AGE-RELATED VARIATION IN SKULLS OF THE PUMA (*PUMA CONCOLOR*)

SAMANTHA W. GAY AND TROY L. BEST

Department of Zoology and Wildlife Science and Alabama Agricultural Experiment Station, 331 Funchess Hall, Auburn University, AL 36849-5414

Measurements of skulls were used to determine if growth continues throughout the lifetime of a puma (*Puma concolor*) and if growth patterns differ between sexes. The dataset included 1,201 adult pumas and consisted of 14 cranial and 5 mandibular measurements. Ages (estimated by the amount of staining and wear of teeth) of specimens examined during our study suggested that few pumas live past ca. 9 years of age in the wild (16 of 609 adult males and 35 of 592 adult females). For both sexes, all of the characters showing no significant variation among age groups were those related to measurements of dentition, indicating that teeth reach their full-grown size by ca. 2 years of age. Growth of the cranium of pumas continues throughout most of the animal's life; males continue to grow to 7–9 years of age, and females continue to grow to 5–6 years of age.

Key words: *Puma concolor,* puma, mountain lion, age variation, North America, South America

The puma (*Puma concolor*) is a morphologically variable and wide-ranging species. The original distribution extended from northwestern Canada to southern Chile and Argentina, and from coast to coast in North and South America (Young and Goldman, 1946). Loss of habitat and persecution by humans have greatly reduced its distribution, yet the puma is the most widely ranging native mammal in the Americas, except for humans (Turbak, 1987). Because of its extensive distribution, the diverse habitats it occupies, and its well-documented morphologic variability, as indicated by >25 subspecies, the puma is an excellent organism in which to study patterns of age variation.

Many species of mammals continue to grow after attaining sexual maturity (e.g., Dice, 1936; Fiscus, 1961; Laird, 1965, 1966; Laird et al., 1965; McClure and Randolph, 1980; Morrison et al., 1977; Quimby, 1951; Smith and Clark, 1994; Zullinger et al., 1984). Shortly after 3 years of age, skull dimensions of African lions (*Panthera leo*) overlap those of older lions (Smuts et al., 1978). Male and female African lions reach sexual maturity at 3–4 years of age (Schaller, 1972). According to growth curves given by Crowe (1975) for bobcats (*Lynx rufus*), mass of male bobcats reaches an asymptote at ca. 450 days of age, whereas females continue to increase in mass through ≥600 days of age. In bobcats, sexual maturity is attained by females within 1 year, and is achieved by males during their 2nd year (Crowe, 1975). Robinette et al. (1961) developed a growth curve for pumas based on mass from birth to 160 weeks of age, at which point pumas were considered mature; they assumed that maturity occurred at 2.5 years of age for females and at 3 years of age for males. Maehr and Moore (1992) used measurements of mass to develop growth curves for three populations of pumas from birth to 120 months of age and found an asymptote at ca. 2 years, which indicated little or no growth after sexual maturity. Herein, we use measurements of the cranium and mandible to determine if growth continues throughout the lifetime of a puma and if growth pat-

