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Systematic relationships of gray wolves *(Canis lupus)* in southwestern North America

MICHAEL A. BOGAN AND PATRICIA MEHLHOP

Abstract

We examined specimens of five subspecies of gray wolves from southwestern North America and assessed their systematic affinities using both univariate and multivariate statistical procedures. Because wolves exhibit considerable sexual dimorphism the sexes were separated for the analyses. Principal components analyses revealed considerable overlap among the individuals, but tended to separate the Mexican wolf *(C. l. baileyi)* from northern wolves *(C. l. youngi)*. Specimens from other subspecies were intermediate to these two. Discriminant function analyses using various groupings of wolves supported these results. Within the southwestern part of North America, we recognize only three subspecies: *C. l. baileyi, C. l. youngi,* and *C. l. nubilus*. Wolves formerly assigned to *C. l. mogollonensis* and *C. l. monstrabilis* are referred to *C. l. baileyi*. As an adjunct to our study, we compared recently collected specimens and captive animals with target groups from the southwest. Recent specimens show clear affinities with *C. l. baileyi*. Captives, although closest to *baileyi,* show some tendencies toward dogs, but whether these tendencies are from hybridization or from the effects of captivity is unknown.

INTRODUCTION

The gray wolf (*Canis lupus* Linnaeus), once a dominant carnivore in southwestern North America, now is restricted primarily to Alaska, parts of Canada, and a few scattered areas in the northern United States. Goldman (1944) studied the taxonomy of wolves in North America but performed no rigorous analysis of geographic variation among the subspecies he recognized. Hall (1981) followed Goldman's taxonomy.

Jolicoeur (1959) was the first investigator to use multivariate techniques to study variation in wolves. Since then, a number of studies have focused on interspecific relationships among canids, many of them with an emphasis on the status of the red wolf of the southeastern United States (Elder and Hayden, 1977; Freeman and Shaw, 1979; Gipson et al., 1974; Lawrence and Bossert, 1967, 1975; and Nowak, 1973, 1979). Studies of variation in the wolves of Canada include those of Jolicoeur (1959, 1975), Kolenosky and Standfield (1975), Pichette and Voight (1971), and Skeel and Carbyn (1977).

We were prompted to study the systematic status of southwestern wolves because of current interest in captive propagation of wolves that were captured in the southwest. We examined most available specimens of the five subspecies thought to occur in or near the southwest (*C. l. baileyi* Nelson and Goldman 1929, *C. l. mogollonensis* Goldman 1937, *C. l. youngi* Goldman 1937, *C. l. monstrabilis* Goldman 1937, and *C. l. nubilus* Say 1823) to determine variation within and among groups of these animals. We also examined recently collected specimens and examples of the two known breeding stocks to assess their affinities with the historic samples of southwestern wolves.

METHODS AND MATERIALS

We examined skulls of 253 adult specimens of *C. lupus* from Mexico, Arizona, Colorado, Kansas, New Mexico, Oklahoma, and Texas (see Specimens Examined; Fig. 1). Sixteen captive animals alleged to have originated from *C. l. baileyi* stock were then compared with these individuals. Small samples of dogs *(C. familiaris)* and coyotes *(C. latrans)* were also examined, and used in some analyses as reference groups. We selected only those dog skulls that resembled wolf skulls in size and shape. Individuals were considered adults when the basisphenoid–basioccipital suture was closed and the postorbital processes pointed. Complete closure of the basisphenoid–basioccipital suture occurs in gray wolves at 12–14 months (Kolenosky and Standfield, 1975). Nowak (1979) stated that maximum skull size is attained by 15 months.

Most of the skull measurements we initially considered were used in other systematic studies of canids: 16 measurements that Lawrence and Bossert (1967) found most useful (15 of these were used by Skeel and Carbyn, 1977); 27 non-ratio measurements used by Kolenosky and Standfield (1975); and 15 measurements used by Goldman (1944). We chose 24 of these that were

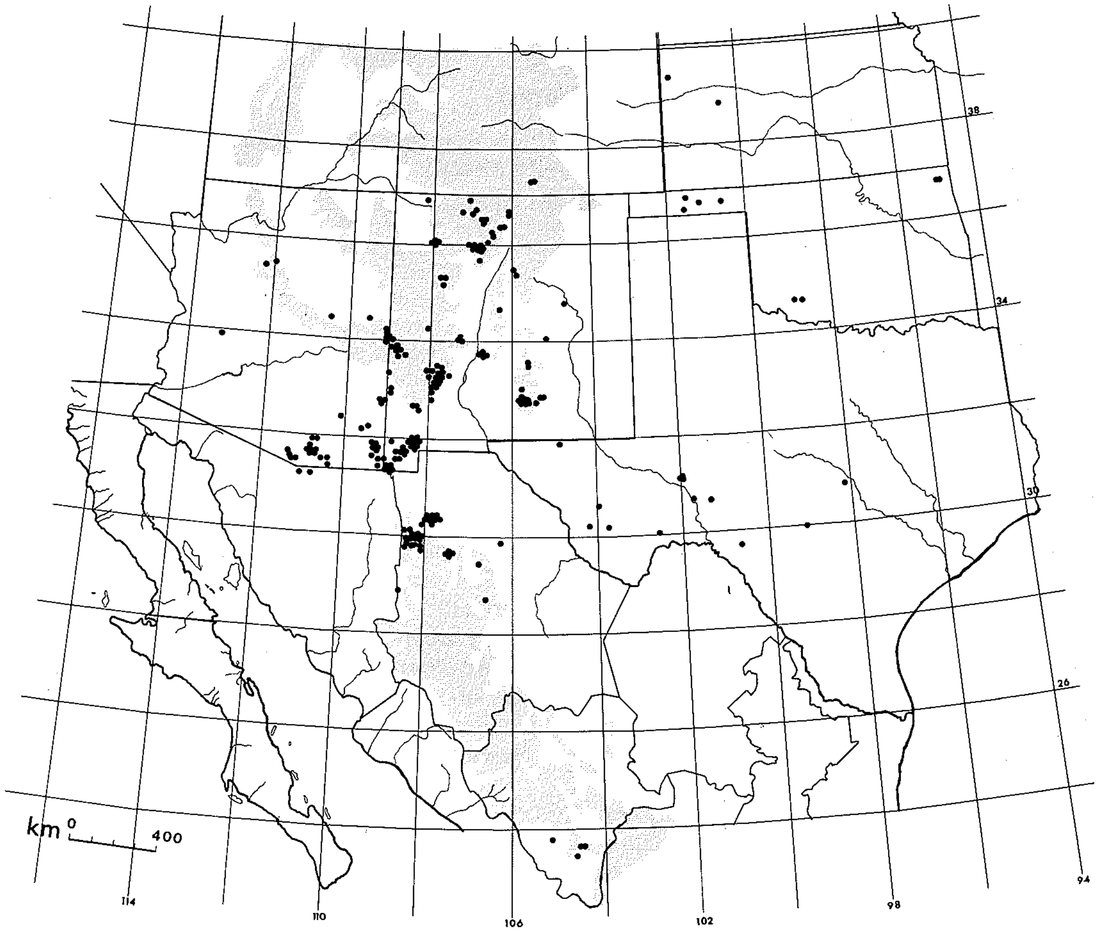

Fig. 1. Localities from which specimens were examined during this study. Three specimens, one each from "Tanks," Arizona; Matamoros, Tamaulipas; and Orizaba, Veracruz, are not mapped (see Discussion). Stippled areas indicate highlands above 2000 m.

