Zoological Journal of the Linnean Society (1996), *117*: 259–282. With 9 figures

Relationships between abiotic variables and geographic variation in skulls of pumas (*Puma concolor*: Mammalia, Felidae) in North and South America

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Received November 1994, accepted for publication May 1995

Relationships between patterns of geographic variation in cranial morphology and selected abiotic variables were studied in the puma (*Puma concolor* Linnaeus). Our dataset consisted of 11 cranial, 6 dental, and 2 mandibular measurements of 1700 adults, which were separated by gender and age class and analysed by univariate and multivariate statistical procedures. Variation in size was correlated with precipitation, but size was more highly correlated with latitude and temperature. The pattern of geographic variation in size of *P. concolor* is consistent with Bergmann's rule; populations with larger pumas occur more distant from the equator than populations with smaller pumas. A combination of climatic and biotic factors contribute to patterns of geographic variation in size of *P. concolor* in North and South America.

ADDITIONAL KEY WORDS: — carnivore – morphology – ecology – Bergmann's rule.

CONTENTS

INTRODUCTION

Geographic variation is the occurrence of morphologic, genetic, or other differences among spatially segregated populations of a species. The morphologic character believed to show the most geographic variation is size, which varies most

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in species that have a large geographic range (Mayr, 1963). Mayr (1963) contended that geographic variation in morphology is caused by geographic variation in the environment. He believed there are two groups of abiotic factors that exert a selective pressure on the phenotype of an animal: climatic and habitat-biotic factors. Examples of parallel variation of morphologic and abiotic characters are widespread and have led to the development of ecogeographic rules. Bergmann's rule claims that races of endothermic species in cooler climates tend to be larger than those in warmer climates (Mayr, 1963). The usual physiologic explanation is that, with an increase in size, the volume of an animal increases more than the surface area. Scholander (1955, 1956) and Irving (1957) challenged the applicability of such ecogeographic rules, stating that other mechanisms, e.g. insulation and behaviour, are more efficient in preventing heat loss than a shift in surface-to-volume ratio. However, as Mayr (1956, 1963) asserted, multiple solutions, not all-or-none solutions, for biological needs are the general rule in evolution. Increased insulation against heat loss still does not eliminate the selective advantage of a decreased surface-to-volume ratio.

James (1970) reformulated Bergmann's rule to state the intraspecific variation in size of homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot and humid conditions, larger size with cooler or drier conditions. It also has been suggested that a larger body will be favoured in environments with greater seasonality (i.e. the seasons are more defined), as opposed to more constant environments (Boyce, 1979, 1985). This is because increased body size would enhance chances for survival during periods of shortages of resources (Lindsey, 1966; Calder, 1974). This enhanced chance for survival is though to be due to the greater percentage of body mass being stored as fat, as size of the mammal increases (Pitts & Bullard, 1968), and to the lower mass-specific rate of metabolism as size increases (Lindstedt & Boyce, 1985). Increased chance for survival during periods of shortages of resources has been suggested to contribute to the pattern of size variation expressed in Bergmann's rule, because cooler climates also tend to be more seasonal and are thus more likely to impose periods of shortages of resources (Lindsey, 1966; Calder, 1974; Lindstedt & Boyce, 1985).

Young & Goldman (1946) conducted an extensive study of pumas (*Puma concolor*) from throughout North and South America, and noted that the larger subspecies *P. c. hippolestes*, *P. c. missoulensis*, and *P. c. olympus* occurred in the northern part of the range, and that *P. c. pearsoni*, also a large subspecies, occurred in the southern area of the range in South America. Young & Goldman (1946) also found geographic variation in the combinations of cranial features that distinguished the subspecies, with a gradual alteration in detail from north to south; cranial characteristics were the primary criteria they used to distinguish among subspecies.

Because of its geographic distribution being the most extensive of any terrestrial mammal (excluding humans) in the Western Hemisphere, the diversity of habitats occupied, and previously documented morphologic variability, we studied geographic variation in the puma to provide additional insight into the applicability of Bergmann's ecogeographic rule to illuminate the reasons for the observed patterns of morphologic variation. The purposes of our study were to elucidate patterns of geographic variation in pumas and to assess relationships between patterns of geographic variation and selected abiotic variables.

MATERIAL AND METHODS

Our dataset included skulls of 1700 adult *P. concolor* (Table 1; Gay, 1994) and consisted of 11 cranial, six dental, and two mandibular measurements (Fig. 1) obtained with dial calipers accurate to the nearest 0.1 mm. Specimens were aged according to the criteria of D. Ashman (in litt.), which assigned specimens to one of five age classes based on wear of canines and incisors and staining of canines (described and illustrated in Gay & Best, 1996; Best & Gay, in press).

TABLE 1. Samples of *Puma concolor* from North and South America used to assess patterns of geographic variation

Sample no.	Code name	Geographic area	Gender		
			Males	Females	Unknown
1	VANCOUVE	Vancouver Island, British Columbia	25	25	21
2	BRCOLUMB	British Columbia	20	22	24
3	ALBERTA	Alberta	17	12	18
4	WASHING	Washington	25	24	8
5	MONTANA	Montana	31	34	20
6	OREGON	Oregon	45	49	13
7	IDAHO	Idaho	9	5	5
8	WYOMING	Wyoming	3	7	4
9	CALIFORN	California	71	56	30
10	NEVADA	Nevada	20	12	13
11	UTAH	Utah	28	39	19
12	COLORADO	Colorado	24	32	39
13	TXOKKSNE	northeastern Texas, Oklahoma, Kansas, and Nebraska	1	2	4
14	NEWENGL	New England	0	0	8
15	ARIZONA	Arizona	66	52	45
16	NEWMEX	New Mexico	69	65	52
17	ARKLOUIS	Arkansas and Louisiana	3	1	2
18	NORTMEX	northern Mexico	14	21	15
19	GRANPEC	between Rio Grande and Pecos rivers	21	25	16
20	PECCOLR	between Pecos and Colorado rivers	26	34	3
21	FLORIDA	Florida	9	12	5
22	WESTMEX	western Mexico	5	5	6
23	EASTMEX	eastern Mexico	4	2	8
24	SMEXCAM	southern Mexico and Central America	5	6	25
25	COLOVENE	Colombia and Venezuela	5	3	4
26	GUSUFRGU	Guyana, Surinam, and French Guiana	12	11	7
27	ECUADOR	Ecuador	15	6	3
28	PERU	Peru	7	2	7
29	WESTBRAZ	western Brazil	9	7	2
30	EASTBRAZ	eastern Brazil	3	4	6
31	BOLIVIA	Bolivia	3	2	11
32	PARAGUAY	Paraguay	2	1	18
33	CHILE	Chile	5	10	8
34	ARGENTIN	Argentina	7	4	30
	Total		609	592	499

Specimens of pumas were divided into samples based upon groupings of collecting localities (Fig. 2). Attempts were made to group specimens within the same physiographic regions (e.g. mountain range, habitat type), but because many of the specimens had little information about collecting locality, limits of most samples were based on political boundaries.

In previous studies of size variation associated with gender and age in pumas, males and females differed significantly in all 19 morphologic characters, and age also contributed to size variation (Gay, 1994; Gay & Best, 1995, 1996; Best & Gay, in press). Thus, males were divided into three age groups (Gay, 1994): age-class II (3–4 years of age); age-class III (5–6 years of age); age-class IV–V (≥ 7 years of age).

