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GEOGRAPHIC VARIATION IN SEXUAL DIMORPHISM OF THE PUMA (*PUMA CONCOLOR*) IN NORTH AND SOUTH AMERICA

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ABSTRACT—Because of its extensive range and the diverse habitats occupied in North and South America, the puma (*Puma concolor*) is an excellent animal in which to document the presence of sexual dimorphism in size, elucidate the pattern of geographic variation in secondary sexual dimorphism in size, and examine the relationship between geographic variation in sexual dimorphism and environmental components, including sympatric taxa. The dataset included 14 cranial and 5 mandibular measurements for 1,201 pumas. Of the 19 morphologic characters, all exhibited secondary sexual dimorphism in size; males were significantly larger than females. No apparent pattern of geographic variation in sexual dimorphism was detected, and none of the environmental variables was correlated with sexual dimorphism. Because none of the broad patterns of environmental variation coincided with the pattern of variation in sexual dimorphism, the causes of sexual dimorphism likely are associated with intraspecific and interspecific interactions. Sexual selection seems to be the most probable explanation for secondary sexual dimorphism in size of the puma.

The puma (*Puma concolor*) is a variable and wide-ranging species; about 30 subspecies generally are recognized (Young and Goldman, 1946). Pumas not only are found in cold-mountainous regions, but also in humid-tropical lowlands and grasslands. The original range of the puma extended from northern British Columbia to southern Chile and Argentina, and from coast to coast in North America (Young and Goldman, 1946). Loss of habitat and persecution by humans have greatly reduced its range. In North America, the present range generally is restricted to mountainous and relatively unpopulated areas, with the largest populations occurring in the western United States and Canada; only small isolated populations exist in eastern North America. In Central and South America, relatively little is known about its ecology and population dynamics (Currier, 1983). However, even with its reduced range, the puma is the most widely ranging native mammal in the Americas, excepting humans (Turbak, 1987). Because of its extensive range and the diverse habitats it occupies, the puma is an excellent animal in which to study geographic variation in sexual dimorphism.

Previous studies of the puma have shown significant sexual dimorphism in size (Goldman, 1946; Kurtén, 1973; Anderson, 1983; Maehr and Moore, 1992; Best and Gay, in press), but none has attempted to elucidate broad geographic patterns in sexual dimorphism. Clutton-Brock and Harvey (1977) have suggested that larger species have fewer competitors, thus relaxing constraints on increasing size of males imposed by the presence of larger species in similar niches. This would allow sexual selection for competitive ability of males to produce relatively larger increases in sizes of males. If this is true, the degree of sexual dimorphism in pumas should be greater in areas where the puma is the largest carnivore. The purposes of our study were to document the presence of sexual dimorphism in size, elucidate the pattern of geographic variation in secondary sexual dimorphism in size, and examine the relationship between geographic variation in sexual dimorphism and environmental components (including sympatric taxa) associated with the puma in North and South America.

MATERIALS AND METHODS—The dataset included 14 cranial and 5 mandibular characters (Fig. 1), measured to the nearest 0.1 mm with dial calipers, for