not redundant and that were sufficiently well described to be replicable; a few were altered slightly to permit measurement when teeth were missing. We added one character, post–palatal length, to provide a measure of length of the cranium. The following 25 characters were used (abbreviations in parentheses are hereafter used to refer to characters): total length of skull from the posteriormost part of the sagittal crest to alveolus of I^1 (MSL); condylobasal length (CBL); crown length of maxillary tooth row (MTR); distance from posterior edge of palate, excluding posterior projection at midline, to occipital condyles at ventro–medial part of foramen magnum (PPL); maximum zygomatic breadth (ZB); minimum interorbital breadth (IOB); rostral breadth across narrowest part of rostrum, at or just posterior to P^1 (RB1); maximum width across P^4 (RB4); maximum breadth of braincase at parieto–temporal suture (BCB); depth of braincase from base of sagittal crest on antero–medial edge of left parietal to midline of basioccipital (BCD); minimum distance from anterior edge of alveolus of M^1 to orbit (OAD); minimum height of jugal at right angles to axis of bone (JH); depth of ramus taken from posterior edge of alveolus of P_4 to ventral surface of ramus (RD); height of coronoid process taken from ventral edge of angular process to dorsal edge of coronoid process (CPH); length of mandible taken from posterior edge of angular process to alveolus of I_1 (ML); maximum antero–posterior length of upper C at alveolus (CL); crown length of P^4 taken labially (P4UL); minimum crown width of P^4 taken between the roots (P4UW); crown length of M^1 taken labially (M1UL); maximum crown width of M^1 (M1UW); maximum crown width of M^2 (M2UW); crown length of P_4 taken labially (P4LL); minimum crown width of P_4 taken between the roots (P4LW); maximum crown length of M_1 taken labially (M1LL); minimum crown width of M_1 taken between the roots (M1LW). Mehlhop measured all specimens to the nearest 0.1 mm with dial calipers. The left side of the skull was used whenever possible.

No ratios of measurements were used. Skeel and Carbyn (1977) gave reasons for excluding characters based on ratios. By using non–ratio data, size could be used to distinguish the various groups in the analysis. When studying differences both within and among species, size may be an important distinguishing characteristic (Nowak, 1979; Skeel and Carbyn, 1977). We calculated the coefficients of variation by sex for each character. Sexual dimorphism in gray wolves has been reported by many researchers (Gipson et al., 1974; Jolicoeur, 1959, 1975; Kolenosky and Standfield, 1975; Nowak, 1979). We tested for sexual dimorphism by using stepwise discriminant function analyses with known males and females for each of the five subspecies. These same analyses were used to classify specimens of unknown sex within each subspecies. Males and females of each subspecies were significantly different (F–tests, $P < 0.05$). All further analyses were therefore made with the sexes separated.

We performed principal components analyses (PCA) on the correlation matrix of standardized characters using the NT–SYS computer programs developed by Rohlf et al. (1972). Skeel and Carbyn (1977) discussed this type of analysis. The multivariate analysis of variance used the ANOVA computer procedure of the Statistical Analysis System (SAS; Helwig and Council, 1979). Statistically significant differences among groups were determined with a Duncan multiple range test. To compare groups of wolves, we used the stepwise discriminant function analysis (DFA) from the Biomedical Computer Programs, (BMD07M; Dixon, 1973). This procedure has been described and discussed by Lawrence and Bossert (1967). Specimens with missing characters were excluded from all analyses.

Skins of 37 individuals of five subspecies were examined to determine if geographic differences were apparent. Twelve quantitative and qualitative characters were selected based on subspecies differences described by Goldman (1944). Winter pelage appeared to be as variable within subspecies groups and small geographic areas as it was among subspecies groups. Summer pelage varied as much as winter pelage among individuals of *C. l. baileyi*. Although geographic differences in pelage may exist, overlap is too great to warrant use of skins for subspecific designations within our study area.

RESULTS

Univariate Analyses.

Basic statistics for nine groups of males and seven groups of females are presented in Table 1. A one–way ANOVA testing the null hypothesis

Table 1. Means and standard deviations (in parentheses) of variables for each geographic group of *Canis lupus* used in this study. Sexes were analyzed separately. Parentheses following group name contain the group sample size.

	MALES								
Variable	Northern New Mexico(15)	Mogollon Plateau(26)	Southern Arizona(6)	Animas Valley(16)	Western Chihuahua(15)	Sacramento Mountains(4)	Texas(9)	Oklahoma(5)	New Mexico Plains(5)
MSL	244.4(8.9)	243.8(9.8)	238.6(9.4)	238.0(6.9)	238.4(6.8)	248.0(10.5)	245.2(13.2)	245.8(11.7)	248.1(4.7)
CBL	232.0(6.7)	226.5(7.9)	220.1(7.9)	222.6(6.1)	223.3(5.2)	229.8(10.7)	228.8(10.4)	229.7(8.7)	225.1(10.9)
MTR	103.1(4.7)	102.0(4.2)	99.0(4.0)	99.6(2.8)	100.1(2.7)	103.3(5.2)	103.1(4.4)	103.6(3.4)	104.4(2.9)
PPL	96.9(3.6)	96.2(2.8)	95.7(3.4)	95.4(2.6)	95.9(2.8)	97.2(3.6)	96.3(5.7)	96.2(4.4)	96.6(1.4)
ZB	135.8(4.1)	136.2(5.7)	133.9(6.8)	132.6(5.8)	133.8(5.9)	135.2(3.8)	133.0(8.4)	128.7(9.7)	136.0(3.6)
IOB	46.3(2.1)	45.2(3.4)	43.6(2.3)	44.1(2.9)	43.3(2.8)	44.6(1.7)	45.2(3.3)	45.2(3.9)	46.7(2.5)
RB1	46.8(1.5)	43.6(3.0)	40.9(2.3)	41.9(2.4)	41.2(1.7)	44.4(2.5)	42.7(4.3)	43.1(3.2)	44.3(2.2)
RB4	81.6(1.5)	78.8(3.2)	75.3(3.0)	77.2(2.2)	76.7(2.4)	78.8(2.8)	76.1(5.4)	77.8(2.3)	80.5(2.8)
BCB	65.9(1.7)	66.2(2.2)	67.0(1.3)	66.1(2.0)	66.8(2.0)	64.9(2.5)	64.6(2.0)	64.8(2.2)	66.6(3.0)
BCD	60.0(1.2)	59.8(1.6)	59.1(1.5)	60.1(1.1)	60.4(2.3)	59.4(1.3)	59.9(2.8)	60.1(2.2)	61.5(3.0)
OAD	39.6(2.0)	39.7(2.5)	40.4(2.6)	39.2(3.7)	39.3(1.8)	40.0(3.0)	39.0(3.1)	38.4(2.0)	39.8(1.1)
JH	18.8(1.1)	18.7(1.0)	18.7(1.8)	18.1(1.5)	18.7(1.4)	19.4(1.9)	17.4(1.8)	18.2(1.0)	19.1(0.9)
RD	29.3(1.4)	29.5(2.3)	29.5(3.0)	29.2(1.7)	29.4(1.2)	28.1(0.5)	28.4(2.6)	28.6(2.7)	30.6(0.8)
CPH	74.3(3.5)	75.9(3.4)	73.4(2.4)	74.7(3.6)	74.7(3.0)	73.4(3.9)	75.7(3.3)	71.8(4.2)	76.0(3.3)
ML	181.5(5.9)	180.2(7.1)	174.3(6.6)	173.5(6.6)	176.1(5.2)	180.3(4.6)	178.3(7.0)	179.4(8.1)	185.1(3.6)
CL	14.4(0.9)	13.7(1.4)	12.5(1.2)	12.5(1.2)	12.7(0.8)	14.4(1.0)	13.9(1.5)	14.9(1.3)	14.2(0.5)
P4UL	24.6(1.2)	24.8(1.2)	24.0(0.8)	24.3(0.9)	24.5(1.1)	25.8(0.9)	24.5(1.6)	24.7(1.1)	25.1(0.3)
P4UW	10.3(0.7)	10.1(0.8)	9.6(0.5)	10.0(0.5)	9.8(0.5)	10.3(0.7)	10.1(1.1)	10.4(0.6)	10.8(0.5)
M1UL	16.3(0.8)	16.0(1.0)	15.6(1.0)	15.6(0.8)	15.7(0.8)	16.6(0.6)	16.1(0.9)	16.5(0.3)	16.9(0.4)
M1UW	21.7(0.9)	21.4(1.3)	20.5(0.6)	20.9(1.0)	20.8(1.0)	22.4(1.3)	21.2(1.4)	23.7(3.2)	21.9(0.5)
M2UW	13.2(0.8)	13.1(1.0)	12.7(1.1)	12.6(0.8)	12.3(0.5)	13.9(0.8)	12.8(1.0)	13.6(0.3)	12.9(0.3)
P4LL	15.0(0.7)	15.4(0.8)	15.2(1.2)	15.1(0.7)	15.1(0.8)	15.9(1.1)	15.3(1.3)	15.7(0.9)	15.8(0.6)
P4LW	8.2(0.5)	7.8(0.6)	7.4(0.5)	7.5(0.4)	7.6(0.6)	8.1(0.6)	7.8(1.0)	8.0(0.6)	8.3(0.3)
M1LL	29.5(1.5)	28.6(1.6)	26.8(1.2)	27.6(1.3)	27.9(0.9)	29.2(1.4)	28.2(2.1)	28.1(1.6)	29.2(1.1)
M1LW	11.9(0.7)	11.2(0.9)	10.3(0.6)	10.8(0.6)	10.8(0.5)	11.4(1.0)	11.2(1.0)	11.3(0.8)	11.8(0.5)