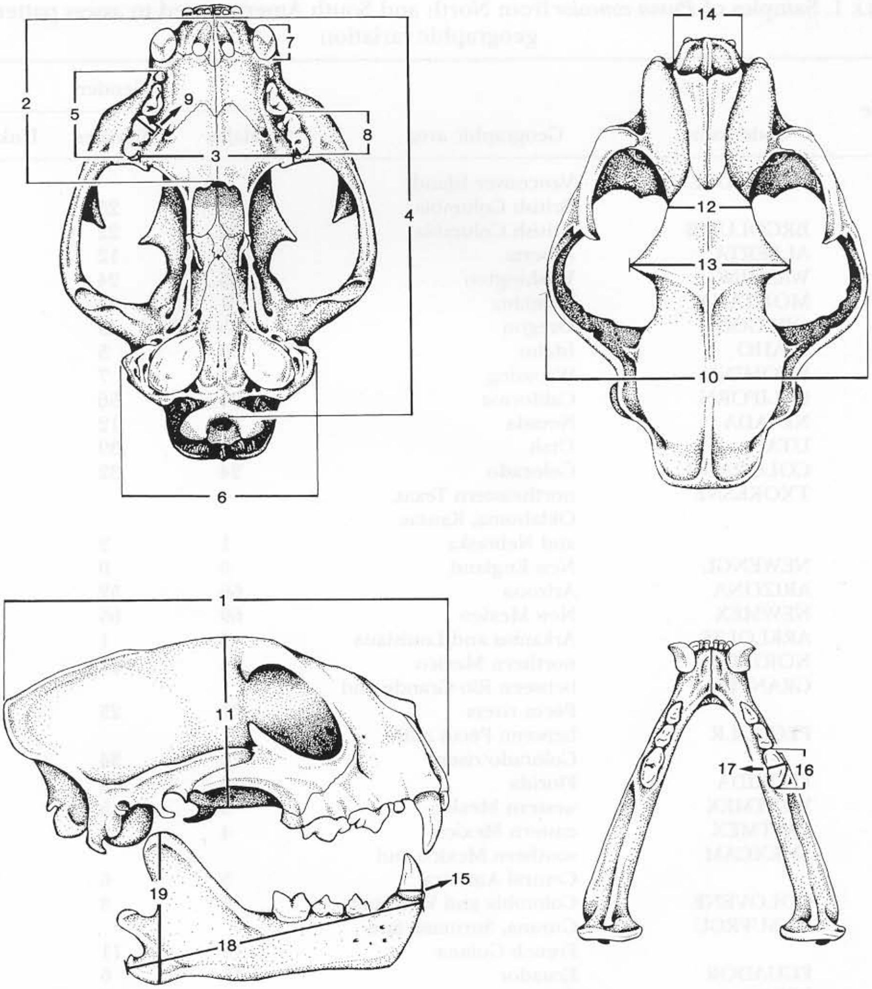

Figure 1. Cranial, tooth, and mandibular measurements used to examine morphometric variation in *Puma concolor* from North and South America: (1) greatest length of skull; (2) palatal length; (3) intermaxillary width; (4) basilar length; (5) length of alveolar toothrow; (6) mastoidal width; (7) greatest 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.

Females were divided into two groups: age-class II (3–4 years of age); age-class III–V (≥ 5 years of age). Each age and gender group was analysed separately.

The gender of animals of unknown gender was determined using discriminant-function analysis (Norusis, 1990) on age-classes II–V separately; age-class I was not included due to small samples. Discriminant-function analysis takes the individuals of known gender and computes an equation, which is used to assign a gender to individuals of unknown gender. Because this procedure would not include specimens with missing data, several analyses were performed. The first analysis included only individuals with complete data. For subsequent analyses, one to three variables were eliminated from the dataset to permit inclusion of individuals with missing data. Individuals of unknown gender with four or more missing variables (93 specimens) were eliminated from the dataset. Results of discriminant-function analysis included a probability estimate that the predicted gender was correct; individuals scoring < 0.7 (33 specimens) were eliminated from the dataset.

For each age class and gender, average and standard deviation were calculated for each character for each sample (a listing of these statistics is provided in Gay, 1994). To determine if the between-group variation was greater than the within-group variation for each character, intersample heterogeneity of each character was tested

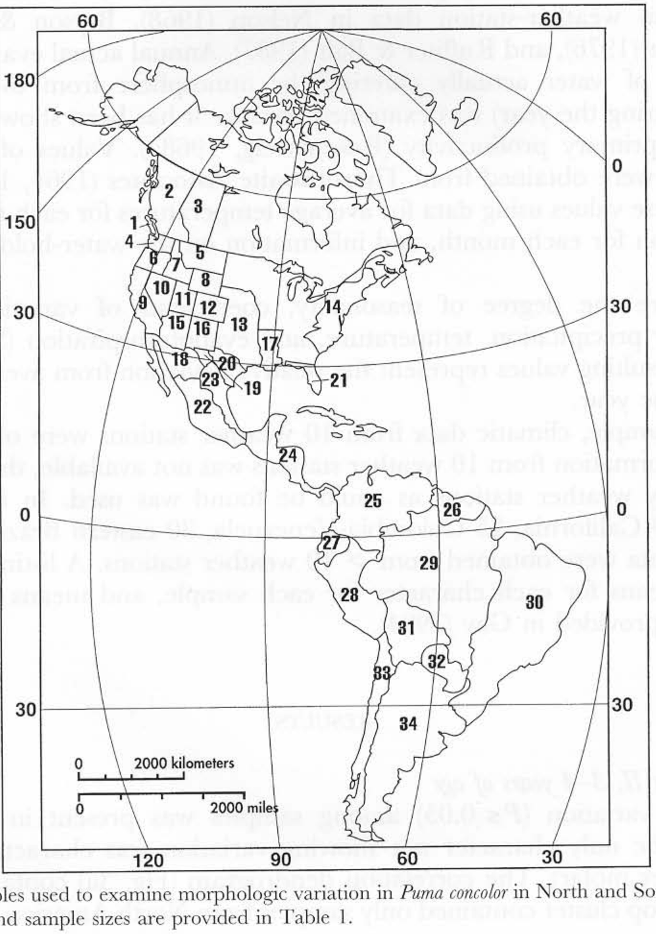

Figure 2. Samples used to examine morphologic variation in *Puma concolor* in North and South America. Code names and sample sizes are provided in Table 1.

with a one-way analysis of variance (Norusis, 1990). For multivariate procedures, the average measurements for each sample were used. Characters were standardized so that each had an average of 0 and a standard deviation of 1. Correlation and distance matrices (Sneath & Sokal, 1973) were calculated and clusters of samples and characters were obtained with the unweighted pair-group method using arithmetic averages; accuracy of the resulting dendrograms in depicting relationships among samples and characters increases from left to right. Principal components were calculated from a correlation matrix among characters and projections of the samples were plotted on the first three components (Rohlf, 1992).

Pearson product-moment correlation coefficients between abiotic variables and principal components of morphologic variation were calculated (Norusis, 1990). To investigate the applicability of Bergmann's rule to morphologic variation of pumas, average annual temperature was obtained. Because latitude and elevation were highly correlated with temperature, the effect of these two variables on body size also was evaluated. To evaluate the hypothesis proposed by James (1970), i.e. body size increases with decreasing temperature and precipitation, the average annual precipitation for the area occupied by each sample was obtained. The relationship with longitude was evaluated because areas in western North America tended to be drier than areas in eastern North America and because similar climatic variation occurs across South America (Watts, 1971). Values for the above variables were obtained from weather-station data in Nelson (1968), Bryson & Hare (1974), Schwerdtfeger (1976), and Ruffner & Bair (1987). Annual actual evapotranspiration (the amount of water actually entering the atmosphere from the soil and the vegetation during the year) was examined because it has been shown to be a good predictor of primary productivity (Rosenzweig, 1968a). Values of actual evapotranspiration were obtained from Thornthwaite Associates (1964, 1965), who had calculated these values using data for average temperatures for each month, amount of precipitation for each month, and information on the water-holding capacity of the soil.

To measure the degree of seasonality, coefficients of variation (CV) were calculated for precipitation, temperature, and evapotranspiration (Sokal & Rohlf, 1981). The resulting values represent the relative deviation from average conditions throughout the year.

For each sample, climatic data from 10 weather stations were obtained. In the event that information from 10 weather stations was not available, then information from as many weather stations as could be found was used. In five larger-area samples (i.e. 9 California, 25 Colombia-Venezuela, 30 eastern Brazil, 33 Chile, 34 Argentina), data were obtained from > 10 weather stations. A listing of specimens examined, means for each character for each sample, and means for the abiotic variables are provided in Gay (1994).