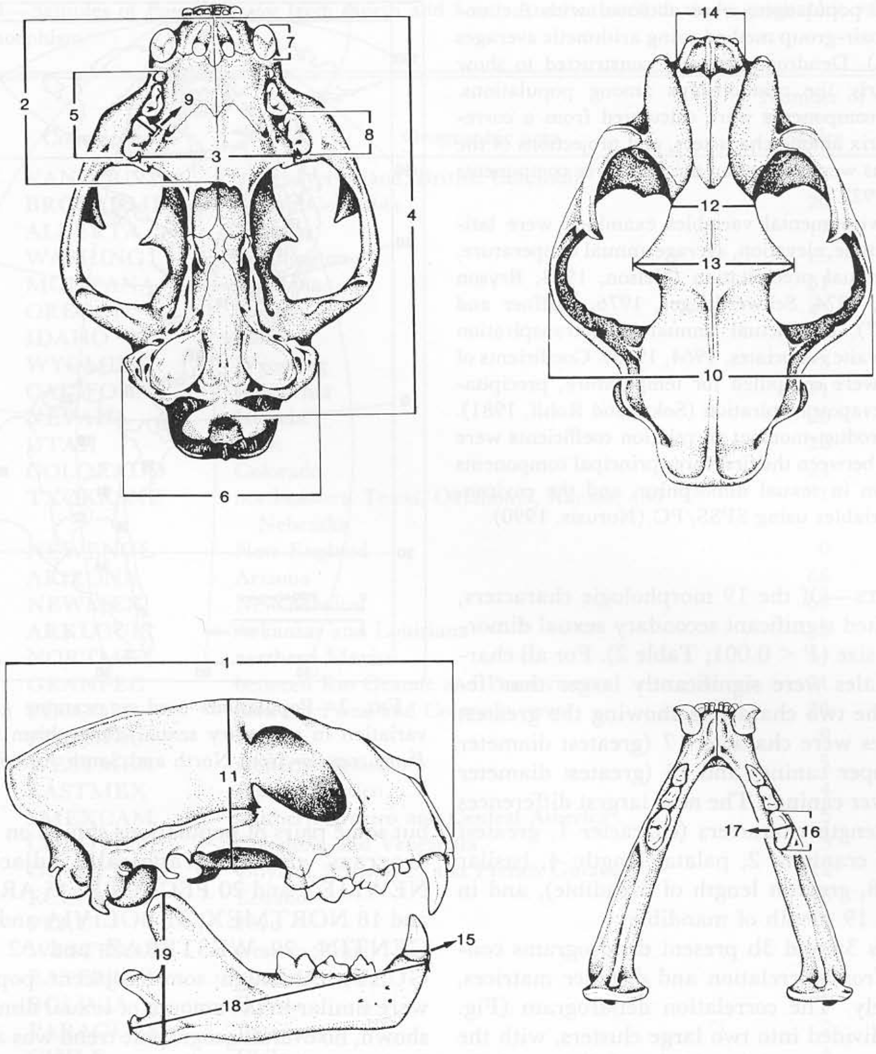

FIG. 1—Cranial, tooth, and mandibular measurements used to examine morphometric variation in *Puma concolor* from North and South America. Names of characters are listed in Table 2.

1,201 pumas (Table 1; a complete list of specimens examined is in Gay, 1994). Only adult specimens that had fully extended canines (D. Ashman, in litt.) were included. One-way analysis of variance (Norusis, 1990) was used to determine if all males and all females differed for each character. Specimens then were divided into 34 populations 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). However, because many specimens had little specific information about collecting locality, most populations were delineated by political boundaries to increase sample sizes. A listing of the populations, abbreviations, and the numbers of males and females in each population is given in Table 1. Population 14 had no individuals in which the gender was known, but it was included in the table to maintain uniformity in population numbers between this study and studies of age variation and geographic variation in cranial morphology (Gay, 1994).

To address geographic variation in sexual dimorphism, averages for each character in each population were calculated using SPSS/PC (Norusis, 1990) and the means for females were subtracted from those of males. The resulting data matrix was standardized so that each population had a mean of 0 and a standard deviation of 1 (Rohlf, 1992). Correlation and distance matrices (Sneath and Sokal, 1973) were calculated and clusters of populations were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Dendrograms were constructed to show more clearly the relationships among populations. Principal components were calculated from a correlation matrix among characters, and projections of the populations were plotted on the first three components (Rohlf, 1992).

The environmental variables examined were latitude, longitude, elevation, average annual temperature, average annual precipitation (Nelson, 1968; Bryson and Hare, 1974; Schwerdtfeger, 1976; Ruffner and Bair, 1987), and actual annual evapotranspiration (Thornthwaite Associates, 1964, 1965). Coefficients of variation were computed for temperature, precipitation, and evapotranspiration (Sokal and Rohlf, 1981). Pearson product-moment correlation coefficients were calculated between the first three principal components of variation in sexual dimorphism and the environmental variables using SPSS/PC (Norusis, 1990).

RESULTS—Of the 19 morphologic characters, all exhibited significant secondary sexual dimorphism in size ($P < 0.001$; Table 2). For all characters, males were significantly larger than females. The two characters showing the greatest differences were characters 7 (greatest diameter of the upper canine) and 15 (greatest diameter of the lower canine). The next largest differences were in length characters (character 1, greatest length of cranium; 2, palatal length; 4, basilar length; 18, greatest length of mandible), and in character 19 (depth of mandible).