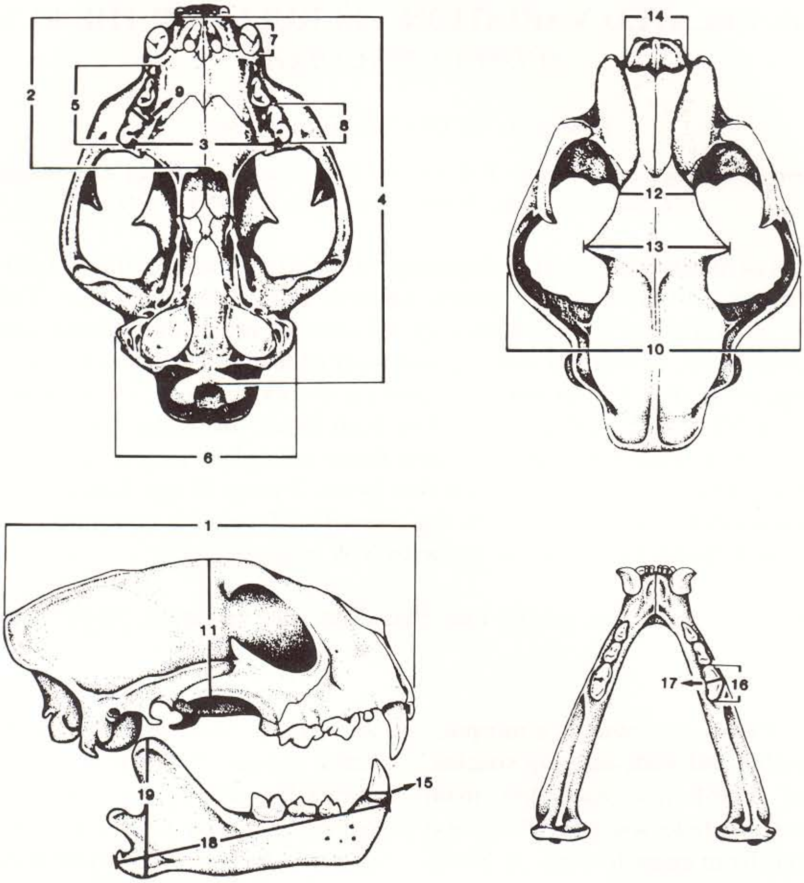

FIG. 1.—Cranial, tooth, and mandibular characters used to examine patterns of age variation in *Puma concolor* from North and South America: 1) greatest length of skull; 2) palatal length; 3) intermaxillary width; 4) basilar length; 5) length of alveolar toothrow; 6) mastoidal width; 7) greatest diameter of upper canine; 8) greatest length of third upper premolar; 9) greatest width of third upper premolar; 10) zygomatic width; 11) depth of cranium; 12) interorbital width; 13) supraorbital width; 14) nasal width; 15) greatest diameter of lower canine; 16) greatest length of lower molar; 17) greatest width of lower molar; 18) greatest length of mandible; 19) depth of mandible.

terns differ between sexes. In addition to providing an estimate of the duration of growth in pumas, documentation of the degree of variation among age groups is essential to any assessment of geographic patterns of morphologic variation (Gay and Best, 1995, in press) and of taxonomic relationships among the numerous subspecies in North and South America.

MATERIALS AND METHODS

Our dataset included 1,201 pumas (609 males and 592 females) from North and South America. A list of specimens examined is provided in Gay (1994). Fourteen cranial and 5 mandibular measurements (Fig. 1) were made with dial calipers accurate to the nearest 0.1 mm. Only adult specimens with canines fully extended were measured. Age of each specimen was estimated by tooth-wear and staining according to D. Ashman (in litt.) using five tooth-wear classes (Fig. 2). For males, tooth-wear classes and corresponding age classes were: age-class I, 2 years of age, canines white with no stain, no wear on incisors or canines; age-class II, 3-4 years of age, canines lightly stained, spot of wear on highest cusp of I^3, I^1, and I^2 with little or no