RESULTS

Males, age-class II, 3–4 years of age

Significant variation ($P \leq 0.05$) among samples was present in 18 of the 19 characters. The only character not showing variation was character 17 (greatest length of lower molar). The correlation dendrogram (Fig. 3a) contained two large clusters. The top cluster contained only samples from North America, with two pairs

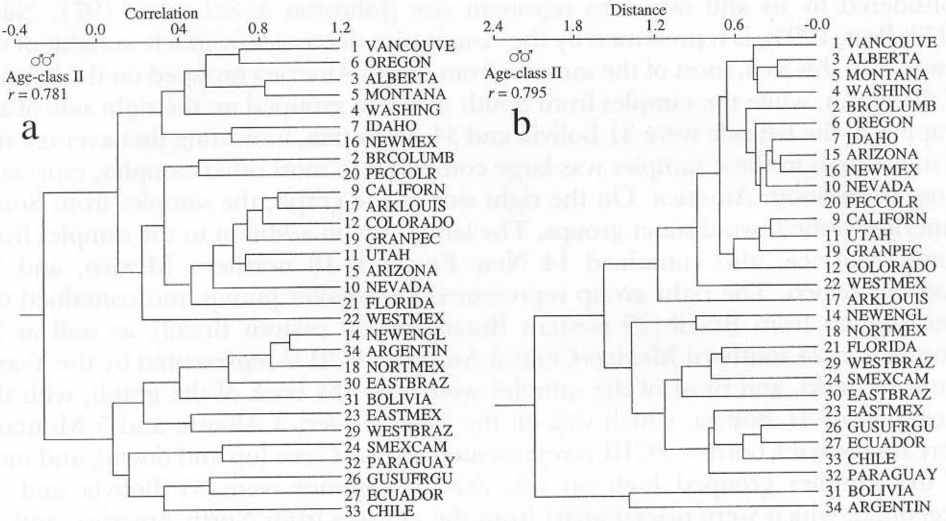

Figure 3. Correlation (a) and distance (b) dendrograms based upon morphometric variation in males of age-class II of *Puma concolor* from North and South America. Numerical identifications and code names are the same as listed in Table 1. The coefficient of cophenetic correlation (r) is provided.

of geographically adjacent samples in this cluster (3 Alberta and 5 Montana, 11 Utah and 15 Arizona). The bottom cluster contained all the samples from South America, as well as 14 New England, 18 northern Mexico, 23 eastern Mexico, and 24 southern Mexico-Central America, but there were no adjacent samples in this cluster. In the distance dendrogram (Fig. 3b), 31 Bolivia and 34 Argentina comprised one cluster and were geographically adjacent. The top cluster contained only samples from North America; 3 Alberta and 5 Montana grouped together and were contiguous samples, and a grouping of seven samples (2 British Columbia, 6 Oregon, 7 Idaho, 15 Arizona, 16 New Mexico, 10 Nevada, and 20 between the Pecos and Colorado rivers) were geographically adjacent. The middle cluster contained the remaining samples from South America, as well as 14 New England, 18 northern Mexico, 21 Florida, 24 southern Mexico-Central America, and 23 eastern Mexico; no geographically contiguous samples clustered together.

The character correlations with principal component I (PCI; Table 2) generally were high (> 0.700) for cranial and mandibular characters, but low for dental ones, i.e. characters 5 (length of alveolar toothrow), 8 (greatest length of third upper premolar), 9 (greatest width of third upper premolar), 13 (supraorbital width), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). On principal component II (PCII), the highest loadings (> 0.400) were for characters 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), 12 (interorbital width), 13 (supraorbital width), 15 (greatest diameter of lower canine), 16 (greatest length of lower molar), 17 (greatest width of lower molar), and 19 (depth of mandible). Principal component III (PCIII) had the highest loadings (> 0.400) for characters 2 (palatal length), 3 (intermaxillary width), and 5 (length of alveolar toothrow).

Groupings evident from the three-dimensional graph of the first three principal components (Fig. 4a) correspond well with the distance dendrogram. PCI, which is considered by us and others to represent size (Johnston & Selander, 1971; Niles, 1973; Best, 1993), is represented by the X-axis (size decreases from left to right) of the graph. On this axis, most of the samples from North America grouped on the left side of the graph, while the samples from South America grouped on the right side of the graph. On the left side were 31 Bolivia and 34 Argentina, indicating that average size of individuals in these samples was large compared to most other samples, especially those from South America. On the right side of the graph, the samples from South America formed two distinct groups. The left group, in addition to the samples from South America, also contained 14 New England, 18 northern Mexico, and 23 eastern Mexico. The right group represented the smaller pumas and contained the two samples from Brazil (29 western Brazil and 30 eastern Brazil), as well as 21 Florida and 24 southern Mexico-Central America. PCII is represented by the Y-axis (front to back), and most of the samples were near the back of the graph, with the exception of 31 Bolivia, which was on the front border; 3 Alberta and 5 Montana were on the back border. PCIII is represented by the Z-axis (up and down), and most of the samples grouped high on this axis. Exceptions were 31 Bolivia and 34 Argentina, which were placed apart from the samples from North America, and 14 New England and 18 northern Mexico, which were placed apart from the samples from South America.

Pearson product-moment correlation coefficients calculated between PCI and nine abiotic variables (Table 3) indicated significant correlations with latitude,

TABLE 2. Character loadings[a] on the first three principal components of intersample phenetic variation among 19 cranial and mandibular characters of males of age-classes II, III, and IV–V of *Puma concolor*

	Age-class II			Age-class III			Age-class IV–V		
Char. no.[b]	I	II	III	I	II	III	I	II	III
1	–0.927	0.238	–0.058	–0.959	0.145	0.060	–0.964	0.020	–0.050
2	–0.875	–0.070	–0.446	–0.900	0.012	0.094	–0.901	–0.069	–0.292
3	–0.837	0.153	0.425	–0.881	0.208	–0.298	–0.843	0.149	0.229
4	–0.937	0.132	–0.146	–0.946	0.168	0.026	–0.955	–0.014	–0.072
5	–0.596	–0.560	–0.513	–0.773	–0.513	0.011	–0.248	–0.762	–0.194
6	–0.891	0.238	–0.054	–0.878	0.130	–0.210	–0.916	–0.063	–0.328
7	–0.858	–0.426	0.145	–0.873	–0.322	0.003	–0.673	–0.299	0.518
8	–0.641	–0.732	0.017	–0.849	–0.393	0.011	–0.275	–0.752	0.030
9	–0.663	–0.670	0.085	–0.855	–0.317	0.139	–0.333	–0.467	0.349
10	–0.882	0.241	–0.135	–0.925	0.227	–0.134	–0.921	0.136	–0.128
11	–0.935	0.217	–0.004	–0.914	0.291	–0.110	–0.950	0.121	0.123
12	–0.838	0.445	0.273	–0.897	0.333	0.162	–0.920	0.154	0.013
13	–0.545	0.647	0.159	–0.737	0.332	0.537	–0.824	0.050	–0.186
14	–0.797	0.239	0.041	–0.895	0.288	0.045	–0.797	0.257	–0.035
15	–0.841	–0.461	0.165	–0.886	–0.242	–0.097	–0.751	–0.262	0.488
16	–0.223	–0.810	0.325	–0.595	–0.738	0.005	–0.022	–0.883	–0.159
17	–0.668	–0.487	0.075	–0.729	–0.479	0.063	0.252	–0.768	–0.181
18	–0.954	0.200	–0.070	–0.947	0.259	–0.112	–0.959	0.067	–0.044
19	–0.813	0.446	–0.041	–0.923	0.168	–0.081	–0.893	0.080	–0.150
Total[c]	63.16	19.81	5.07	74.95	11.05	2.86	58.74	16.10	5.63

[a] Correlations of sample average values (*n*=30,34, and 28 for age-classes II, III, and IV–V, respectively) of individual characters with the component axes.

[b] Character numbers correspond to the list of characters under Fig. 1.

[c] Percent of total phenetic variance explained.

longitude, average annual temperature, average annual precipitation, actual annual evapotranspiration, and coefficient of variation (CV) of temperature. PCII showed no significant relationships with any of the abiotic variables, but PCIII was