Figures 3a and 3b present dendrograms constructed from correlation and distance matrices, respectively. The correlation dendrogram (Fig. 3a) was divided into two large clusters, with the upper cluster containing 13 populations and the lower cluster containing 20 populations. Each cluster contained a mixture of populations from North and South America, populations from eastern and western parts of the range, populations from near the equator, and populations distant from the equator. Thus, there was no consistent geographic pattern in this dendrogram, although there were three pairs of populations on the dendrogram that were geographically contiguous (i.e., 22 WESTMEX and 24 SMEXCAM, 29 WESTBRAZ and 32 PARAGUAY, 2 BRCOLUMB and 3 ALBERTA), and there was one group of three contiguous populations (9 CALIFORN, 15 ARIZONA, and 18 NORTMEX). The distance dendrogram (Fig. 3b) contained no large clusters that exhibited geographic affinities, but some pairs of populations shown on the dendrogram were geographically adjacent (16 NEWMEX and 20 PECCOLR; 15 ARIZONA and 18 NORTMEX; 31 BOLIVIA and 34 ARGENTIN; 29 WESTBRAZ and 32 PARAGUAY). Although some adjacent populations were similar in the amount of sexual dimorphism shown, no overall geographic trend was apparent in the correlation or distance dendrograms.

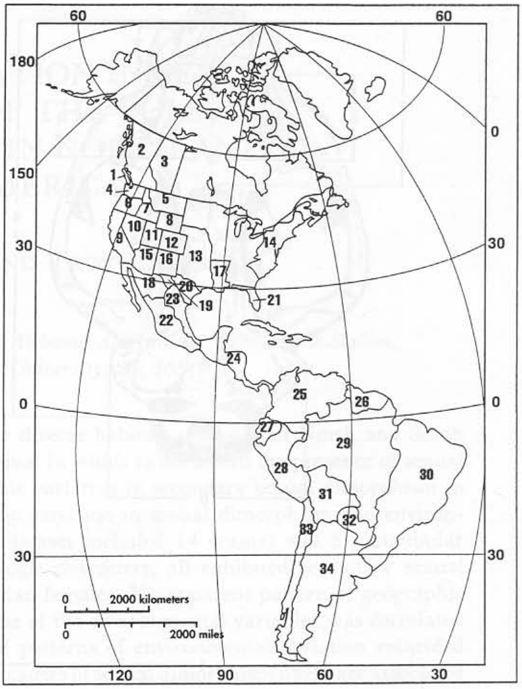

FIG. 2—Populations used to examine geographic variation in secondary sexual dimorphism in size of *Puma concolor* from North and South America.

The loadings of characters on the first three principal-component axes are presented in Table 3 and three-dimensional projections are depicted in Fig. 4. The character correlations with principal component I (PCI) were high (>0.500) for all characters, but characters 1 (greatest length of cranium) and 18 (greatest length of mandible) had loadings >0.900. PCI accounted for ca. 62% of the phenetic variation. Following the reasoning of Johnston and Selander (1971) and Niles (1973) this component may be taken to represent overall size in both sexes, because it accounted for most of the covariation among characters. On PCII, the highest loadings (>0.400) were for characters 5 (length of alveolar toothrow), 7 (greatest diameter of upper canine), 8 (greatest length of

TABLE 1—Samples of *Puma concolor* from North and South America used to study geographic variation in sexual dimorphism.

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

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); these were characters of the dentition. PCII accounted for ca. 14% of the phenetic variation. PCIII had the highest loadings (>0.400) for characters 2 (palatal length), 13 (supraorbital width), and 15 (greatest diameter of lower canine), and accounted for ca. 6% of the phenetic variation. Thus, the three components explained ca. 82% of the total character variation (Table 3), indicating that most of the variation was represented in the first three principal-component axes.

A three-dimensional plot of populations onto the first three principal-component axes is shown in Fig. 4. PCI was represented along the X-axis; populations with the most secondary sexual dimorphism in size were placed on the left side of the graph, e.g., 23 EASTMEX and 33 CHILE. The least secondary sexual dimorphism in size was shown on the right side by 13 TXOKKSNE. In this population, females were larger than males for nine of the 19 characters.

TABLE 2—Secondary sexual dimorphism in size of 19 cranial and mandibular characters of specimens of known gender of *Puma concolor* from North and South America. Dimensions are in mm; asterisks indicate characters that exhibit significant secondary sexual dimorphism in size ($P < 0.001$).