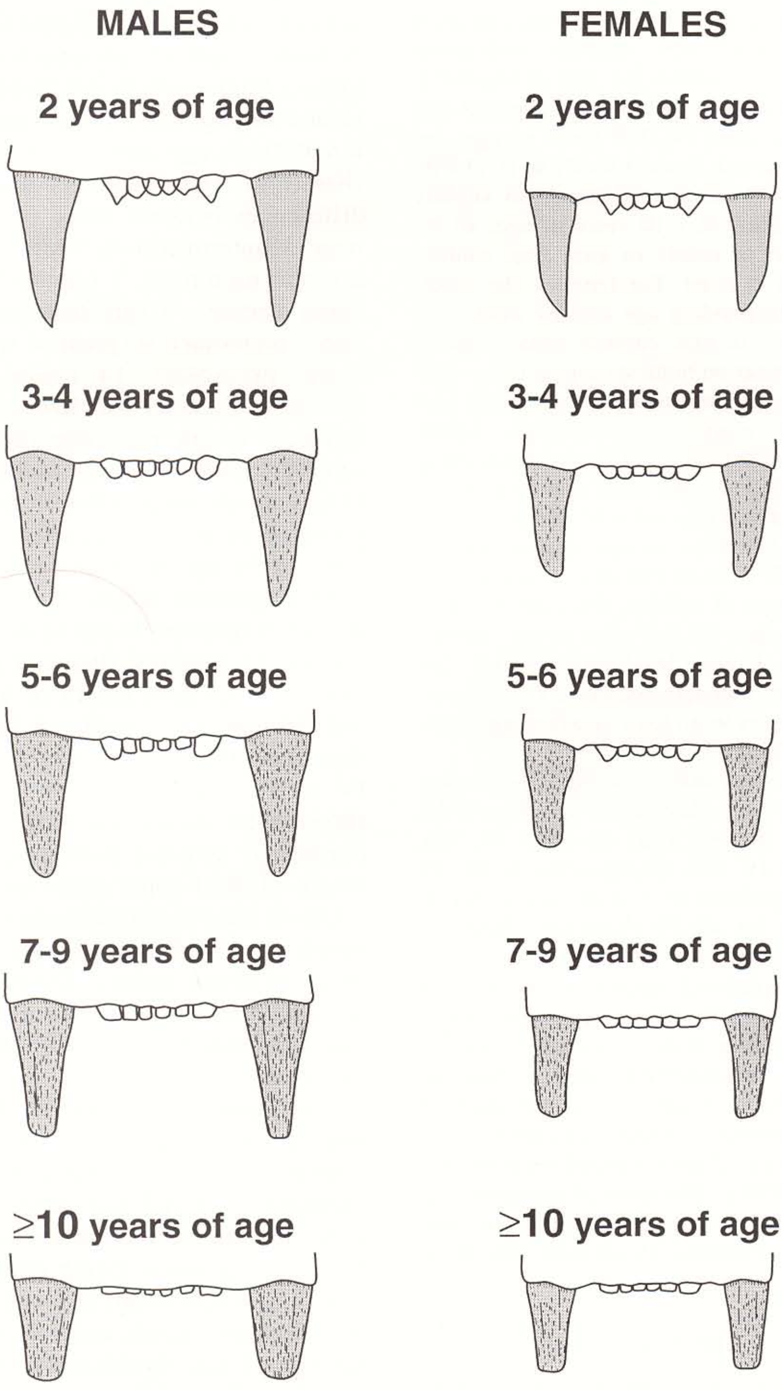

FIG. 2.—Age classes of *Puma concolor* based on staining and wear of teeth (D. Ashman, in litt.). Males: a) age-class I, 2 years of age; b) age-class II, 3–4 years of age; c) age-class III, 5–6 years of age; d) age-class IV, 7–9 years of age; e) age-class V, ≥10 years of age. Females: f) age-class I, 2 years of age; g) age-class II, 3–4 years of age; h) age-class III, 5–6 years of age; i) age-class IV, 7–9 years of age; j) age-class V, ≥10 years of age.

wear, tips of canines with slight wear; age-class III, 5–6 years of age, canines moderately stained, I^3 worn to within 3-4 mm of crest of I^1 and I^2, tips of canines with obvious wear (3 mm worn off); age-class IV, 7–9 years of age, canines darkly stained, I^3 worn nearly to level with I^1 and I^2, tips of canines flattened to slightly rounded; age-class V, ≥10 years of age, all incisors worn to or nearly to gum line, canines worn rounded to blunt. For females, the toothwear and corresponding age classes were: age-class I, 2 years of age, canines white with no stain, spot of wear on highest cusp of I^3, no wear on I^1 or I^2, tips of canines with slight wear; age-class II, 3–4 years of age, canines lightly stained, I^3 worn flat (3–4 mm across) along crest, I^1 and I^2 with slight wear along entire crest, tips of canines with obvious wear (2 mm worn off); age-class III, 5–6 years of age, canines moderately stained, I^3 worn to within 1–2 mm of crest of I^1 and I^2, tips of canines flat with 3–5 mm worn off; age-class IV, 7–9 years of age, canines darkly stained, I^3 worn level with I^1 and I^2, tips of canines worn rounded; age-class V, ≥10 years of age, all incisors worn to or nearly to gum line, canines worn blunt.

Sample sizes for males and females, respectively, for each age class were: age-class I, 13, 30; age-class II, 139, 180; age-class III, 336, 278; age-class IV, 105, 69; age-class V, 16, 35. Because of significant ($P \leq 0.05$) sexual dimorphism in size for all 19 characters (Best and Gay, in press; Gay and Best, 1995), males and females were analyzed separately. Analysis of variance was used to determine if age classes were different with respect to each of the 19 morphometric measurements and a Student-Newman-Keuls, a posteriori test for multiple comparisons among averages, was used to determine which age classes differed from the others (Norusis, 1990). The level of statistical significance was corrected for multiple comparisons with the sequential Bonferroni test (Rice, 1989).