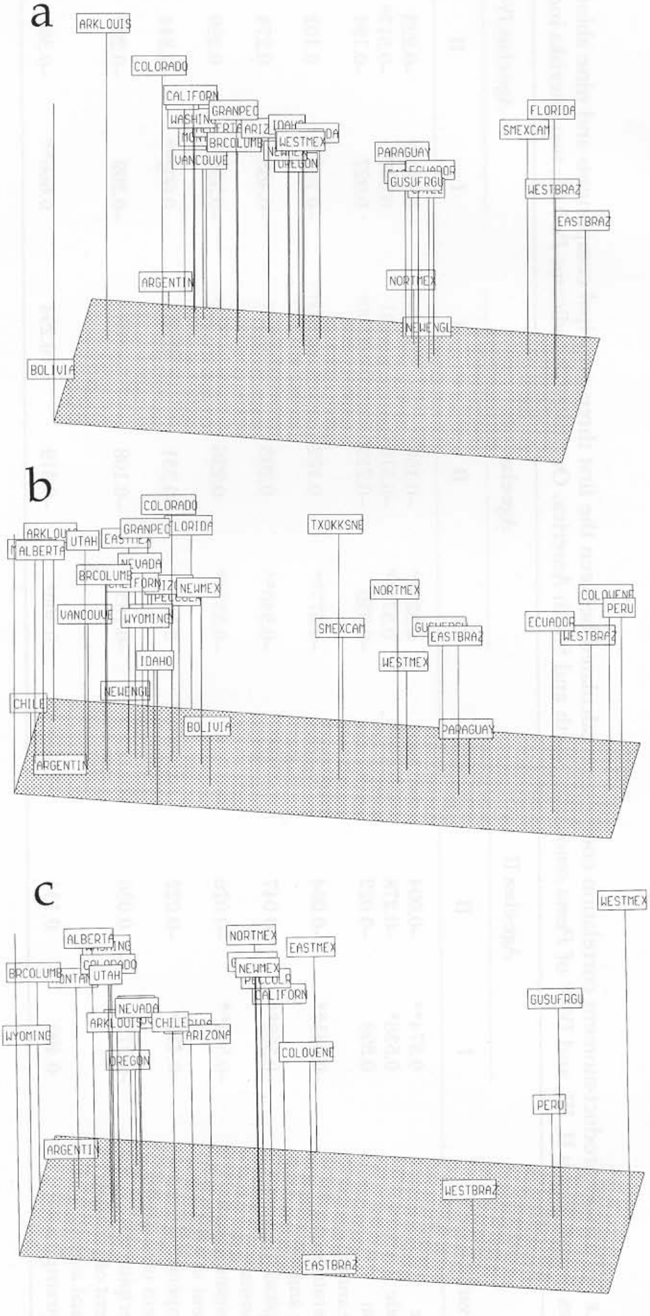

Figure 4. Three-dimensional graphs of the first three principal components of morphometric variation in males of age-classes II (a), III (b), and IV-V (c) of *Puma concolor* from North and South America.

TABLE 3. Pearson product-moment correlation coefficients calculated between the first three principal components and nine abiotic variables for males of age-classes II, III, and IV–V of *Puma concolor* in North and South America. One asterisk indicates $P \leq 0.01$; two asterisks indicate $P \leq 0.001$

	Age-class II			Age-class III			Age-class IV–V		
Abiotic variable	I	II	III	I	II	III	I	II	III
Latitude	0.574**	–0.004	–0.505*	0.823**	–0.150	0.278	0.851**	–0.223	–0.221
Longitude	0.538*	–0.278	–0.424*	0.579**	–0.510*	0.231	0.547*	–0.517*	–0.405
Elevation	0.398	–0.022	0.244	–0.036	–0.219	0.400*	0.027	–0.194	0.043
Average annual temperature	–0.641**	–0.064	0.374	–0.677**	0.172	–0.539**	–0.742**	0.102	0.209
Average annual precipitation	–0.562**	–0.047	0.241	–0.546**	0.203	–0.318	–0.468*	0.274	0.104
Actual annual evapotranspiration	–0.552**	–0.026	0.364	–0.537**	0.236	–0.468*	–0.538*	0.289	0.031
Coefficient of variation of temperature	0.432*	–0.022	–0.448*	0.543**	–0.331	0.381	0.602**	–0.244	–0.098
Coefficient of variation of precipitation	–0.073	0.036	0.182	–0.185	–0.108	–0.087	–0.399	–0.297	–0.451*
Coefficient of variation of actual annual evapotranspiration	0.400	0.134	–0.485*	0.506*	–0.319	0.294	0.660**	–0.368	–0.209

significantly correlated with latitude, longitude, CV of temperature, and CV of actual annual evapotranspiration.

Males, age-class III, 5–6 years of age

For this group, all 19 characters showed significant variation among samples ($P \leq 0.05$). The correlation dendrogram (Fig. 5a) consisted of four clusters. The top cluster contained three adjacent samples; 1 Vancouver Island, 4 Washington, and 6 Oregon. The second cluster contained only samples from North America. Within this cluster, there were four groups of contiguous samples; 2 British Columbia, 3 Alberta, and 5 Montana; 11 Utah, 12 Colorado, and 13 Texas-Oklahoma-Kansas-Nebraska; 9 California, 15 Arizona, 16 New Mexico, and 18 northern Mexico; 19 between Rio Grande and Pecos rivers and 23 eastern Mexico. The third cluster contained a pair of adjacent samples (7 Idaho and 8 Wyoming) along with 28 Peru. The bottom cluster contained most of the samples from South America, as well as 14 New England, 22 western Mexico, and 24 southern Mexico-Central America; 31 Bolivia, 32 Paraguay, 33 Chile, and 34 Argentina formed a contiguous grouping in this cluster. The distance dendrogram (Fig. 5b) was composed of two large clusters with each cluster containing samples from North and South America. The top cluster contained three pairs of adjacent samples (3 Alberta and 5 Montana, 7 Idaho and 8 Wyoming, 33 Chile and 34 Argentina) and a group of seven adjacent samples (6 Oregon, 9 California, 15 Arizona, 16 New Mexico, 19 between Rio Grande and Pecos rivers, 20 between Pecos and Colorado rivers, and 23 eastern Mexico). The bottom cluster contained mostly samples from South America and Mexico and had four adjacent samples (25 Colombia-Venezuela, 27 Ecuador, 28 Peru, and 29 western Brazil).

The character correlations with PCI (Table 2) were high (> 0.700) for all characters except 16 (greatest length of lower molar). On PCII, the highest loadings

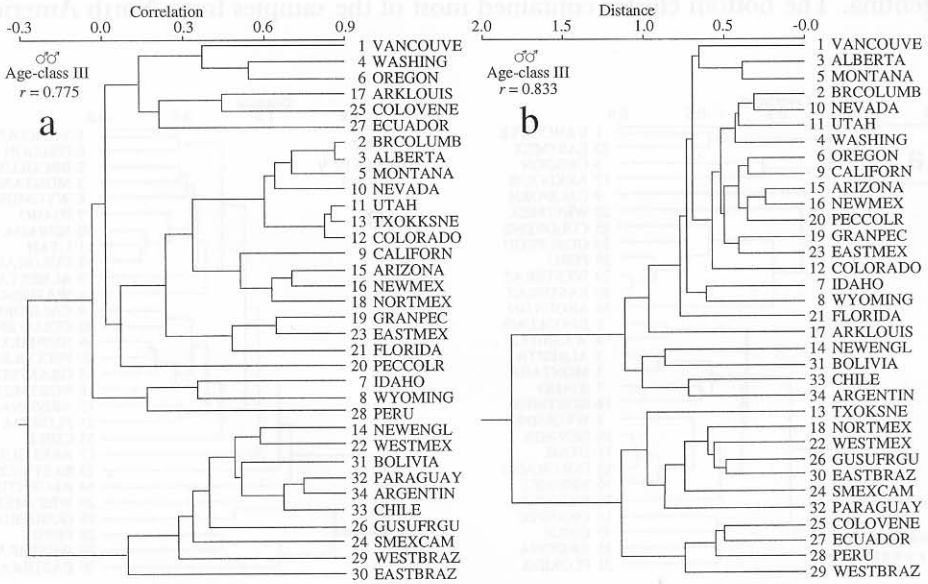

Figure 5. Correlation (a) and distance (b) dendrograms based upon morphometric variation in males of age-class III of *Puma concolor* from North and South America. Numerical identifications and code names are the same as listed in Table 1. The coefficient of cophenetic correlation (r) is provided.

(> 0.400) were for characters 5 (length of alveolar toothrow), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). PCIII had the highest loadings (> 0.500) for character 13 (supraorbital width).

In the three-dimensional graph of the first three principal components (Fig. 4b), most of the samples from North America grouped together on the left side of the graph. Also contained in this group were 31 Bolivia, 33 Chile, and 34 Argentina, but these were low on PCIII and away from the samples from North America. Also in this group, 14 New England was low on PCIII. The remaining samples from South America were on the right side of the graph and most of the samples from Mexico and 13 Texas-Oklahoma-Kansas-Nebraska were near the middle.

Correlation coefficients calculated between PCI and nine abiotic variables (Table 3) indicated significant correlations with latitude, longitude, average annual temperature, average annual precipitation, actual annual evapotranspiration, CV of temperature, and CV of actual annual evapotranspiration. PCII was significantly correlated with longitude, and PCIII was significantly correlated with elevation, average annual temperature, and actual annual evapotranspiration.