Char. no.	Character	Character averages: Males	Character averages: Females	Analysis of variance: *d.f.*	Analysis of variance: *F*-ratio
1	Greatest length of cranium	203.2	184.6	1,1087	684.3*
2	Palatal length	75.4	68.6	1,1124	679.6*
3	Intermaxillary width	66.8	62.8	1,1137	279.6*
4	Basilar length	164.7	150.1	1,1050	607.3*
5	Length of alveolar toothrow	43.2	40.6	1,1188	486.6*
6	Mastoidal width	85.0	77.5	1,1018	565.0*
7	Greatest diameter of upper canine	13.9	12.1	1,1162	845.9*
8	Greatest length of third upper premolar	23.4	22.1	1,1174	419.0*
9	Greatest width of third upper premolar	11.9	11.1	1,1192	394.3*
10	Zygomatic width	139.5	126.4	1,1070	506.8*
11	Depth of cranium	74.3	68.1	1,1131	473.3*
12	Interorbital width	40.9	37.1	1,1162	267.5*
13	Supraorbital width	72.5	69.0	1,1087	108.1*
14	Nasal width	34.1	30.6	1,1076	381.8*
15	Greatest diameter of lower canine	13.4	11.7	1,1146	860.0*
16	Greatest length of lower molar	17.3	16.2	1,1159	361.8*
17	Greatest width of lower molar	8.3	7.8	1,1168	392.0*
18	Greatest length of mandible	138.8	125.8	1,1155	619.8*
19	Depth of mandible	67.6	59.2	1,1158	624.5*

PCII is shown along the Y-axis in Fig. 4. This principal component generally appeared to be positively correlated with cranial characters and negatively correlated with dental characters; populations with higher loadings on PCII showed more secondary sexual dimorphism in cranial characters and those with lower loadings on PCII showed more secondary sexual dimorphism in dental characters. However, the direction of increasing sexual dimorphism on this axis is unclear. For example, the differences between genders for 23 EASTMEX were smaller than between genders of 33 CHILE for characters 5 (length of alveolar toothrow) and 7 (greatest diameter of upper canine), but was larger for characters 16 (greatest length of lower molar) and 17 (greatest width of lower molar). The opposite occurs for 32 PARAGUAY and 24 SMEXCAM. Here differences between genders for 32 PARAGUAY were larger than between genders of 24 SMEXCAM for characters 5 (length of alveolar toothrow) and 7 (greatest diameter of upper canine) and differences between genders were smaller for characters 16 (greatest length of lower molar) and 17 (greatest width of lower molar). Differences between genders for 29 WESTBRAZ were larger than between genders of 7 IDAHO for characters 5 (length of alveolar toothrow), 7 (greatest diameter of upper canine), and 16 (greatest length of lower molar) and were the same for character 17 (greatest width of lower molar). Thus, this axis did not seem to be a reliable indicator of differences between genders among the populations, because it was difficult to determine in which direction the amount of secondary sexual dimorphism increased.

PCIII is depicted along the Z-axis in Fig. 4. Sexual dimorphism increased from bottom to top on this axis, but caution should be used in interpreting this axis. Comparisons of populations on this axis are best accomplished among populations that are in proximity to each other based on the X- and Y-axes, because of the greater variation explained by the first two axes. For example, 8 WYOMING showed more sexual dimorphism than 31 BOLIVIA, but 31 BOLIVIA showed more sexual dimorphism than 17 ARKLOUIS.

The Pearson product-moment correlation coefficients calculated between the first three principal components of secondary sexual dimorphism in size and nine environmental variables are listed in Table 4. None of the correlations was significant ($P > 0.05$).