Results

For males, 15 of the 19 characters exhibited significant ($P \leq 0.0026$) variation among age classes (Table 1). The four characters that did not differ among age classes were characters 8 (greatest length of third upper premolar), 9 (greatest width of third upper premolar), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). Student-Newman-Keuls analysis revealed that age-class I was significantly different from age-class II in 10 of the 19 characters. The characters that showed no differences between these two age classes were 3 (intermaxillary width), 5 (length of alveolar toothrow), 7 (greatest diameter of upper canine), 8 (greatest length of third upper premolar), 9 (greatest width of third upper premolar), 14 (nasal width), 15 (greatest diameter of lower canine), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). Age-class II was significantly different from age-class III in 14 of the 19 characters. The characters exhibiting no significant differences were 8 (greatest length of third upper premolar), 9 (greatest width of third upper premolar), 15 (greatest diameter of lower canine), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). Age-class III was different from age-class IV in 14 characters. The five characters showing no significant differences were 5 (length of alveolar toothrow), 8 (greatest length of third upper premolar), 9 (greatest width of third upper premolar), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). There were no significant differences between age-class IV and age-class V for any of the characters examined.

For females, 16 of the 19 characters exhibited significant ($P \leq 0.0026$) variation among age classes (Table 1). The three characters that did not differ among ages were 15 (greatest diameter of lower canines), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). Student-Newman-Keuls analysis revealed that age-class I was significantly different from age-class II in 15 of the 19 characters. Characters that showed no differences between these two age classes were 7 (greatest diameter of upper canine), 15 (greatest diameter of lower canines), 16 (greatest length of lower molar), and 17 (greatest

TABLE 1.—*Results of one-way analysis of variance in size of 19 cranial and mandibular characters (Fig. 1) among five age classes of* Puma concolor *from North and South America. Averages and results of Student-Newman-Keuls analysis are given for each age class.*

Char. no.	Gender	*d.f.*	*F*-ratio	*P*[a]	Age class I	II	III	IV	V
1	♂♂	4,542	36.2	0.0000[a]	182.8[b]	194.7[b]	204.6[b]	208.1	211.0
	♀♀	4,537	20.1	0.0000[a]	173.6[b]	181.4[b]	186.6	187.0	189.7
2	♂♂	4,566	42.3	0.0000[a]	67.6[b]	72.0[b]	76.1[b]	78.2	77.9
	♀♀	4,550	17.9	0.0000[a]	64.7[b]	67.6[b]	69.2	69.6	70.6
3	♂♂	4,572	18.4	0.0000[a]	63.7	64.5[b]	67.1[b]	68.8	69.0
	♀♀	4,557	9.6	0.0000[a]	59.5[b]	62.3	62.9	63.7	64.6
4	♂♂	4,518	40.4	0.0000[a]	145.7[b]	157.3[b]	166.4[b]	170.6	169.1
	♀♀	4,524	22.0	0.0000[a]	140.1[b]	147.5[b]	151.6	152.6	154.7
5	♂♂	4,598	6.6	0.0000[a]	41.5	42.5[b]	43.5	43.5	43.2
	♀♀	4,582	4.6	0.0011[a]	39.4[b]	40.4	40.8	40.7	40.7
6	♂♂	4,516	17.6	0.0000[a]	78.4[b]	82.5[b]	85.6[b]	87.4	86.1
	♀♀	4,494	6.5	0.0000[a]	73.6[b]	77.0	77.8	78.5	79.0
7	♂♂	4,584	4.8	0.0008[a]	13.2	13.6[b]	13.9[b]	14.2	13.8
	♀♀	4,570	5.3	0.0003[a]	11.6	11.9	12.1	12.1[b]	12.6
8	♂♂	4,591	1.8	0.1256	23.1	23.2	23.4	23.5	23.0
	♀♀	4,575	6.1	0.0001[a]	21.3[b]	22.0	22.2	22.1	22.2
9	♂♂	4,599	2.0	0.0813	11.9	11.8	11.9	12.0	11.6
	♀♀	4,585	6.2	0.0001[a]	10.6[b]	11.0[b]	11.1	11.0	11.2
10	♂♂	4,530	50.8	0.0000[a]	122.9[b]	131.2[b]	140.9[b]	147.0	145.4
	♀♀	4,532	22.7	0.0000[a]	116.9[b]	123.9[b]	127.2	129.1[b]	132.7
11	♂♂	4,564	32.0	0.0000[a]	66.7[b]	71.1[b]	74.8[b]	77.3	76.2
	♀♀	4,559	11.0	0.0000[a]	64.4[b]	67.4[b]	68.4	69.2	69.8
12	♂♂	4,578	35.8	0.0000[a]	35.0[b]	38.4[b]	41.4[b]	43.3	42.4
	♀♀	4,576	10.8	0.0000[a]	34.0[b]	36.4[b]	37.4	38.2	38.9
13	♂♂	4,529	59.7	0.0000[a]	63.7[b]	67.5[b]	73.4[b]	77.4	76.1
	♀♀	4,550	36.9	0.0000[a]	64.2[b]	66.7[b]	69.7[b]	71.6[b]	73.7
14	♂♂	4,531	20.3	0.0000[a]	30.7	32.5[b]	34.4[b]	35.7	35.0
	♀♀	4,537	9.5	0.0000[a]	28.2[b]	30.2[b]	31.0	31.2	31.5
15	♂♂	4,579	5.8	0.0001[a]	12.7	13.2	13.4[b]	13.7	13.2
	♀♀	4,559	4.1	0.0027	11.3	11.7	11.7	11.7	12.1
16	♂♂	4,583	3.5	0.0068	16.9	17.1	17.3	17.6	17.2
	♀♀	4,568	1.9	0.1035	15.9	16.2	16.3	16.3	16.4
17	♂♂	4,589	1.6	0.1564	8.3	8.2	8.3	8.4	8.2
	♀♀	4,571	1.2	0.2803	7.6	7.8	7.8	7.8	7.8
18	♂♂	4,584	47.2	0.0000[a]	123.8[b]	131.8[b]	140.3[b]	144.7	144.4
	♀♀	4,563	19.6	0.0000[a]	117.3[b]	123.8[b]	127.0	127.8	130.0
19	♂♂	4,585	50.9	0.0000[a]	57.5[b]	63.0[b]	68.4[b]	71.8	70.9
	♀♀	4,565	16.3	0.0000[a]	54.2[b]	58.1[b]	59.8	60.5	61.6