Males, age-class IV–V, ≥ 7 years of age

Twelve of the 19 characters showed significant ($P \leq 0.05$) variation among samples. Characters that did not show significant differences were 2 (palatal length), 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), 15 (greatest diameter of lower canine), and 17 (greatest width of lower molar). The correlation dendrogram (Fig. 6a) contained two large clusters. The top cluster contained most of the samples from South America and Mexico, as well as 1 Vancouver Island, 6 Oregon, 9 California, and 17 Arkansas-Louisiana. It also contained one group of adjacent samples; 25 Colombia-Venezuela, 26 Guyana-Surinam-French Guiana, 28 Peru, 29 western Brazil, 30 eastern Brazil, and 34 Argentina. The bottom cluster contained most of the samples from North America,

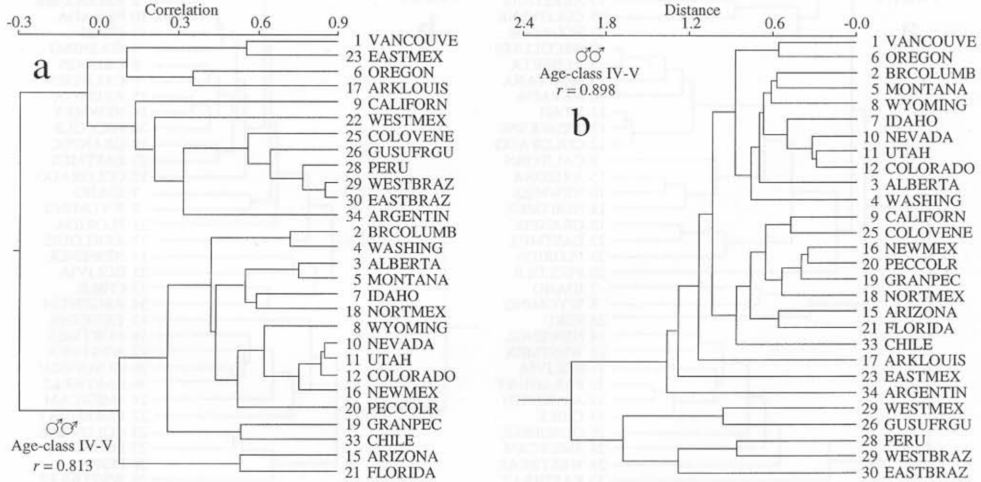

Figure 6. Correlation (a) and distance (b) dendrograms based upon morphometric variation in males of age-class IV–V of *Puma concolor* from North and South America. Numerical identifications and code names are the same as listed in Table 1. The coefficients of cophenetic correlation (*r*) is provided.

as well as 33 Chile. The bottom cluster also contained two pairs of geographically adjacent samples (2 British Columbia and 4 Washington, 3 Alberta and 5 Montana) and a group of six adjacent samples (8 Wyoming, 10 Nevada, 11 Utah, 12 Colorado, 16 New Mexico, and 20 between Pecos and Colorado rivers). The distance dendrogram (Fig. 6b) contained two clusters. In the top cluster, the top 11 samples made up a geographically adjacent grouping, and there also was a group of four adjacent samples (16 New Mexico, 18 northern Mexico, 19 between Rio Grande and Pecos rivers, and 20 between Pecos and Colorado rivers) within this cluster. There were only five samples in the bottom cluster; three of these were adjacent (28 Peru, 29 western Brazil, and 30 eastern Brazil).

The character correlations with PCI were high (> 0.700; Table 2) for all characters except 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), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). On PCII, the highest loadings (> 0.400) were for characters 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). PCIII had the highest loadings (> 0.400) for characters 7 (greatest diameter of upper canine) and 15 (greatest diameter of lower canine).

In the three-dimensional graph of the first three principal components (Fig. 4c), once again most of the samples from North America grouped together on the left side of the graph. Again, 33 Chile and 34 Argentina were in this group, but only 34 Argentina grouped apart by being low on the axis of PCIII. Toward the middle, there was a mixture of samples from North (mostly the Southwest) and South America. Only samples from South America were on the right side of the graph.

Pearson product-moment correlation coefficients calculated between PCI and nine abiotic variables (Table 3) indicated significant correlations with latitude, longitude, average annual temperature, average annual precipitation, actual annual evapotranspiration, CV of temperature, and CV of actual annual evapotranspiration. PCII was significantly correlated with longitude, and PCIII was significantly correlated with CV of precipitation.

Females, age-class II, 3–4 years of age

For this group, 16 of the 19 characters showed significant geographic variation ($P \leq 0.05$). Those characters not showing significant variation were characters 5 (length of alveolar toothrow), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). The correlation dendrogram (Fig. 7a) contained two large clusters, with each containing a mixture of samples from North and South America. Only one group of adjacent samples was present (1 Vancouver Island, 2 British Columbia, 3 Alberta, and 5 Montana). The distance dendrogram (Fig. 7b) also contained two clusters; all but one (34 Argentina) of the samples in the top cluster were samples from North America. There was one pair of adjacent samples in the top cluster (4 Washington and 7 Idaho) and a group of five geographically adjacent samples (2 British Columbia, 3 Alberta, 5 Montana, 11 Utah, and 12 Colorado). The bottom cluster contained most of the samples from South America, along with 18 northern Mexico and 23 eastern Mexico and had one pair of adjacent samples (28 Peru and 31 Bolivia).

All character correlations with PCI loaded high (> 0.700; Table 4) with the exception of character 17 (greatest width of lower molar). On PCII, the highest

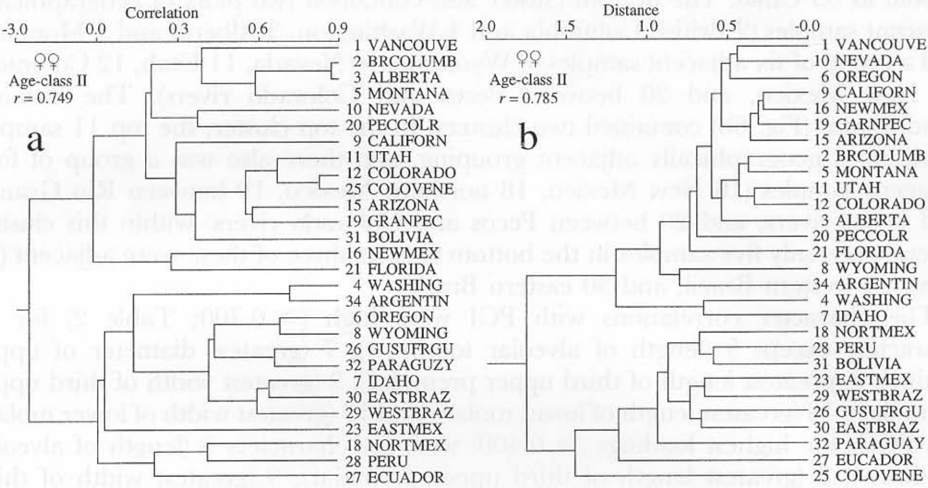

Figure 7. Correlation (a) and distance (b) dendrograms based upon morphometric variation in females of age-class II of *Puma concolor* from North and South America. Numerical identifications and code names are the same as listed in Table 1. The coefficient of cophenetic correlation (r) is provided.

loadings (> 0.400) were for characters 5 (length of alveolar toothrow), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). The highest loadings (> 0.200) for PCIII were for characters 4 (basilar length), 6 (mastoidal width), 10 (zygomatic width), and 13 (supraorbital width).

In the three-dimensional graph of the first three principal components (Fig. 8a), most of the samples from North America grouped closely near the center of the graph, and most of the samples from South America were scattered across the right side of the graph. On the far left side of the graph were 4 Washington and 7 Idaho, indicating that these samples contained the largest pumas. Near the samples from North America was 34 Argentina.

Correlation coefficients calculated between PCI and nine abiotic variables (Table 5) indicated significant correlations with latitude, longitude, average annual temperature, average annual precipitation, actual annual evapotranspiration, CV of temperature, and CV of actual annual evapotranspiration. No significant relationships were found between PCII or PCIII and the abiotic variables.