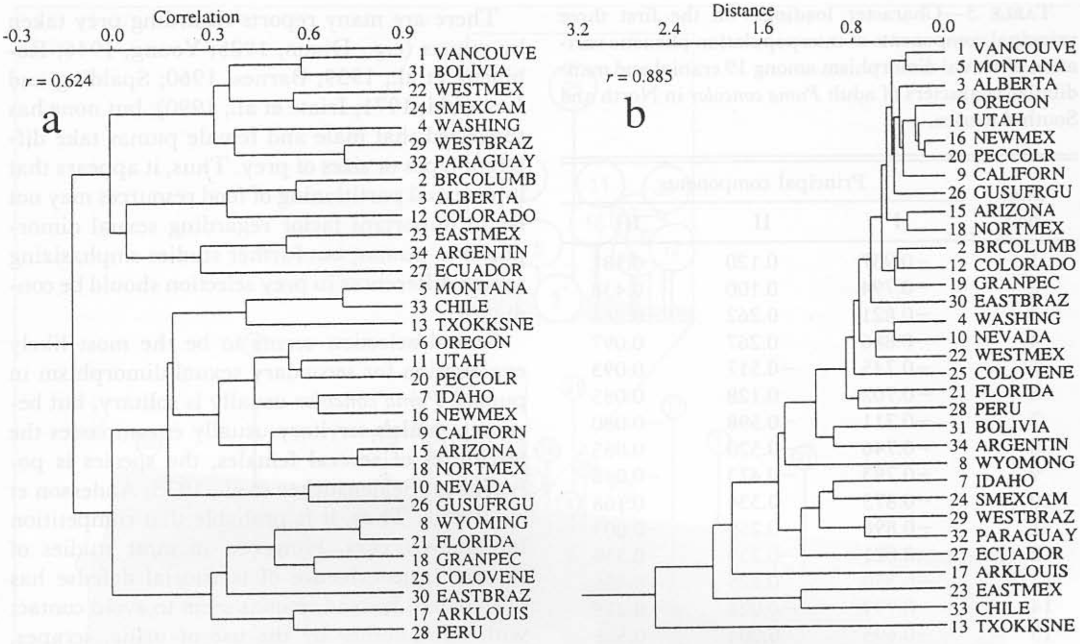

FIG. 3—Correlation (a) and distance (b) dendrograms based on secondary sexual dimorphism in size of *Puma concolor* from North and South America. Accuracy of the diagrams in depicting interpopulation relationships increase from left to right. Cophenetic correlation coefficients (*r*) are provided for each dendrogram. Numerical identifications and code names are the same as listed in Table 1.

DISCUSSION—Males and females differed significantly for each of the 19 characters examined. These results support previous reports of sexual dimorphism in the puma (Goldman, 1946; Kurtén, 1973; Anderson, 1983; Maehr and Moore, 1992; Best and Gay, in press). The characters with the greatest differences were greatest diameter of upper canine (character 7) and greatest diameter of lower canine (15). This is similar to the findings of Kurtén (1973), where the greatest differences were in size of canines and interorbital width. In our study, sexual dimorphism was no greater for interorbital width than for most other characters.

Two of the most commonly cited explanations for sexual dimorphism are niche partitioning (Selander, 1966; Schoener, 1977; Slatkin, 1984) and sexual selection (Schoener, 1977; Slatkin, 1984; Gould and Gould, 1989; Payne, 1984). In niche partitioning, intersexual competition for food causes sexual dimorphism to evolve to allow the sexes to exploit different food resources. Sexual selection usually involves competition between males for mates. This presumably would increase size of males so they might become more successful competitors. Also, defense of a territory often involves selective advantages for larger size in males and may be associated with pronounced sexual dimorphism in size favoring males (Ralls, 1977).

Kennedy and Schnell (1978) found geographic variation in width of third molars in the Ord kangaroo rat (*Dipodomys ordii*) and suggested that the variability might be related to intersexual competition for food. Giannico and Nagorsen (1989) found that in martens (*Martes americana*) the increased morphologic distance between the sexes may promote different feeding niches and reduce intersexual competition. Selander (1966) presented evidence of an adaptive function of sexual dimorphism in size in two species of woodpeckers (*Centurus aurifrons* and *C. striatus*) by relating degrees of morphologic and sexual divergence in foraging behavior. Dayan et al. (1990) found each of three sympatric small felids (*Caracal caracal, Felis chaus,* and *F. silvestris*) in Israel to be strongly sexually dimorphic for average diameter of canines. Treating each gender as a morphospecies, they found that the size ratios between adjacent morphospecies in a size-ranking was re-

TABLE 3—Character loadings[a] on the first three principal components of interpopulation phenetic variation of sexual dimorphism among 19 cranial and mandibular characters of adult *Puma concolor* in North and South America.