[a] Significant based on sequential Bonferroni minimum table-wide significance level set at 0.0026 for a table of 19 tests for each gender.

[b] Indicates that the age class is significantly different from the age class to the right.

width of lower molar). Age-class II was significantly different from age-class III in 11 characters. Characters exhibiting no significant differences were 3 (intermaxillary width), 5 (length of alveolar toothrow), 6 (mastoidal width), 7 (greatest diameter of upper canine), 8 (greatest length of third upper premolar), 15 (greatest diameter of lower canine), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). Age-class III was different from age-class IV for only one character; 13 (supraorbital width). Age-class IV was significantly different from age-class V for three characters (7, greatest diameter of upper canine; 10, zygomatic width; 13, supraorbital width).

Discussion

Maximum longevity of pumas in the wild is unknown (Anderson, 1983), but reported life spans of captive pumas range from 4 to 19.5 years (Eaton and Velander, 1977; Young and Goldman, 1946). Young and Goldman (1946) calculated an average longevity of 7.5 years, and Spector (1956) reported an average life span of 9 years. The ages of specimens examined during our study suggest that few pumas live past ca. 9 years of age in the wild (16 of 609 adult males and 35 of 592 adult females).

For both sexes, characters without significant variation among age groups were all measurements of dentition. This suggests that teeth reach full size by ca. 2 years of age. Perhaps, the relatively rapid acquisition of full-grown teeth is related to capturing and killing prey beginning early in adult life.

Changes in the cranium of an individual puma are great during its lifetime. The cranium of juveniles (ca. <1 year) is smooth and round, and the braincase is large in comparison with the facial parts of the cranium and mandible. There are only faint suggestions of the postorbital processes and the sagittal crest that later become prominent structures. As the animal grows older, the bones thicken, the maxillary and mandibular regions of the cranium increase in size relative to the braincase, and various ridges and processes develop (Grinnell et al., 1937). By eliminating juveniles and subadults (i.e., pumas <2 years of age) from analyses of morphologic variation in skulls from southwestern North America, Best and Gay (in press) believed that they eliminated most of the variation associated with age, but their analyses and those presented herein demonstrated that significant growth continues during most of the adult life of a puma. Even in age-classes IV and V, we noticed a tendency for more pronounced sagittal crests in older individuals, particularly in males.