Females, age-class III–V, ≥ 5 years of age

All 19 characters showed significant geographic variation among samples ($P \leq 0.05$). The correlation dendrogram (Fig. 9a) contained five clusters. The first cluster contained a geographic mixture of samples, but it also contained a group of four adjacent samples (10 Nevada, 11 Utah, 12 Colorado, and 16 New Mexico) and a pair of adjacent samples (20 between Pecos and Colorado rivers and 23 eastern Mexico). Within the second cluster, there was a pair of adjacent samples (15 Arizona and 18 northern Mexico) and a group of three adjacent samples (3 Alberta, 5 Montana, and 7 Idaho). The third cluster consisted of the adjacent pair of 4 Washington and 6 Oregon, the fourth cluster consisted of 8 Wyoming, 22 western Mexico, and 25 Colombia-Venezuela, and the fifth cluster contained mostly samples from South America, as well as 17 Arkansas-Louisiana and 21 Florida. The distance dendrogram (Fig. 9b) contained three clusters. The top cluster consisted mostly of samples from North America (excluding Mexico). In this cluster there were four pairs of adjacent samples (4 Washington and 6 Oregon, 5 Montana and 7 Idaho, 15 Arizona and 16 New Mexico, 19 between Rio Grande and Pecos rivers and 20 between Pecos and Colorado rivers) and a group of three (10 Nevada, 11 Utah, and 12 Colorado). The second cluster contained most of the samples from Mexico and South America. There were two pairs of contiguous samples in this cluster (18 northern Mexico and 22 western Mexico, 26 Guyana-Surinam-French Guiana and 29 western Brazil). The bottom cluster contained 17 Arkansas-Louisana.

The character correlations with PCI were high (> 0.700; Table 4) for all characters, except 5 (greatest length of alveolar toothrow), 13 (supraorbital width), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). For PCII, the highest loadings (> 0.400) were for characters 5 (length of alveolar toothrow), 8 (greatest length of third upper premolar), 9 (greatest width of third upper premolar), 13 (supraorbital width), 16 (greatest length of lower molar), and 17 (greatest width of lower molar). For PCIII, the highest loadings (> 0.300) were for characters 5 (length of alveolar toothrow), 15 (greatest diameter of lower canine), and 17 (greatest width of lower molar).

In the three-dimensional graph of the first three principal components (Fig. 8b), the samples were somewhat evenly spaced throughout the graph. Samples from North America were positioned on the left side of the graph and samples from South America were on the right side. At the extremes on the PCI axis were 17 Arkansas-

TABLE 4. Character loadings[a] on the first three principal components of intersample phenetic variation among 19 cranial and mandibular characters of females of age-classes II and III–V of *Puma concolor*

	Age-class II			Age-class III–V		
Char. no.[b]	I	II	III	I	II	III
1	–0.972	0.150	0.064	–0.959	–0.009	0.174
2	–0.951	0.023	–0.039	–0.873	–0.037	0.248
3	–0.920	0.172	0.149	–0.859	0.347	–0.197
4	–0.943	0.066	0.251	–0.964	0.101	0.205
5	–0.743	–0.471	–0.079	–0.651	–0.560	0.387
6	–0.852	0.243	–0.382	–0.925	–0.074	–0.102
7	–0.928	–0.090	–0.187	–0.813	–0.398	0.033
8	–0.868	–0.341	0.087	–0.852	–0.434	0.040
9	–0.848	–0.350	0.158	–0.788	–0.466	–0.029
10	–0.922	0.129	0.222	–0.915	0.301	–0.010
11	–0.934	0.245	0.091	–0.938	0.249	0.017
12	–0.938	0.255	0.006	–0.904	0.265	0.107
13	–0.810	0.307	–0.330	–0.660	0.604	0.018
14	–0.903	0.162	0.172	–0.901	0.127	0.136
15	–0.934	–0.133	–0.160	–0.743	0.177	–0.497
16	–0.744	–0.423	–0.141	–0.431	–0.687	–0.203
17	–0.589	–0.674	–0.011	–0.632	–0.499	–0.412
18	–0.972	0.067	–0.004	–0.959	0.175	0.005
19	–0.942	0.232	0.025	–0.914	0.210	–0.146
Total[c]	78.25	8.19	2.91	70.04	12.87	4.46

[a] Correlations of sample average values ($n=28$ and 34 for age-classes II and III–V, respectively) of individual characters with the component axes.

[b] Character numbers correspond to the list of characters under Fig. 1.

[c] Percent of total phenetic variance explained.

Louisiana on the left side and 24 southern Mexico-Central America and 26 Guyana-Surinam-French Guiana on the right side. Representing the extremes of PCII were 27 Ecuador on the front and 17 Arkansas-Louisiana on the back. For PCIII, the lower extreme was 17 Arkansas-Louisiana and the upper extreme was 24 southern Mexico-Central America.

Pearson product-moment correlation coefficients calculated between PCI and nine abiotic variables (Table 5) indicated significant correlations with latitude, longitude, average annual temperature, average annual precipitation, actual annual evapotranspiration, CV of temperature, and CV of actual annual evapotranspiration. PCII was significantly correlated with longitude and actual annual evapotranspiration, but PCIII was not significantly correlated with any of the abiotic variables.

DISCUSSION

Numerous studies of morphologic variation have been conducted on mammals, and many of these studies have addressed the relationship between the observed patterns of variation and ecogeographic rules. For example, larger white-footed mice (*Peromyscus leucopus* Rafinesque) occurred in areas of lower temperature, moisture, and

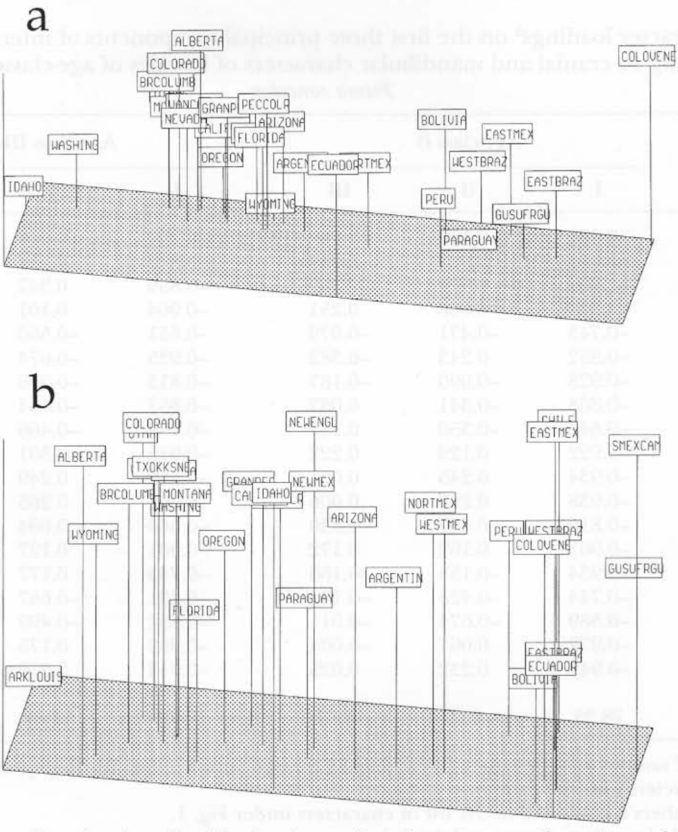

Figure 8. Three-dimensional graphs of the first three principal components of morphometric variation in females of age-classes II and III–V of *Puma concolor* from North and South America.

TABLE 5. Pearson product-moment correlation coefficients calculated between the first three principal components and nine abiotic variables for females of age-classes II and III–V of *Puma concolor* in North and South America. One asterisk indicates $P \leq 0.01$; two asterisks indicate $P \leq 0.001$

	Age-class II			Age-class III–V		
Abiotic variable	I	II	III	I	II	III
Latitude	0.849**	0.012	–0.422	0.826**	–0.338	0.046
Longitude	0.816**	–0.176	–0.192	0.680**	–0.430*	0.121
Elevation	0.186	–0.117	0.133	0.068	–0.103	0.280
Average annual temperature	–0.800**	0.099	0.214	–0.704**	0.317	–0.147
Average annual precipitation	–0.626**	0.041	0.179	–0.563**	0.334	–0.161
Actual annual evapotranspiration	–0.743**	0.097	0.020	–0.537**	0.408*	–0.081
Coefficient of variation of temperature	0.587**	–0.198	–0.286	0.672**	–0.355	0.274
Coefficient of variation of precipitation	–0.159	–0.001	0.008	–0.281	–0.184	0.196
Coefficient of variation of actual annual evapotranspiration	0.640**	–0.088	–0.114	0.702**	–0.252	0.216

productivity, and higher seasonality (Owen, 1989). Snell & Cunnison (1983) demonstrated that meadow voles (*Microtus pennsylvanicus* Ord) showed a pattern of size variation that was the reverse of Bergmann's rule, with voles being larger where it was warm and smaller where it was cold. Because small size reduces total expenditure of energy, they predicted that smaller voles would be less energetically