Char. no.[b]	Principal components I	II	III
1	−0.937	0.120	0.181
2	−0.794	0.100	0.438
3	−0.821	0.262	−0.264
4	−0.886	0.267	0.097
5	−0.745	−0.517	0.093
6	−0.702	0.128	0.085
7	−0.711	−0.598	−0.080
8	−0.746	−0.520	0.085
9	−0.793	−0.473	−0.048
10	−0.873	0.334	0.168
11	−0.896	0.259	−0.003
12	−0.821	0.239	−0.350
13	−0.550	0.625	−0.456
14	−0.799	−0.021	0.217
15	−0.695	0.004	−0.558
16	−0.698	−0.472	−0.208
17	−0.627	−0.575	−0.162
18	−0.915	0.199	0.208
19	−0.843	0.355	0.214
Total[c]	62.10	13.92	6.37

[a] Correlations between the average values of individual characters and the component axes.

[b] Character numbers correspond to the list of characters in Table 2.

[c] Percent of total phenetic variance explained.

markably equal and suggested that intraspecific and interspecific competition for food had selected for these equal ratios of size of canines. However, they also noted that an alternative hypothesis would entail ethologic interactions mediated by display or use of canines in fighting. Similar results were found in a study of mustelids (*Mustela erminea, M. frenata,* and *M. nivalis*) in North America (Dayan et al., 1989). Conversely, Ralls and Harvey (1985), in studying the same species of mustelids, suggested that the principal cause of sexual dimorphism in *M. erminea* and *M. frenata* was sexual selection for large size in males. They also found no evidence of character displacement between any pairs of species. Likewise, Kennedy and Lindsay (1984) and Ritke (1990) have suggested that sexual dimorphism in the raccoon (*Procyon lotor*) probably is related to intraspecific defense of territories, rather than intersexual partitioning of resources.

There are many reports regarding prey taken by pumas (e.g., Dixon, 1925; Young, 1946; Robinette et al., 1959; Barnes, 1960; Spalding and Lesowski, 1971; Iriate et al., 1990), but none has suggested that male and female pumas take different types or sizes of prey. Thus, it appears that intersexual partitioning of food resources may not be an important factor regarding sexual dimorphism in pumas, but further studies emphasizing sexual differences in prey selection should be conducted.

Sexual selection seems to be the most likely explanation for secondary sexual dimorphism in pumas. *Puma concolor* usually is solitary, but because a male's territory usually encompasses the territories of several females, the species is polygynous (Seidensticker et al., 1973; Anderson et al., 1992). Thus, it is probable that competition for mates occurs. However, in most studies of pumas, little evidence of territorial defense has been noted. Instead, pumas seem to avoid contact with one another by the use of urine, scrapes, scratches in suitable substrate, and scent from anal or other glands (Hornocker, 1969; Seidensticker et al., 1973). Hornocker (1969) emphasized that because pumas are solitary, and thus must obtain food by themselves, pumas cannot afford the luxury of a potentially damaging agonistic encounter. However, fighting between mature male pumas has been noted (Grinnell et al., 1937; Lesowski, 1963; Henberg, 1994), and Sweanor (1990) found intraspecific fighting and killings as the highest mortality factor of pumas in her study area in New Mexico. Bailey (1974) has suggested that for bobcats (*Lynx rufus*) most male–male competition may be for territories and subsequent access to associated females, even though overt defense of areas is believed to be minimal or absent. Some other carnivores also hold territories, but show minimal overt defense of these territories (Lockie, 1966; Erlinge, 1968; Gerrell, 1970).

In addition to our determination that characters exhibiting the most sexual dimorphism in size were greatest diameters of upper and lower canines, sexual dimorphism in size of canines also occurs in many other mammals, e.g., raccoons (*Procyon lotor*—Grau et al., 1970), black bears (*Ursus americanus*—Rausch, 1961; Sauer, 1966), and some primates (Garn et al., 1966). Ritke (1990) suggested that wider canines should help prevent breakage during combat. Also, threat behavior is based, among other things, on display