	FEMALES						
Variable	Northern New Mexico(9)	Mogollon Plateau(18)	Southern Arizona(5)	Animas Valley(7)	Western Chihuahua(11)	Sacramento Mountains(4)	Texas and Oklahoma(5)
MSL	232.4(6.4)	237.4(8.0)	217.2(7.5)	224.4(6.5)	221.6(7.2)	230.8(3.3)	232.4(12.4)
CBL	218.7(4.9)	220.5(6.7)	203.4(5.5)	210.9(4.7)	210.4(7.4)	212.9(4.9)	217.5(12.5)
MTR	99.4(3.0)	100.5(3.2)	91.7(3.6)	94.7(2.2)	95.3(3.6)	95.1(3.1)	98.7(3.4)
PPL	91.2(3.0)	93.0(2.7)	87.0(4.6)	89.9(2.6)	89.6(3.6)	91.5(1.4)	89.1(4.1)
ZB	126.9(4.8)	128.8(6.6)	120.0(4.0)	125.4(5.1)	125.2(5.0)	123.6(2.5)	126.8(8.3)
IOB	42.1(3.0)	42.5(3.6)	38.7(1.0)	40.7(2.1)	40.8(1.7)	42.1(1.5)	42.8(4.4)
RB1	42.0(1.7)	42.0(2.9)	38.6(1.7)	38.9(1.6)	38.5(1.4)	40.1(1.1)	40.9(4.1)
RB4	76.8(1.8)	75.8(3.0)	70.9(2.1)	72.8(2.0)	72.7(2.2)	73.1(1.2)	74.4(4.1)
BCB	64.4(1.4)	64.9(2.6)	64.2(1.7)	64.0(2.3)	65.5(1.5)	64.3(2.9)	63.9(1.7)
BCD	57.5(2.1)	59.1(1.9)	59.8(3.4)	60.1(4.2)	59.6(1.8)	58.7(2.1)	59.0(0.9)
OAD	37.1(2.0)	37.9(2.0)	35.6(1.3)	36.0(1.1)	36.0(1.7)	36.8(1.5)	38.2(4.0)
JH	17.4(1.0)	17.2(1.0)	16.8(1.1)	16.8(1.2)	17.2(0.8)	16.2(0.1)	17.2(1.2)
RD	27.3(1.0)	27.4(1.5)	26.5(1.3)	26.8(1.1)	26.8(2.0)	26.9(0.6)	27.8(3.6)
CPH	71.4(2.5)	71.4(3.0)	64.7(2.7)	69.4(2.1)	66.9(1.5)	69.0(0.8)	69.0(4.0)
ML	173.3(3.8)	175.0(5.2)	160.6(4.6)	166.5(5.0)	165.0(6.1)	173.6(3.8)	171.6(7.8)
CL	13.1(0.8)	13.0(0.9)	11.1(0.7)	11.8(0.5)	11.5(0.8)	12.7(0.5)	13.2(1.5)
P4UL	23.6(0.7)	24.2(0.8)	22.2(1.1)	23.3(0.6)	23.5(1.0)	23.6(0.6)	23.5(0.9)
P4UW	10.1(0.4)	10.0(0.6)	8.8(0.4)	9.3(0.3)	9.2(0.4)	9.6(0.2)	9.7(0.8)
M1UL	15.8(0.8)	16.3(1.2)	14.8(0.9)	15.2(0.5)	15.3(0.7)	15.5(0.6)	15.8(0.9)
M1UW	21.1(1.1)	21.3(0.7)	19.0(1.4)	20.1(0.8)	20.5(1.0)	21.0(1.3)	20.6(0.7)
M2UW	13.2(0.8)	13.3(0.5)	11.5(1.0)	11.7(0.5)	12.1(0.7)	13.2(0.8)	11.6(0.5)
P4LL	14.4(1.0)	14.8(0.6)	14.4(1.1)	14.7(0.2)	14.6(0.7)	14.4(0.7)	14.8(0.5)
P4LW	7.6(0.5)	7.6(0.3)	6.8(0.5)	6.8(0.5)	7.0(0.4)	7.6(0.3)	7.5(0.6)
M1LL	28.3(1.3)	27.7(1.0)	24.9(1.6)	26.8(0.8)	26.3(0.9)	26.9(0.9)	26.7(0.9)
M1LW	11.0(0.4)	10.9(0.6)	9.5(0.6)	10.2(0.5)	10.0(0.3)	10.2(0.1)	10.5(0.8)

of no geographic variation among nine groups of males was rejected ($P < 0.05$) for 12 of the 25 variables: CBL, RB1, RB4, MTR, CL, M1UL, M1UW, M2UW, P4LW, M1LL, M1LW, and ML. For seven of the 12 characters, two varying subsets of samples were significantly different from each other. The two subsets always overlapped, and the only consistent result was that the three groups (southern Arizona, Animas Valley, and western Chihuahua) that included most specimens of *baileyi* had smaller means than the other samples and never differed significantly from one another. Three characters exhibited three overlapping subsets of samples, and a fourth character had four overlapping subsets. In canine length, the subsets were non–overlapping; the three groups containing most *baileyi* were significantly smaller than all other groups.

On the basis of the ANOVA for females we rejected ($P < 0.05$) the hypothesis of no geographic variation for 17 of the 25 variables: CBL, MSL, RB1, RB4, MTR, PPL, CL, P4UL, P4UW, M1UL, M1UW, M2UW, P4LW, M1LL, M1LW, CPH, and ML. Most variables showed varying numbers of overlapping subsets. There were four variables with four subsets, seven with three subsets, and three with two subsets. Three variables had non–overlapping subsets. The southern Arizona group was significantly different from all others in P4UL; the three groups of *baileyi* and the Texas–Oklahoma group were significantly different from the other three groups in M2UW; and the three groups of *baileyi* were significantly different from all other samples in P4LW. In general, wolves from northern New Mexico *(youngi)*, the Mogollon Plateau *(mogollonensis)*, and Texas averaged larger in most characters than the three groups of *baileyi*. Among males, most character means for male *youngi* were the largest, but among females, most character means for female *mogollonensis* were the largest.