In our study, size of samples varied dramatically among age classes, i.e., from 16 to 278 specimens for males and from 13 to 336 for females. Small samples may obscure differences among age classes because they tend to increase overlap in variances. However, even the small samples of males and females in age-class I usually were adequate to distinguish this age class from the others. It is possible that the small samples for age-class V contributed to its lack of significant differences from age-class IV, but any significant affect of small samples is reduced because comparisons between age-classes III and IV indicate that growth has stopped before age-class V is attained. Thus, it was reasonable to expect no differences between age-classes IV and V. Size of samples must be considered carefully in interpretation of results of statistical analyses of morphologic variation.

Many features of the skull (especially length) continue to grow well into adulthood. For females, this growth continues until 5–6 years of age (age-class III), and for males, this growth continues until 7–9 years of age (age-class IV). The pattern of males growing to a larger size than females and reaching maximum size at a later age also has been shown to occur in another large carnivore, the polar bear (*Ursus maritimus*—Kingsley, 1979). However, Best and Gay (in press) found that male and female pumas from southwestern North America did not differ as to when growth of the cranium stopped, i.e., in both sexes, significant growth continued until 5–6 years of age. They postulated that growth continued for pumas in age-class III (5–6 years of age), because this age class was significantly different from pumas in age-class II

(3–4 years of age) in several characters. They also postulated that growth eventually ceased while pumas were in age-class III, because age-classes IV and V (7–>10 years of age) were not significantly different from age-class III. Reasons for the difference in age at cessation of growth for males between the previous study (5–6 years of age; Best and Gay, in press) and the present study (7–9 years of age) are unknown, especially considering that the 616 specimens examined by Best and Gay (in press) were a portion of the dataset examined herein. However, it is possible that when specimens from the remainder of North America and South America were included in analyses, either a more accurate estimation of age variation was obtained or male pumas from southwestern North America continue to grow for a shorter period of time than those from elsewhere in the range.

Growth of the cranium of pumas continues throughout most of the animal's life. Males continue to grow to 7–9 years of age, and females continue to grow to 5–6 years of age. Our findings are not fully consistent with studies of growth of the skull based on a smaller geographic area (Best and Gay, in press), body mass (Maehr and Moore, 1992), or size of feet (Shaw, 1983). Maehr and Moore (1992), however, were interested in growth rates based upon body mass of different geographic populations. They found that rate of growth did not vary by gender, but did vary geographically. In our study, geographic variation in patterns of growth was not considered due to lack of adequate samples for comparisons. Shaw (1983) suggested that feet of pumas continue to grow until 3–4 years of age, and that males grow more rapidly than females. It also is likely that increases in size of the cranium and mandible do not correspond to increases in body mass, size of feet, or other characters of the animal. Thus, it appears that more can be learned from future studies of the relationships among size of skull, geographic variation in growth pattern, body mass, and size of feet. Our study also indicates that age variation should be considered in studies involving assessment of morphologic variation among pumas.

Acknowledgments

This paper was extracted from a graduate thesis (Gay, 1994) submitted in partial fulfillment of the Master of Science in Zoology at Auburn University. We thank individuals maintaining personal collections and curatorial personnel of the numerous institutions for allowing access to specimens in their care. Data collection, analyses, and preparation of the manuscript were partially funded by The University of New Mexico Research Allocations Committee and the Alabama Agricultural Experiment Station. W. Barber, L. L. Janecek, and P. Chappell assisted in caring for loans of specimens sent to The University of New Mexico Museum of Southwestern Biology. We also thank G. F. Folkerts and J. B. Armstrong for help with computer software, F. S. Dobson, G. Halpin, and M. C. Wooten for statistical advice, C. D. Hilton and J. D. Wigginton for providing access to some of the literature, M. D. Gay for assistance in checking the data and analyses in various stages of this project, T. Haagenstad and T. E. Rodriguez for preparing figures, and R. S. Boyd, R. S. Lishak, R. E. Mirarchi, L. C. Wit, and two anonymous reviewers for critically evaluating an early draft of the manuscript. This is journal article no. 15-944873 of the Alabama Agricultural Experiment Station.

Literature Cited

Anderson, A. E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife, Special Report, 54:1–91.

Best, T. L., and S. W. Gay. In press. Morphometric assessment of the taxonomic status of the Yuma puma (*Puma concolor browni*). Arizona Game and Fish Department, Special Report.

Crowe, D. M. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. Journal of Mammalogy, 56:177–198.