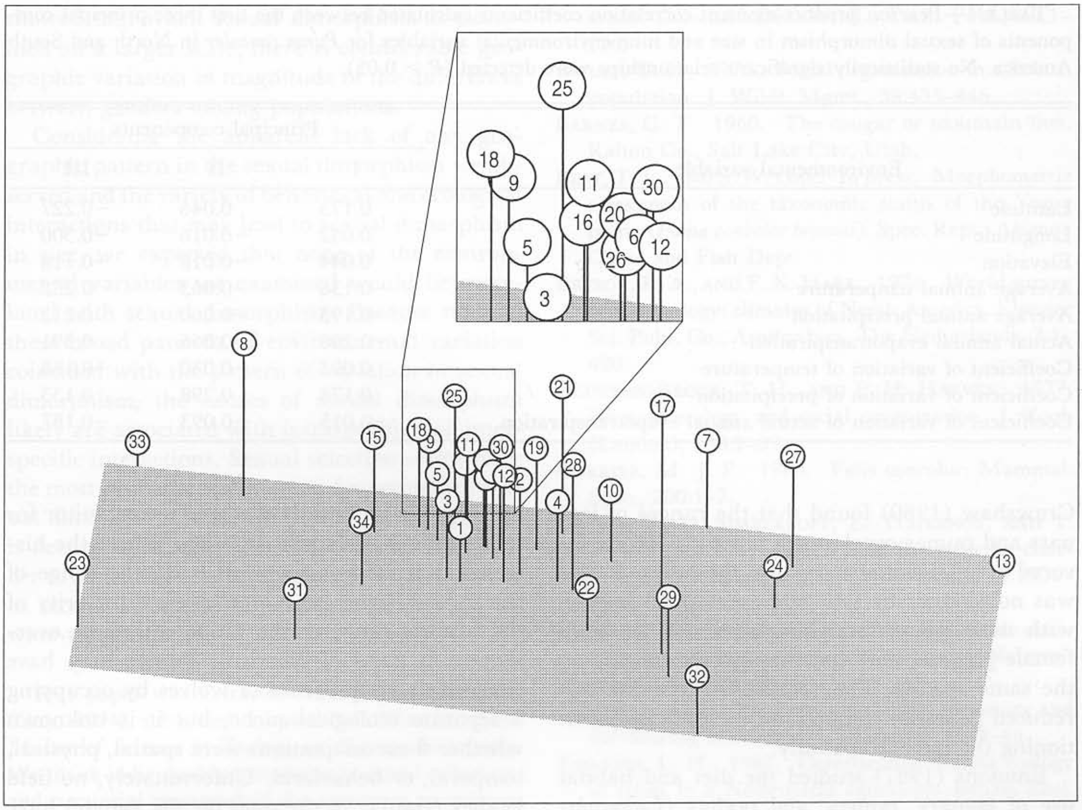

FIG. 4—Three-dimensional plot of the first three principal components of sexual dimorphism in size for *Puma concolor* in North and South America.

of the weapons used in attack. In carnivores, at least part of such behavior consists of showing the teeth by opening the mouth and, in some species, by a stylized raising of the lip to bare the canine teeth (Ewer, 1973). It is possible that a large amount of secondary sexual dimorphism in size of canines could result from some form of sexual selection mediated by display of canines or by fights involving the canines (Dayan et al., 1989). In pumas, this type of threat behavior could be important in avoiding actual combat.

Clutton-Brock and Harvey (1977) suggested that larger species have fewer competing species, thus relaxing constraints on increasing size of males imposed by the presence of larger species in similar niches. This would allow sexual selection for competitive ability of males to produce relatively larger increases in size of males. Pumas are the largest felid competitor, except where jaguars (*Panthera onca*) exist. It has been reported that in Belize, at least one puma travelled within the ranges of several male jaguars and appeared to be feeding on smaller prey items (Rabinowitz and Nottingham, 1986). If Clutton-Brock and Harvey's (1977) suggestion applies to pumas, then the degree of sexual dimorphism in pumas should be reduced in areas where the puma coexists with the jaguar. The jaguar's past range includes all the study localities of South America, Central America, and Mexico as well as 9 CALIFORN, 15 ARIZONA, 16 NEWMEX, 20 PECCOLR, 13 TXOKKSNE, and 17 ARKLOUIS. It does not appear that this factor significantly contributes to geographic variation in sexual dimorphism, because these populations do not group together, and in fact 23 EASTMEX and 33 CHILE show the most sexual dimorphism in size (Fig. 4).