Coefficients of variation ranged from 3.1 to 8.9% for males and from 3.1 to 7.0% for females (Table 2). For most characters, males were more variable ($< 2\%$) than females. Females were more variable ($< 1\%$) in IOB, BCB, BCD, and M1UL. The extent of sexual dimorphism varied among groups. Three of four groups examined (northern New Mexico, *baileyi* from the Animas Valley, and *baileyi* from western Chihuahua) showed the same relative amount of sexual dimorphism with character means ranging from zero to 11% larger for males. However, in the group from the Mogollon Plateau, females were larger in two characters (M1UL and M2UW) and males were from 0.5 to 7.7% larger in the other characters. Sample sizes for males were 15 to 26; sample sizes for females were smaller and ranged from 7 to 18. The sample size for wolves from the Mogollon Plateau was among the largest available.

Table 2. Coefficients of variation (in percent) for males and females for each of the variables used in morphological analyses of *Canis lupus*. Specimens with incomplete data sets were omitted.

Variable	Males (n = 101)	Females (n = 59)
MSL	3.8	3.3
CBL	3.4	3.2
MTR	3.8	3.3
PPL	3.5	3.5
ZB	4.5	4.5
IOB	6.6	7.0
RB1	6.0	5.8
RB4	3.8	3.5
BCB	3.1	3.3
BCD	3.1	4.0
OAD	6.6	5.5
JH	7.2	5.9
RD	6.7	6.4
CPH	4.5	3.7
ML	3.6	3.1
CL	8.9	6.9
P4UL	4.7	3.6
P4UW	7.0	5.0
M1UL	5.4	5.9
M1UW	5.9	4.5
M2UW	6.5	5.2
P4LL	5.6	4.9
P4LW	7.4	5.9
M1LL	5.2	3.9
M1LW	6.8	4.8

Multivariate Analyses.

Principal components analysis of males ($n = 104$) revealed considerable overlap among specimens assigned to the five taxa (Fig. 2). The animals were arranged primarily by size on the first PC, with most *baileyi* to the left in Fig. 2, most *youngi* to the right, and specimens of other taxa

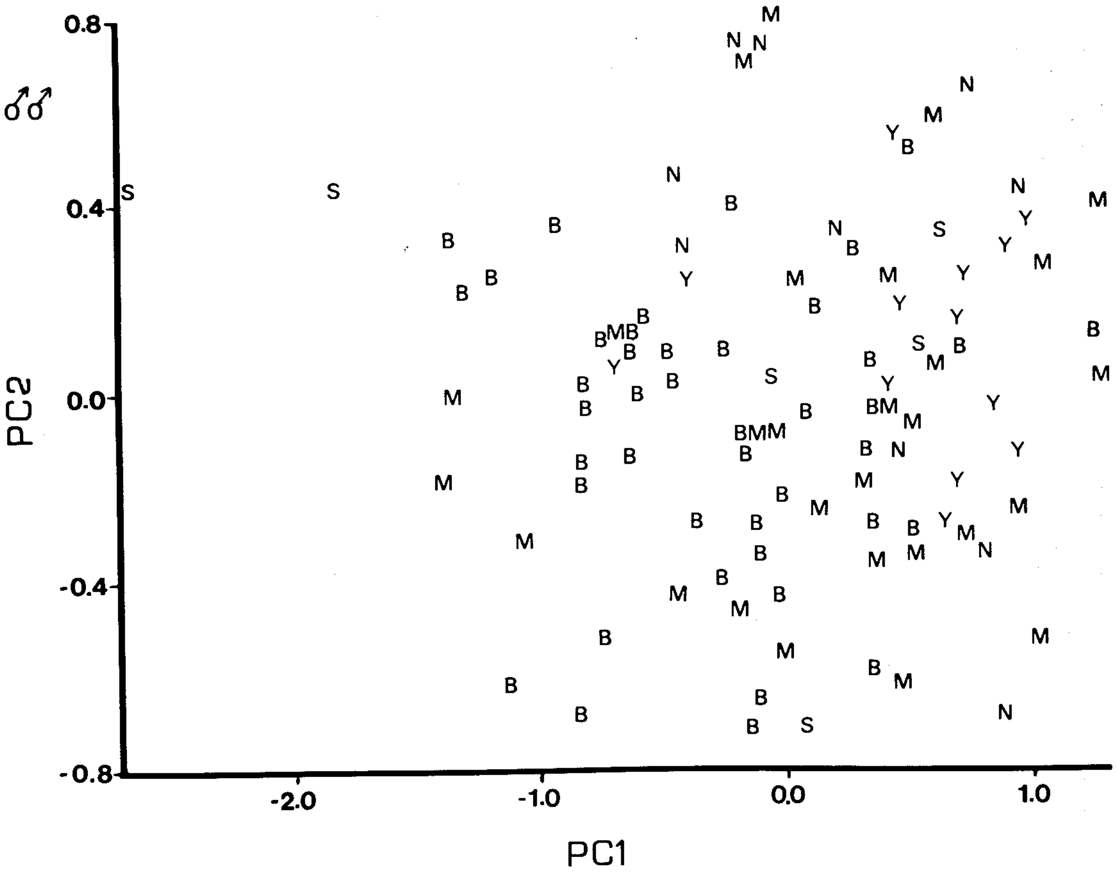

Fig. 2. Distribution of male wolves on the first two principal components. Letters represent the subspecies used in this study: B, *C. l. baileyi;* M, *C. l. mogollonensis;* N, *C. l. nubilus;* S, *C. l. monstrabilis;* and Y, *C. l. youngi.* PC I accounts for 77% of the variation, PC II for 17%.

generally in an intermediate position. All variables had positive correlations with the first PC (Table 3), with most length variables loading somewhat higher than measurements of breadth or depth. No clear pattern of ordination was evident on PC II; all tooth measurements loaded positively and all other variables loaded negatively.

The principal component analysis of females (n = 64) yielded results similar to those for males (Fig. 3). The first PC was a size factor and all variables loaded positively (Table 3). Specimens of *baileyi* were generally to the left in Fig. 3, with specimens of *mogollonensis* and *youngi* to the right. The second PC contrasted dental characters and braincase depth with other measures of skull size. The major difference between the two analyses was the positioning of *mogollonensis*. Among the males, *mogollonensis* occupied an intermediate position between *baileyi* and *youngi,* whereas in the analysis of females, *mogollonensis* was phenetically closer to specimens of *youngi*.

Our initial discriminant analyses examined Goldman's (1944) taxonomy for southwestern wolves. Specimens were assigned to one of five subspecies based either upon Goldman's own assignment, or by using his characters and range map. The analysis of males (n = 104) revealed that the two most distinct subspecies of southwestern wolves were *baileyi* and *youngi* (Fig. 4). *Canis l. mogollonensis* showed considerable overlap with both of these subspecies, with *nubilus* and *monstrabilis* in an intermediate position

Table 3. Character loadings of variables on the first two principal components.