Dice, L. R. 1936. Age variation in Peromyscus maniculatus gracilis. Journal of Mammalogy, 17:55–57.

Eaton, R. L., and K. A. Velander. 1977. Reproduction in the puma: biology, behavior and ontogeny. Pp. 45–70, *in* The world's cats (R. L. Eaton, ed.). Carnivore Research Institute, Burke Museum, University of Washington, Seattle, 3:1–144.

Fiscus, C. H. 1961. Growth in the Steller sea lion. Journal of Mammalogy, 42:218–223.

Gay, S. W. 1994. Morphologic variation in pumas (*Puma concolor*) and its relationship to selected climatic and biotic variables. M.S. thesis, Auburn University, Alabama, 184 pp.

GAY, S. W., AND T. L. BEST. 1995. Geographic variation in sexual dimorphism of the puma (*Puma concolor*) in North and South America. The Southwestern Naturalist, 40:148–159.

———. In press. Relationships between abiotic variables and geographic variation in skulls of pumas (*Puma concolor*: Mammalia, Felidae) in North and South America. Zoological Journal of the Linnean Society.

GRINNELL J., J. S. DIXON, AND J. M. LINSDALE. 1937. Fur-bearing mammals of California: their natural history, systematic status, and relations to man. University of California Press, Berkeley, 777 pp.

KINGSLEY, M. C. S. 1979. Fitting the von Bertalanffy growth equation to polar bear age-weight data. Canadian Journal of Zoology, 57:1020–1025.

LAIRD, A. K. 1965. Dynamics of relative growth. Growth, 29:249–263.

———. 1966. Postnatal growth of birds and mammals. Growth, 30:349–363.

LAIRD, A. K., S. A. TYLER, AND A. D. BARTON. 1965. Dynamics of normal growth. Growth, 29:233–248.

MAEHR, D. S., AND C. T. MOORE. 1992. Models of mass growth for 3 North American cougar populations. The Journal of Wildlife Management, 56:700–707.

MCCLURE, P. A., AND J. C. RANDOLPH. 1980. Relative allocation of energy to growth and development of homeothermy in the eastern wood rat (*Neotoma floridana*) and hispid cotton rat (*Sigmodon hispidus*). Ecological Monographs, 50:199–219.

MORRISON, P., R. DIETERICH, AND D. PRESTON. 1977. Body growth in sixteen rodent species and subspecies maintained in laboratory colonies. Physiological Zoology, 50:294–309.

NORUSIS, M. J. 1990. SPSS/PC+ Statistics 4.0 for the IBM PC/XT/AT and PS/2. SPSS, Inc., Chicago, paged by chapter.

QUIMBY, D. C. 1951. The life history and ecology of the jumping mouse, *Zapus hudsonius*. Ecological Monographs, 21:61–95.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution, 43:223–225.

ROBINETTE, W. L., J. S. GASHWILER, AND O. W. MORRIS. 1961. Notes on cougar productivity and life history. Journal of Mammalogy, 42:204–217.

SCHALLER, G. B. 1972. The Serengeti lion: a study of predator-prey relations. The University of Chicago Press, Chicago, 480 pp.

SHAW, H. G. 1983. Mountain lion field guide. Arizona Game and Fish Department, Special Report, 9:1–38.

SMITH, K. G., AND J. D. CLARK. 1994. Black bears in Arkansas: characteristics of a successful translocation. Journal of Mammalogy, 75:309–320.

SMUTS, G. L., J. L. ANDERSON, AND J. C. AUSTIN. 1978. Age determination of the African lion (*Panthera leo*). Journal of Zoology (London), 185:115–146.

SPECTOR, W. S. (ED.). 1956. Handbook of biological data. W. B. Saunders Company, Philadelphia, 584 pp.

TURBAK, G. 1987. North America. Pp. 32–57, *in* Kingdom of cats (H. F. Robinson, ed.). National Wildlife Federation, Washington, D.C., 207 pp.

YOUNG, S. P., AND E. A. GOLDMAN. 1946. The puma: mysterious American cat. American Wildlife Institute, Washington, D.C., 358 pp.

ZULLINGER, E. M., R. E. RICKLEFS, K. H. REDFORD, AND G. M. MACE. 1984. Fitting sigmoidal equations to mammalian growth curves. Journal of Mammalogy, 65:607–636.

Submitted 24 January 1995. Accepted 4 May 1995.

Associate Editor was Patricia W. Freeman.