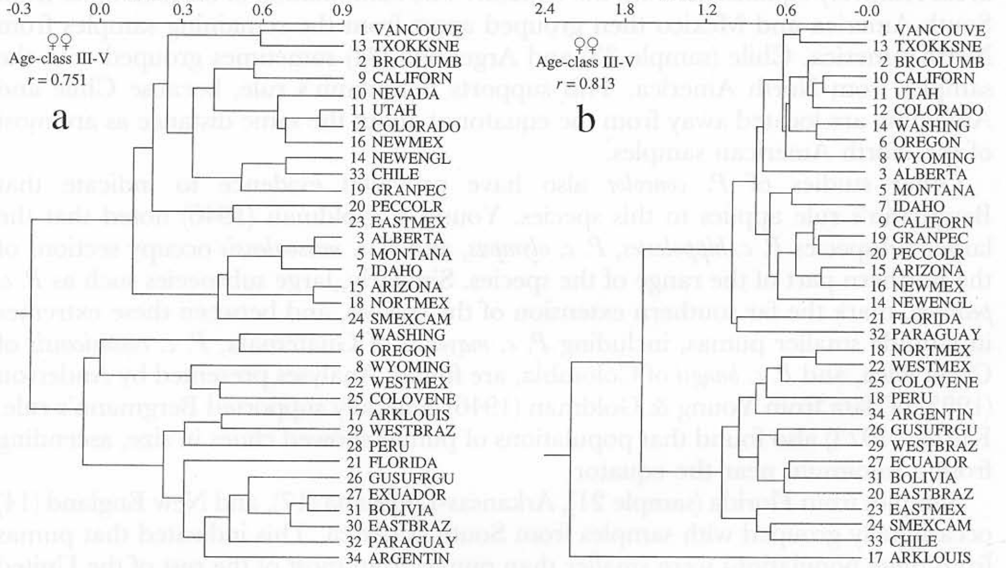

Figure 9. Correlation (a) and distance (b) dendrograms based upon morphometric variation in females of age-class III–V of *Puma concolor* from North and South America. Numerical identifications and code names are the same as listed in Table 1. The coefficient of cophenetic correlation (r) is provided.

stressed than larger voles and that large size would thus be selected against. Larger body size of snowshoe hares (*Lepus americanus* Erxleben) was correlated with areas of greater precipitation in July, large annual evapotranspiration, cold temperatures in winter, spring, and autumn, and great seasonality in temperatures (Nagorsen, 1985). In raccoons (*Procyon lotor* Linnaeus), larger body size was correlated with high seasonality and low primary productivity (Ritke & Kennedy, 1988). Body size of muskrats (*Ondatra zibethicus* Linnaeus) was largest in regions of high annual precipitation and low seasonality in rainfall patterns (Boyce, 1978), and also was negatively correlated with variability of water level. It was suggested that variability of water level resulted in areas of low availability of resources, which would cause small size to be adaptive, because less energy would be needed for growth and maintenance (Donohoe, 1966). Rosenzweig (1968b) believed that a measure of total primary productivity was one of the better correlates of body size in mammalian carnivores, especially in areas of lower primary productivity. Greater availability of energy was believed to be correlated with increased body size because body size must be maintained by a sufficient food supply. In addition, Fuentes & Jaksic (1979) found that interspecific interactions in Chilean foxes (*Pseudalopex* Burmeister) were correlated with body size and could overrule latitudinal tendencies predicted by Bergmann's rule, annual precipitation, or average size of potential prey.

Results of our study indicate that there is significant geographic variation in *P. concolor*. In analyses in which some of the characters did not show significant variation (e.g. males of age-class IV–V), these characters were almost always associated with the dentition. This is consistent with the observations of Best & Gay (in press) and those of Young & Goldman (1946), who noted that dental characters were remarkably uniform among subspecies, with only minor differences in size and occlusal relief.

Results of several analyses consistently grouped most samples from South America (excluding the Southern Cone) with those from Mexico. These samples represent areas relatively equidistant from the equator. The combination of these samples from South America and Mexico then grouped apart from the remaining samples from North America. Chile (sample 33) and Argentina (34) sometimes grouped with the samples from North America. This supports Bergmann's rule, because Chile and Argentina are located away from the equator at about the same distance as are most of the North American samples.

Other studies of *P. concolor* also have provided evidence to indicate that Bergmann's rule applies to this species. Young & Goldman (1946) noted that the larger subspecies *P. c. hippolestes*, *P. c. olympus*, and *P. c. missoulensis* occupy sections of the northern part of the range of the species. Similarly, large subspecies such as *P. c. pearsoni*, mark the far southern extension of the species, and between these extremes in latitude smaller pumas, including *P. c. mayensis* of Guatemala, *P. c. costaricensis* of Costa Rica, and *P. c. bangsi* of Colombia, are found. Analyses presented by Anderson (1983) of data from Young & Goldman (1946) generally supported Bergmann's rule. Kurtén (1973) also found that populations of pumas showed clines in size, ascending from a minimum near the equator.

Samples from Florida (sample 21), Arkansas-Louisiana (17), and New England (14) occasionally grouped with samples from South America. This indicated that pumas from these populations were smaller than pumas from most of the rest of the United States and Canada. The samples from Florida and from Arkansas and Louisiana probably represented the subspecies *P. c. coryi*, but recent genetic studies indicate considerable differentiation within the Florida population (Barone *et al.*, 1994). The sample from New England represented *P. c. couguar*. Young & Goldman (1946) noted that the skulls of these two subspecies were similar and individuals were medium in size.

Correlations between size (PCI) and several abiotic variables further supported the contention that pumas adhere to Bergmann's rule, regardless of whether one interprets the rule as an effect of latitude or temperature. Latitude and average annual temperature were highly correlated with size, but in most cases latitude had a higher correlation than temperature. This agrees with Rosenzweig (1968b) who found that temperature and latitude were good predictors of body size in several species of mammalian carnivores (*P. concolor* was not included); he also found that latitude was a better predictor of size than temperature.

The correlations between body size and a number of abiotic variables also supported James' (1970) hypothesis that size is related to a combination of climatic variables, which include temperature and moisture. She stated that small size should be associated with hot-humid conditions and larger size with cooler or drier conditions. Results of our study consistently showed that size is inversely correlated with average annual precipitation and actual annual evapotranspiration, i.e. larger pumas occur in drier areas.

Correlations also were present between size and coefficients of variation for temperature and evapotranspiration. Boyce (1978) argued that seasonality is a major factor selecting for large body size in muskrats and other organisms. During seasonal periods of abundance of resources, natural selection favors individuals with rapid growth to a large size, while concurrently enhancing survivorship through oncoming periods of shortages of resources. Similarly, Geist (1987) suggested that body size is a function of availability of nutrients and energy during periods of growth. His results indicated that in large mammals (*Alopex lagopus* Linnaeus, *Canis lupus* Linnaeus, *Ovibos moschatus* Zimmermann, *Ovis dalli* Nelson, *O. nivicola* Eschscholtz, *Rangifer tarandus* Linnaeus, *Ursus arctos* Linnaeus) body size increased with latitude, but then decreased between 53 and 65°N; thus, small body sizes occurred at the lowest and highest latitudes, where availability of nutrients decreased. Unfortunately, the geographic range of the puma does not extend far enough north to test this hypothesis.

In addition to abiotic variables, other factors have been suggested to be important determinants of body size. Rosenzweig (1966) noted that differences in body size allow similar species of carnivores to coexist, and Gittleman (1985) found that prey size increased with body mass. McNab (1971) stated that a correlation of body size with latitude in carnivores seemed simply to reflect the size of available prey, which in turn is influenced by the distribution of other predators with which they must share the prey. He further stated that in a set of similar carnivores, a positive correlation of size and latitude usually is found in the smaller carnivores beyond the northern limits of distribution of the larger species and represents character displacement along the latitudinal axis of species diversity. McNab (1971) demonstrated that *P. concolor* was smallest within the range of the jaguar (*Panthera onca* Linnaeus), beyond which it increased in size in both North and South America.

Several authors have noted that pumas and jaguars live sympatrically in portions of Central and South America (Schaller & Crawshaw, 1980; Rabinowitz & Nottingham, 1986; Emmons, 1987), but little information is available to elucidate the amount of competition between these two species. Schaller & Crawshaw (1980) determined that pumas and jaguars were sympatric in much of southwestern Brazil.