Variable	Males		Females	
	PC I	PC II	PC I	PC II
MSL	0.865	−0.209	0.905	−0.171
CBL	0.869	−0.140	0.909	−0.253
MTR	0.873	−0.004	0.821	−0.145
PPL	0.660	−0.309	0.714	−0.325
ZB	0.653	−0.544	0.752	−0.198
IOB	0.628	−0.349	0.709	−0.205
RB1	0.814	−0.041	0.842	−0.019
RB4	0.814	−0.080	0.865	−0.087
BCB	0.208	−0.300	0.312	−0.146
BCD	0.334	−0.262	0.234	0.144
OAD	0.596	−0.475	0.798	−0.255
JH	0.602	−0.307	0.578	−0.261
RD	0.582	−0.500	0.682	−0.502
CPH	0.649	−0.377	0.826	−0.085
ML	0.870	−0.195	0.897	−0.175
CL	0.796	0.310	0.799	0.259
P4UL	0.740	0.378	0.829	0.206
P4UW	0.777	0.296	0.848	0.225
M1UL	0.674	0.411	0.654	0.213
M1UW	0.648	0.444	0.761	0.429
M2UW	0.646	0.362	0.522	0.426
P4LL	0.606	0.252	0.577	0.108
P4LW	0.752	0.273	0.738	0.162
M1LL	0.812	0.359	0.843	0.305
M1LW	0.791	0.384	0.850	0.248
Variance accounted for	77%	17%	83%	9%

and overlapping primarily *mogollonensis*. The amount of phenetic overlap was shown by the percentage of misclassified individuals: *youngi*, 0%; *monstrabilis*, 9%; *baileyi*, 15%; *nubilus*, 30%; and *mogollonensis*, 32%. One male *baileyi* (USNM 232446) from 30 mi SE Animas, New Mexico, consistently was misclassified as a *youngi* (P = 100%); we suspect that the locality information for this specimen is incorrect. Four *baileyi* were classified with *mogollonensis* and one with *monstrabilis*, results that might be expected of interbreeding populations. Nine *mogollonensis* were misclassified, two as *youngi*, five as *baileyi*, and one each as *monstrabilis* and *nubilus*. Two *nubilus* were misclassified as *monstrabilis* and one as *mogollonensis*. One *monstrabilis* was assigned to *mogollonensis*. All subspecies pairs were significantly different except for *baileyi* and *mogollonensis* (Table 4). The first 10 characters and their order of entry into the discriminant function were RB1, BCB, MSL, CPH, RD, CPL, ML, P4LL, RB4, and M1LL.

Specimens of females of the five subspecies showed little overlap when plotted on the first two canonical variates (Fig. 5). *Canis l. baileyi* is clearly separated from all other groups and only *mogollonensis* exhibits any overlap with other subspecies. Of 64 individuals, only two were misclassified (*mogollonensis* as *youngi*). Females thus exhibited less phenetic overlap among groups, were more distinct geographically, and agreed better with Goldman's taxonomy. Female *mogollonensis* were closer to female *youngi*. The F–tests among groups showed *baileyi* was significantly different from all groups (Table 4). *Canis l. mogollonensis* was significantly different from *baileyi* and *nubilus* but not from *youngi* or *monstrabilis*. The first 10 variables and their order of entry in the discriminant function were M2UW, CL, BCD, MTR, ML, RB4, P4UL, M1LL, ZB, and CPH.

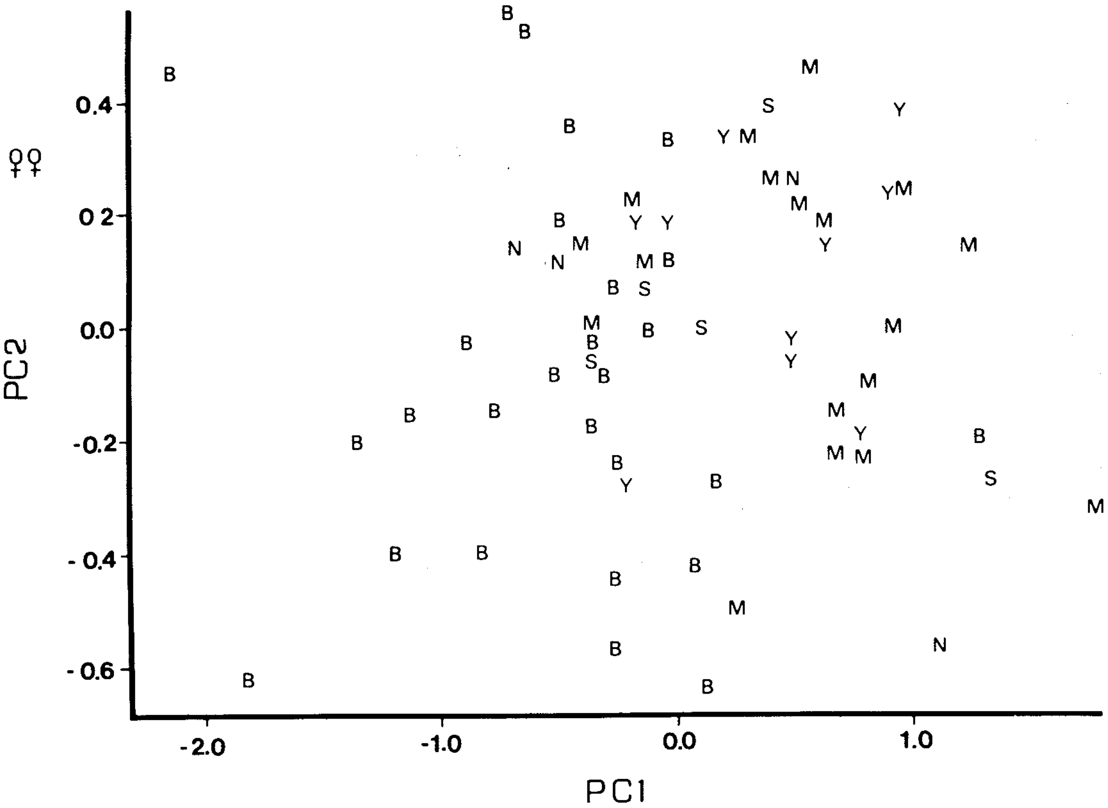

Fig. 3. Distribution of female wolves on the first two principal components. See Fig. 2 for explanation of symbols. PC I accounts for 83% of the variation, PC II for 9%.

We also performed a two–group DFA using samples of *youngi* and *baileyi* as references and the specimens of *mogollonensis* as unknowns. Between the two groups of reference males, only USNM 232446 was misclassified (*baileyi* as *youngi*). Of 26 *mogollonensis*, 8 were assigned to *youngi* and 18 to *baileyi*. The five most important characters differentiating male *baileyi* from *youngi* were RB1, CPH, ML, JH, and M2UW. The plot of specimens on the first canonical variate (not shown) supported the classification analysis; most *mogollonensis* were closer to *baileyi* than *youngi*, although there was considerable overlap among the three groups. A similar analysis of females revealed no misclassification of the reference groups (*baileyi* and *youngi*) and classified 12 *mogollonensis* as *youngi* and 6 as *baileyi*. Characters separating female *baileyi* and *youngi* were P4UW, P4LL, RB1, P4LW, and BCD. Again, a plot of the individuals on the first variate (not shown) showed considerable overlap but with most *mogollonensis* closer to *youngi*. In both analyses *baileyi* and *youngi* were significantly different (F–test, $P < 0.05$).

To better assess the degree of distinctness, we assigned specimens from areas of relative climatic and physiographic homogeneity to discrete geographic groups (see Specimens Examined) and then studied these groups with discriminant function analyses. The analysis of males revealed that the two most distinct groups were from northern New Mexico *(youngi)* and from Oklahoma *(nubilus)*. Other groups of wolves exhibited considerable overlap when plotted on the first two canonical variates (Fig. 6). Particularly striking was the degree of overlap among wolves from the Mogollon Plateau, southern New Mexico, Arizona, and the Sierra Madre Occidental of northern Mexico. Samples of *monstrabilis* from southeastern New Mexico and Texas overlapped

