely represents the true situation with respect to growth of cougars from several populations (Table 3, Fig. 2).

The estimated value (1.52, Table 3) of the curve shape parameter placed the inflection point at the age corresponding to 45% of attainment of adult mass. Averaged over both sexes, these ages were 7.0, 8.7, and 10.2 months for the Nevada, Florida, and California populations respectively. The limits of the 95% confidence interval for the curve shape parameter were approximately 1 and 2, suggesting that the Gompertz and logistic versions of the Richards curve are unsuitable models for mass growth of cougars.

We estimated unrealistically high birth mass in most of the 6 data sets (\bar{x} = 5.4 kg, Table 1) and in the SC-selected model (7.5 kg, Table 3). Indeed, in every model we investigated, estimated birth mass was high relative to mass of newborn cougars (1.16–1.25 kg for 2 Fla. males 14 days old; D. S. Maehr, unpubl. data). Obtaining data for very young cougars (0–4 months) should allow estimation of reasonable values of birth mass.

The possibility of sex-dependence in either curve shape or birth mass was entertained by the model selection criteria. Because birth mass was unreliably estimated, we placed little emphasis on models permitting birth mass to vary by sex. In fact, the phenomenon may have more to do with birth mass acting as a surrogate for curve shape, a parameter that may truly depend on sex but was forced constant in those models. A sex effect on curve shape has been demonstrated in at least 1 other species (wood duck [*Aix sponsa*]; Brisbin et al. 1986a,b) and, with additional data, may be found in cougars.

In least squares modeling, bias in parameter estimates should be anticipated when the in-

dependent variable is subject to measurement error (Draper and Smith 1981:122–125, Seber and Wild 1989:12). Leberg et al. (1989) determined that parameter estimates of Richards curves fit to mass of male white-tailed deer (*Odocoileus virginianus*) suffered negligible bias (within $\pm 1\%$) when deer were imprecisely aged (to the nearest month) but could be substantially biased (within $\pm 19\%$) when deer were inaccurately aged (assigned to the wrong year class). Age was estimated for all cougars except the 20 youngest kittens (≤ 10 months old) from Florida. Error in age estimation undoubtedly occurred in every sample, but errors as great as 12–24 months likely occurred only beyond the point where the curve reached the adult mass plateau. If, as we believe, error in age estimation increases proportionally with age, then bias in all parameters may be minimal.

Zullinger et al. (1984) provided the only other parametric model of cougar growth of which we are aware. They reported parameter estimates for 15 points fit to a Gompertz model, but their objective of finding a single model formulation for comparing growth of diverse mammalian taxa did not guarantee that other models were inferior. Their data comprised known points from repeatedly-measured hand-reared individuals, interpolated points from a hand-drawn curve of wild cougar growth, and an age range too limited (< 30 months) for stable estimation of adult mass (E. M. Derrickson, Loyola Coll., Baltimore, Md., pers. commun.). We believe that differences in study objectives and sample characteristics precluded meaningful statistical comparison of parameters in their model and ours.

Whereas latitude separation was 11° between the Florida and California sites and $2\text{--}5^\circ$ between the California and Nevada sites, adult mass and growth rate were similar in the distant Florida and California cougar populations and different in the closer Nevada and California populations. We suspect that larger adult mass and faster growth rate in Nevada cougars was attributable to higher altitude (1,500–2,700 m) and larger prey (Iriarte et al. 1990) in Nevada than elsewhere. Similar adult mass and growth rate in Florida and California populations may result from similar food niche breadth width; both populations prey heavily upon the medium-sized wild hog (*Sus scrofa*) (Hopkins 1989, Maehr et al. 1990). Deer occurred less frequently in the diet of cougars studied by Hopkins

(1989) than of those elsewhere in California (Dixon 1925, Iriarte et al. 1990).

MANAGEMENT AND RESEARCH IMPLICATIONS

Prediction of Florida cougar age from mass becomes more uncertain as mass increases (Fig. 1). Beyond 27 kg in females and 41 kg in males, where the horizontal distance between the 95% prediction limits approaches animal age (Fig. 1), these curves lose their utility as rough indicators of age. We do not recommend indiscriminate use of mass growth models as an aging tool, especially for cougars > 24 months old.

Researchers of *F. concolor* should handle wild kittens 0–5 months of age and provide mass measurements to increase precision of the growth model. Age of kittens should be determined to within 1 day for kittens ≤ 28 days old and to within 1 week for kittens 4–24 weeks old to reduce estimation bias. We encourage other cougar researchers to examine their mass growth data by utilizing the Richards curve and improving upon our initial application of this approach for the species.

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