These species overlapped in size, and male pumas weighed as much as small female jaguars. They also noted that the two species preyed largely on the same species, but avoided each other spatially. In Peru, Emmons (1987) observed jaguars to use riparian areas more than did pumas, suggesting that the two species differed in use of habitats and possibly food habits. A study of the ecology of jaguars in Belize revealed that at least one puma travelled within the ranges of several male jaguars and appeared to be feeding on smaller prey items (Rabinowitz & Nottingham, 1986). Kiltie (1984) cited competitive character displacement as a possible explanation for the constant ratios in maximum gape of *Herpailurus yagouraoundi* (Lacepede), *Leopardus pardalis* (Linnaeus), *P. concolor*, and *Panthera onca*.

Iriate *et al.* (1990) found that food habits of different subspecies of pumas varied with latitude. Subspecies from temperate habitats generally ate larger prey and specialized on a smaller number of prey taxa, whereas, in tropical habitats, pumas preyed on smaller, more varied prey. Large prey represented *c.* 78% of the puma's diet in North America, but the Florida subspecies (*P. c. coryi*) did not follow the North American pattern. For this subspecies, white-tailed deer (*Odocoileus virginianus* Zimmermann) accounted for only 28% of prey in its faeces, the lowest proportion of the diet for all the North American subspecies. The study by Iriate *et al.* (1990) supported the idea of Hornocker (1970) that prey selection by pumas largely depends on availability and vulnerability of prey. Other felids also have been shown to hunt opportunistically (Sunquist & Sunquist, 1989; Johnson *et al.*, 1993). Hornocker (1970) found that pumas in Idaho killed equal numbers of elk (*Cervus elaphus* Linnaeus; 175 kg) and mule deer (*Odocoileus hemionus* Rafinesque; 64 kg), although mule deer were more abundant. Elk apparently were more vulnerable in the winter when they were forced into terrain offering ideal hunting conditions for pumas. In southwestern Florida, feral hogs (*Sus scrofa* Linnaeus) were the most common prey of pumas (Maehr *et al.*, 1990). Iriate *et al.* (1990) suggested that the high incidence of feral hogs and nine-banded armadillos (*Dasypus novemcinctus* Linnaeus) in the diet of pumas in Florida was due to the noisy foraging and slow escape behaviours of these species.

Van Valkenburgh & Ruff (1987) have suggested that shape of canines reflects the forces produced during killing and feeding. The typical kill by a felid results from one of the canine teeth entering between two neck vertebrae, forcing them apart and breaking the spinal cord. The canines in different species are specifically adapted in size and shape to deal in this way with the neck vertebrae of their principal prey species (Ewer, 1973). Although results of our study showed no geographic variation in some of the dental characters, these characters mostly were related to the cheek teeth. Significant geographic variation was shown for most characters associated with the canines.

Our observations of geographic variation in size of *P. concolor* show trends consistent with Bergmann's rule. The variation in size also is correlated with precipitation, and thus is consistent with the hypothesis as stated by James (1970). However, size has a greater correlation with latitude and temperature than with precipitation variables. Size also is correlated with size of prey (Iriate *et al.*, 1990), and seems to be influenced by the presence of the jaguar (McNab, 1971). Thus, it appears that a combination of climatic and biotic factors are contributing to patterns of geographic variation in size of *P. concolor* in North and South America.

ACKNOWLEDGEMENTS

This paper was extracted from a graduate thesis (Gay, 1994) submitted in partial fulfillment of the Master of Science in Zoology at Auburn University. 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 thank the individuals maintaining personal collections and the curatorial personnel of the following institutions for allowing access to specimens in their care: Allen E. Anderson, Montrose, CO; Alberta Fish and Wildlife Service, Edmonton, Alberta, and Calgary, Alberta, Canada; Arizona Department of Game and Fish, Phoenix, AZ; University of Alberta, Edmonton, Alberta, Canada; American Museum of Natural History, New York, NY; Academy of Natural Sciences, Philadelphia, PA; Provincial Museum of Alberta, Edmonton, Alberta, Canada; Angelo State University, San Angelo, TX; Arizona State University, Tempe, AZ; Arkansas State University, Jonesboro, AR; University of Arizona, Tucson, AZ; British Columbia Provincial Museum, Victoria, British Columbia, Canada; Bell Museum, University of Minnesota, Minneapolis, MN; British Museum (Natural History), London, United Kingdom; Ball State University, Muncie, IN; California Academy of Sciences, San Francisco, CA; College of Idaho and Idaho Department of Game and Fish, Caldwell, ID; Carnegie Museum of Natural History, Pittsburg, PA; Condon Museum of Geology, University of Oregon, Eugene, OR; Colorado State University, Fort Collins, CO; California State University, Sacramento, CA; Cameron University, Lawton, OK; Delaware Museum of Natural History, Greenville, DL; Denver Museum of Natural History, Denver, CO; Fort Collins Field Station Museum, National Fish and Wildlife Laboratory, Fort Collins, CO; Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; Field Museum of Natural History, Chicago, IL; Florida State Museum, Gainesville, FL; Oregon State University, Corvallis, OR; Harold E. Broadbooks, Edwardsville, IL; Humboldt State University, Arcata, CA; Earlham College, J. Moore Museum, Richmond, IN; Kelowna Centennial Museum, Kelowna, British Columbia, Canada; University of Kansas, Museum of Natural History, Lawrence, KS; Los Angeles County Museum of Natural History, Los Angeles, CA; California State University, Long Beach, CA; Louisiana State University, Baton Route, LA; Museo Civico de Storia Naturale, Genova, Italy; Museum of Comparative Zoology, Harvard University, Cambridge, MA; Montana Department of Game and Fish, Bozeman, MT; Museum d'Histoire Naturelle, Geneva, Switzerland; Museum National d'Histoire Naturelle, Paris, France; M.L. Bean Museum, Brigham Young University, Provo, UT; Manitoba Museum of Man and Nature, Winnipeg, Manitoba, Canada; Mississippi Museum of Natural Science, Jackson, MS; Museum of Northern Arizona, Flagstaff, AZ; Museum fur Naturkunde der Humboldt Universitat, Berlin, Germany; Michigan State University, East Lansing, MI; University of Montana, Missoula, MT; Museum of Vertebrate Zoology, University of California, Berkeley, CA; Midwestern State University, Wichita Falls, TX; National Museum of Canada, Ottawa, Ontario, Canada; New Mexico State University, Las Cruces, NM; Naturhistoriska Riksmuseet, Stockholm, Sweden; Oklahoma State University, Stillwater, OK; Yale University, Peabody Museum, New Haven, CN; University of Puget Sound, Tacoma, WA; Royal Ontario Museum, Toronto, Ontario, Canada; Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; Santa Barbara Museum of Natural History, Santa Barbara, CA; San Diego Natural History Museum, San Diego, CA; San Francisco State University, San Francisco, CA; Strecker Museum, Baylor University, Waco, TX; Saskatchewan Museum of Natural History, Regina, Saskatchewan, Canada; Staatliches Museum fur Naturkunde, Stuttgart, Germany; Sul Ross State University, Alpine, TX; Shippensburg State College, Shippensburg, PA; Southwest Research Station, American Museum of Natural History, Portal, AZ; Texas Cooperative Wildlife Collection, College Station, TX; Texas Memorial Museum, University of Texas, Austin, TX; Texas Tech University, Lubbock, TX; University of British Columbia, Vancouver, British Columbia, Canada; University of California, Davis, CA; University of California, Los Angeles, CA; University of Colorado, Boulder, CO; University of Connecticut, Storrs, CN; University of California, Santa Barbara, CA; University of Illinois, Urbana, IL; University of Kentucky, Lexington, KY; University of Missouri, Columbia, MO; University of Michigan Museum of Zoology, Ann Arbor, MI; University of Nebraska State Museum, Lincoln, NB; University of New Mexico Museum of Southwestern Biology, Albuquerque, NM; United States National Museum of Natural History, Washington, DC; Utah State University, Logan, UT; University of Texas at El Paso, El Paso, TX; Vertebrate Paleontology Lab, Balcones Research Center, Austin, TX; University of Utah, Salt Lake City, UT; University of Vermont, Burlington, VT; University of Wyoming, Laramie, WY; Washington State University, Pullman, WA; Western New Mexico University, Silver City, NM; Weber State College, Ogden, UT; Zoologisches Institut und Zoologisches Museum, Hamburg, Germany. We also thank G.W. 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 for preparing Figure 1, T. Rodriguez for preparing Figure 2 and the figures of dendrograms, and G.D. Baumgardner, R.S. Boyd, G.W. Folkerts, N.R. Holler, B.D. Patterson, and L.C. Wit for critically evaluating an early draft of the manuscript. This is journal article no. 15-944871 of the Alabama Agricultural Experiment Station.

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