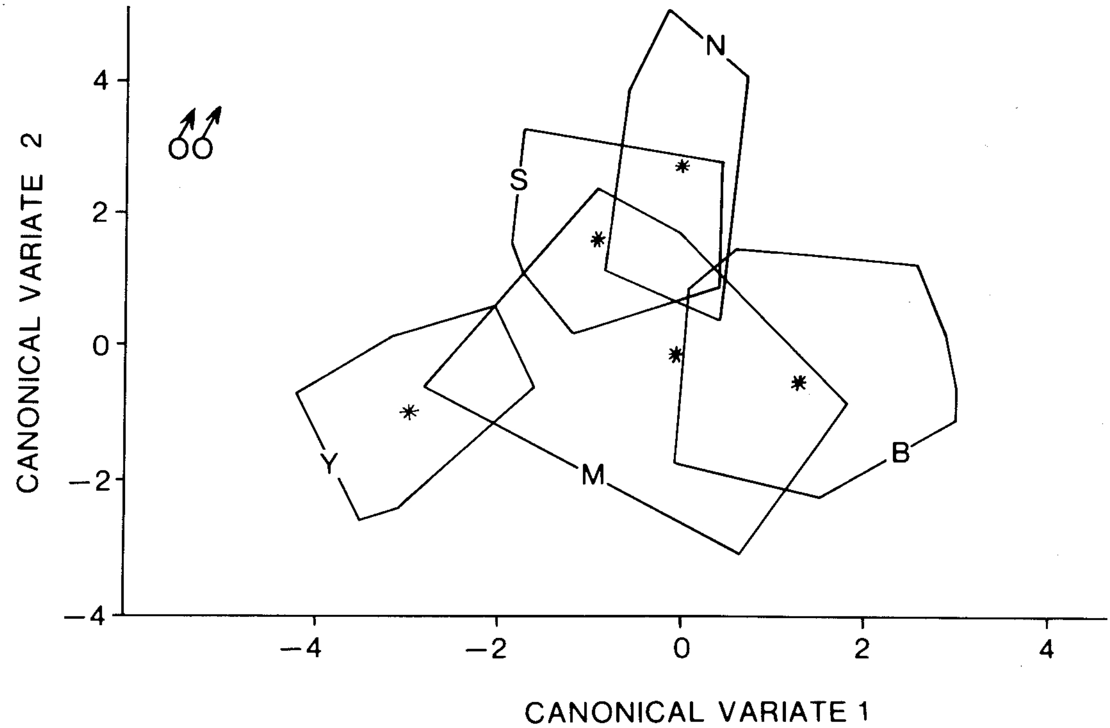

Fig. 4. Distribution of males of five subspecies of wolves on the first two canonical variates. Polygons enclose all individuals of each group. Letters designate the subspecies given in Fig. 2; an asterisk is placed at each group centroid. The first canonical variate accounts for 51% of the variation, the second for 32%.

Table 4. Matrix of F-values for testing significant differences among five subspecies of *Canis lupus* in discriminant function analyses using 25 characters. Males and females were analyzed separately. F-values for females are on the upper diagonal, males on the lower diagonal. Degrees of freedom (numerator/denominator) are 25/35 for females and 25/75 for males.

Group	*baileyi*	*mogollonensis*	*nubilus*	*monstrabilis*	*youngi*
baileyi		9.01**	2.31*	4.19**	8.71**
mogollonensis	1.55		2.07*	0.95	1.72
nubilus	3.48**	2.40**		1.66	1.97*
monstrabilis	3.27**	1.97**	1.70*		2.49**
youngi	6.29**	3.30**	4.36**	3.00**	

* = $P < 0.05$
** = $P < 0.01$

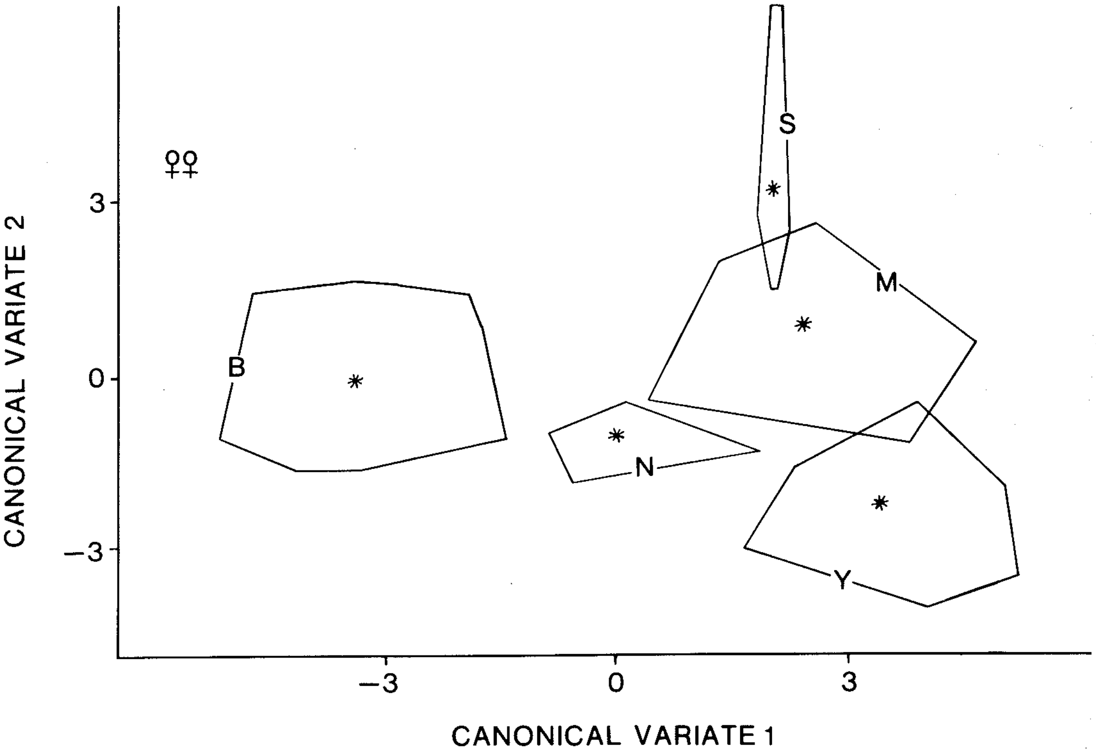

Fig. 5. Distribution of females of five subspecies of wolves on the first two canonical variates. Polygons enclose all individuals in each group. Letters designating the subspecies are those used in Fig. 2; an asterisk is placed at each group centroid. The first canonical variate accounts for 74% of the variation, the second for 15%.

these groups as well as the sample of *nubilus*. There were no misclassifications among specimens from northern New Mexico *(youngi)*. Among males from the Mogollon Plateau, 46% were misclassified; two as *youngi*, the remainder with wolves from elsewhere in New Mexico, Texas, or Mexico. Misclassifications among wolves from southern Arizona, New Mexico, and northern Mexico ranged from 17 to 27%. These three groups represented *baileyi* as defined by Goldman. Specimens from the Trans–Pecos region of Texas were misclassified (44%) as specimens from the Mogollon Plateau and northern Mexico. There were few other misclassifications. The first 10 characters in their order of entry into the discriminant function were RB1, CL, CPH, RB4, ML, CPL, P4UL, M1LL, M1UW, and JH.

The results of the DFA on seven geographic groups of females revealed much less overlap among the groups plotted on the first two canonical variates (Fig. 7). The first canonical variate separated the three groups of *baileyi* from wolves from elsewhere in New Mexico. The second variate provided some separation between wolves from northern New Mexico *(youngi)*, the Mogollon Plateau, and the Sacramento Mountains *(monstrabilis)*. These results again showed the close phenetic relationship between female *youngi* and females from the Mogollon Plateau. The analysis also revealed phenetic similarity between wolves from Texas and Oklahoma and wolves representing *baileyi* (Fig. 7). The first 10 variables and their order into the discriminant function were M2UW, CL, BCD, M1LL, MTR, P4UL, ML, RB4, CPH, and RD. The percentage of misclassifications was quite low with four of the six groups showing no misclassifications. One female from the Mogollon Plateau was classified