Although Rabinowitz and Nottingham (1986) suggested that pumas and jaguars might be taking different sized prey, other studies have indicated that pumas and jaguars take mostly the same prey species. In studying the movement patterns of jaguars in southwestern Brazil, Schaller and

TABLE 4—Pearson product-moment correlation coefficients calculated between the first three principal components of sexual dimorphism in size and nine environmental variables for *Puma concolor* in North and South America. No statistically significant relationships were detected ($P > 0.05$).

Environmental variable	Principal components I	 II	 III
Latitude	0.173	0.046	−0.227
Longitude	0.052	−0.016	−0.300
Elevation	0.044	−0.018	−0.118
Average annual temperature	−0.136	−0.063	0.252
Average annual precipitation	−0.193	−0.060	0.213
Actual annual evapotranspiration	−0.208	−0.066	0.391
Coefficient of variation of temperature	0.093	−0.030	−0.188
Coefficient of variation of precipitation	0.178	0.298	0.133
Coefficient of variation of actual annual evapotranspiration	−0.015	−0.093	−0.187

Crawshaw (1980) found that the ranges of jaguars and pumas overlapped, but each species favored areas not much used by the other. It also was noted that the two cats overlapped in size, with male pumas weighing as much as small female jaguars, and that they preyed largely on the same species. They concluded that the cats reduced potential competition for prey by partitioning the habitat spatially.

Emmons (1987) studied the diet and habitat use of jaguars, pumas, and ocelots (*Leopardus pardalis*), and populations of their mammalian prey in an undisturbed rainforest in southeastern Peru. Pumas and jaguars weighed about the same in this area, diversity of prey was high, and the felids evidently took any readily captured vertebrate. All three felids seemed to hunt by opportunistic encounter of prey. Jaguars often used waterside habitats, where they captured caimans (*Caiman*) and river turtles (*Podocnemis unifilis*). Pumas did not use these habitats or resources, although the samples of pumas and prey species were too small for much inference. There also was evidence that the big cats avoided each other temporally, both intraspecifically and interspecifically.

Data from Rabinowitz and Nottingham (1986) indicated that pumas rarely were observed where jaguars were abundant. Thus, pumas and jaguars appeared to coexist by avoiding each other both spatially and temporally. This type of avoidance may secondarily result in different prey being taken, as Emmons (1987) noted, but is not the primary factor involved in the partitioning of habitats by pumas and jaguars.

The gray wolf (*Canis lupus*) is similar in size to the puma and may have been a competitor for food in much of North America. Where the historic range of the gray wolf ends, the range of the jaguar begins, and both cover a majority of the historic range of the puma (all three overlapped in parts of Mexico). Pumas may have adapted to the presence of wolves by occupying a separate ecological niche, but it is unknown whether these adaptations were spatial, physical, temporal, or behavioral. Unfortunately, no field studies (similar to the ones on the jaguar) have been conducted where wolves and pumas are sympatric.

In our multivariate analysis, no apparent trend of geographic variation was found in sexual dimorphism in size of pumas (Fig. 4). The population with the least amount of sexual dimorphism (13 TXOKKSNE), grouped apart from the other populations, but the significance of this distinction is questionable because the population covered a large geographic area and contained only three individuals. The three populations with the greatest amount of sexual dimorphism (23 EASTMEX, 33 CHILE, and 8 WYOMING) also grouped apart from the other populations. Most of the remaining populations grouped together near the center of the graph. This tight grouping of the populations indicates that these populations exhibit similar amounts of sexual dimorphism in size. Our study generally supports the findings of Maehr and Moore (1992) who compared body mass of pumas from California, Florida, and Nevada. They found that mass of adults was greater in males than females in all populations, and the size of the difference was similar among populations. However, our results showed that when sexual dimorphism is examined on a larger scale, there is considerable geographic variation in magnitude of the differences between genders among populations.

Considering the apparent lack of any geographic pattern in the sexual dimorphism we observed and the variety of behavioral and ecological interactions that may lead to sexual dimorphism in size, we expected that none of the environmental variables we examined would be correlated with sexual dimorphism. Because none of these broad patterns of environmental variation coincided with the pattern of variation in sexual dimorphism, the causes of sexual dimorphism likely are associated with intraspecific and interspecific interactions. Sexual selection seems to be the most probable explanation for secondary sexual dimorphism in size of pumas. More research is needed concerning prey selection by each gender to assess the relationship of niche partitioning to secondary sexual dimorphism in size of this wide-ranging felid.

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