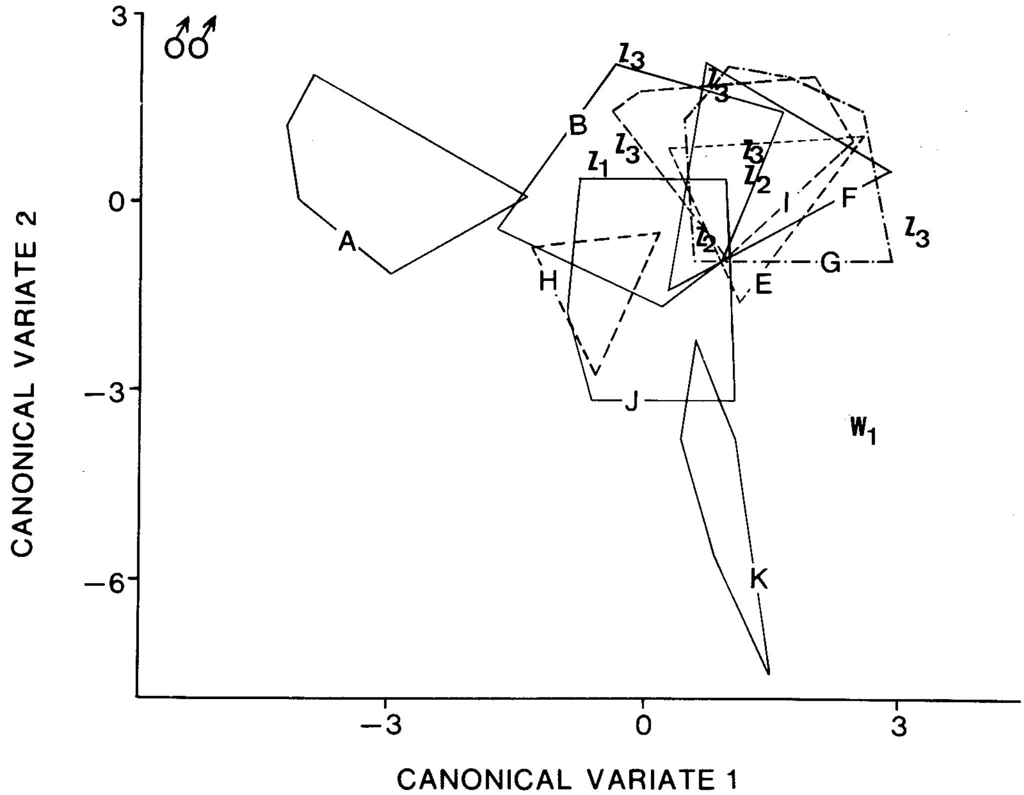

Fig. 6. Distribution on the first two canonical variates of male *C. lupus* from the geographic groups. Assignment of specimens to the geographic groups is given in the Specimens Examined. Abbreviations for these groups are as follows: A, northern New Mexico; B, Mogollon Plateau; E, New Mexico Plains; F, southern Arizona; G, Animas Valley; H, Sacramento Mountains, New Mexico; I, Chihuahua; J, Texas; K, Oklahoma. Polygons enclose all individuals in each group and letters identifying each group are placed at the group margin. Specimens of captive wolves from the ASDM and WCSRC lines are designated Z and W, respectively. The first canonical variate accounts for 37% of the variation, the second for 26%.

with the northern group *(youngi)*, and one animal from southern New Mexico was classified with the northern Mexico group.

The F–tests among the male groups showed that *youngi* was significantly different from all other groups except those from the Sacramento Mountains (Table 5). Wolves from the Mogollon Plateau were significantly different only from *youngi* and the sample of *nubilus* from Oklahoma. The three *baileyi* samples were not significantly different from each other, but were significantly different from *youngi* and *nubilus*. The sample from the Sierra Madre also was significantly different from wolves from Trans–Pecos Texas. Among females, *youngi* was significantly different from all samples except those from the Mogollon Plateau. Mogollon Plateau wolves were significantly different from all other groups except for the Sacramento Mountains group. The groups of *baileyi* were not significantly different among themselves, but differed from most other geographic groups. Texas–Oklahoma wolves were not significantly different from the samples of *baileyi*.

Recent Specimens.

Wolves taken in the southwest since 1945 were entered as unknowns in discriminant analyses to investigate their affinities. We used coyotes, dogs, and wolves from each of the three southern geographic areas that represent *C. l. baileyi,* and wolves from northern New Mexico as reference

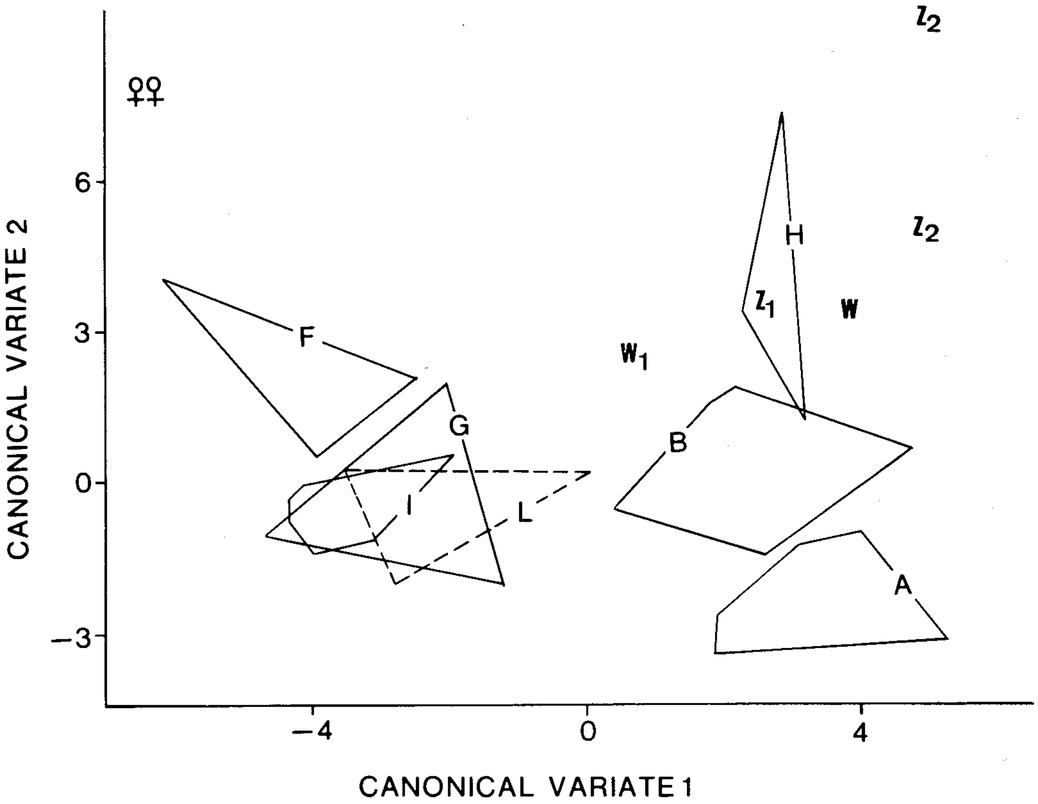

Fig. 7. Distribution on the first two canonical variates of female wolves from the geographic groups. See Fig. 6 for explanation. Group L represents Texas and Oklahoma females. The first canonical variate accounts for 64% of the variation, the second for 16%.

groups. For males, the first canonical variate accounted for 90% of the total dispersion and the second for 6%. For females, the first canonical variate accounted for 82% of the total dispersion and the second for 11%. All recent specimens were classified with greater than 99% probability into the three groups of southern wolves. One male taken in 1950 from Sonora, Mexico (USNM 285754), and one female taken in 1956 from Durango, Mexico (MSU 863), were between southern wolves and dogs on the plots of the canonical variables (not shown), but the probability that these individuals belonged with southern wolves rather than with dogs was 100%.

We also entered the post–1945 individuals as unknowns and used just the geographic groups of wolves as references. Wolves from the three southern areas representing *C. l. baileyi* were combined into a single group. For males, the first canonical axis accounted for 39% of the total dispersion, and the second for 31%. For females, the first canonical axis accounted for 72% of the total dispersion, and the second for 15%. Seven of the 10 recently captured males were classified as southern wolves *(baileyi)* with probabilities greater than 65%; these were taken from Chihuahua, Durango, and the Trans–Pecos region of Texas. An eighth individual, taken from the Mogollon Plateau in Arizona, was classified with the Mogollon Plateau group with 54% probability. Another, from Chihuahua, had a 68% probability with the Mogollon Plateau group and 16% with the southern group. The tenth individual (from Sonora) was classified with the Sacramento Mountains group with a probability of 98%. The F–tests among reference groups showed that the Mogollon Plateau group was not significantly different from either the Sacramento Mountains group

Table 5. Matrix of F-values for testing significant differences among geographic groups of *Canis lupus* in discriminant function analyses using 25 characters. Males and females were analyzed separately. F-values for females are on the upper diagonal, males on the lower diagonal. Degrees of freedom (numerator/denominator) are 25/28 for females, 25/68 for males. Blanks indicate no comparison was made.

Group	Northern New Mexico	Mogollon Plateau	Southern Arizona	Animas Valley	Western Chihuahua	Sacramento Mountains	Texas–Oklahoma	Texas	Oklahoma
Northern New Mexico		1.48	5.29**	3.56**	5.80**	2.42*	3.19**		
Mogollon Plateau	2.91**		4.52**	3.65**	6.31**	1.17	3.11**		
Southern Arizona	3.22**	1.07		1.28	1.13	2.99**	1.50		
Animas Valley	4.66**	1.36	0.93		0.84	2.78**	1.35		
Western Chihuahua	4.03**	0.89	0.83	0.84		4.09**	1.87		
Sacramento Mountains	1.43	0.80	0.98	1.52	1.28		2.83**		
Texas	2.91**	1.55	1.65	2.00*	1.80*	1.05			
Oklahoma	4.47**	3.35**	2.52**	3.43**	3.52**	1.45		2.17**	
New Mexico Plains	3.28**	1.46	1.45	1.90*	1.64	1.52		2.23**	2.35**

* = $P < 0.05$
** = $P < 0.01$

or the southern wolf group ($P < 0.05$). The Sacramento Mountains group was significantly different, however, from the southern group ($P < 0.05$). Three females from southern New Mexico and northern Chihuahua were classified with the southern wolves with greater than 98% probability. Of two taken from Durango, one showed affinities with both the southern ($P = 46\%$) and Mogollon Plateau ($P = 35\%$) groups; and the second only with the latter group ($P = 100\%$). The southern group is statistically different from the Mogollon Plateau group (F–test, $P < 0.05$). Curtis Carley (pers. comm.) believed that one, and possibly both, recent captures from the Trans–Pecos region of Texas showed some dog characters. These individuals had 0% probability for classification with dogs in our analyses.

Captive Specimens.

Individuals from two lines of captive specimens were entered as unknowns in two series of discriminant function analyses. We examined eight males and three females from a line that originated at the Arizona Sonoran Desert Museum (ASDM). The dam of the original parental stock of this line was bred with a son. Two of our specimens (here referred to as Z_1 individuals), were offspring from this backcross. Two littermates from the backcross were mated several times. Four of our specimens (Z_2), two males and two females, came from this cross. Two progeny from this cross were then mated several times; we had five males (Z_3) from these litters.

The second line of captive animals came from the Wild Canid Survival and Research Center (WCSRC). We examined four individuals from this line: the parents (W), and a male and a female offspring (W_1). Because the character RB4 could not be taken on the sire of the WCSRC line, that individual was initially eliminated from the analyses. Later, analyses with males were repeated, and data from the sire were included by eliminating RB4 from the character set. The deletion of a single character did not change the results with respect to the position of target groups and unknowns, and it permitted us to discuss the position of all captive individuals in discriminant space.

In the first series of discriminant function analyses, the target groups were coyotes, dogs, the three groups of southern wolves representing *C. l. baileyi,* and the group of wolves from northern New Mexico. The Z_1 and Z_2 individuals fell outside the polygons enclosing southern wolves (Figs. 8, 9). The Z_3 individuals fell completely within these polygons. With one exception, all of the captive ASDM individuals were classified with greater than 99% probability into the southern wolf groups based on their discriminant function scores. The exception, a female Z_2, was classified into the northern wolf group. The sire of the WCSRC line was classified with 100% probability into the southern wolf groups. The dam of this line was classified as dog (P = 100%), although her coordinates on the plot of the first two canonical variates were not within the area delineating our sample of dogs (Fig. 9). The W_1 individuals were classified with southern wolves with greater 80% probability.

We also analyzed captive specimens as unknowns and used wolves from the geographic groups as references. Six of the 10 captive males were assigned with greater than 62% probability to either the southern Arizona or Animas Valley groups. These included the two Z_2 specimens and four of the five Z_3. The fifth Z_3 had probabilities with wolves from the Animas Valley (P = 38%), Mogollon Plateau (P = 29%), and southern Arizona (P = 19%). The Z_1 male had affinities with the Texas group (P = 35%), the southern Arizona group (P = 26%), and the Mogollon Plateau group (P = 20%). The male progeny from the WCSRC cross was classified with the Oklahoma group (P = 95%). The sire of the WCSRC line was classified with the Animas Valley group (P = 35%), the Mogollon Plateau group (23%), and the southern Arizona group (17%). The two Z_2 females were classified with 100% probability to the Sacramento Mountains group. The remaining three captive females (Z_1, W, W_1) were assigned to the Mogollon Plateau group with greater than 80% probability. All these individuals except the WCSRC sire are depicted in Figs. 6 and 7.

DISCUSSION

The principal components analyses, in which animals were not assigned to any a priori geographic or taxonomic grouping, allowed an ob-

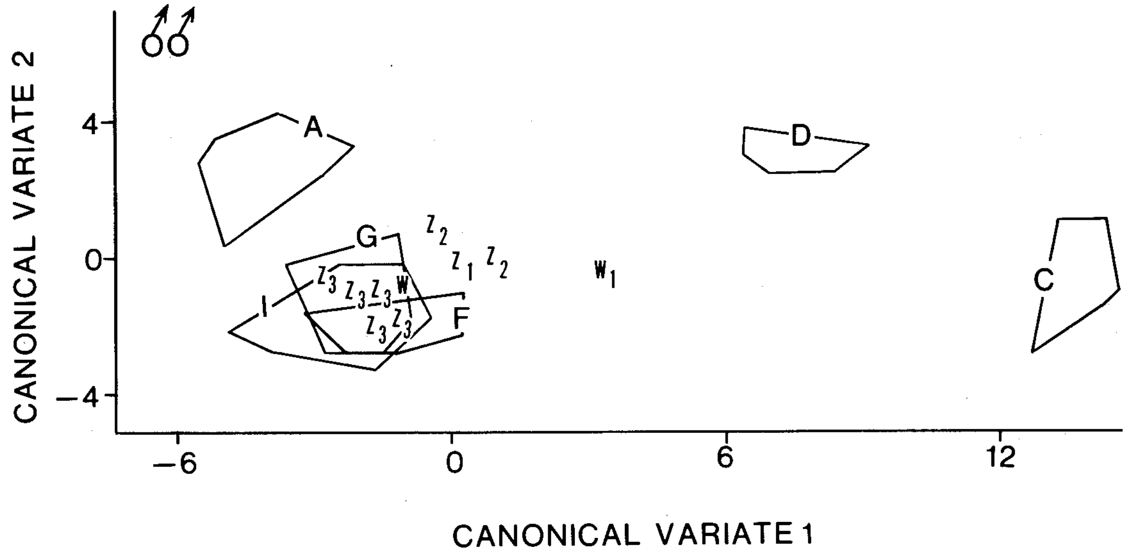

Fig. 8. Distribution of *Canis latrans* (C), *C. familiaris* (D), and four of our samples of male *C. lupus* (A, F, G, I) on the first two canonical variates. This analysis used 24 variables as RB4 was omitted. See Fig. 6 for explanation. The first canonical variate accounts for 84% of the variation, the second for 10%.

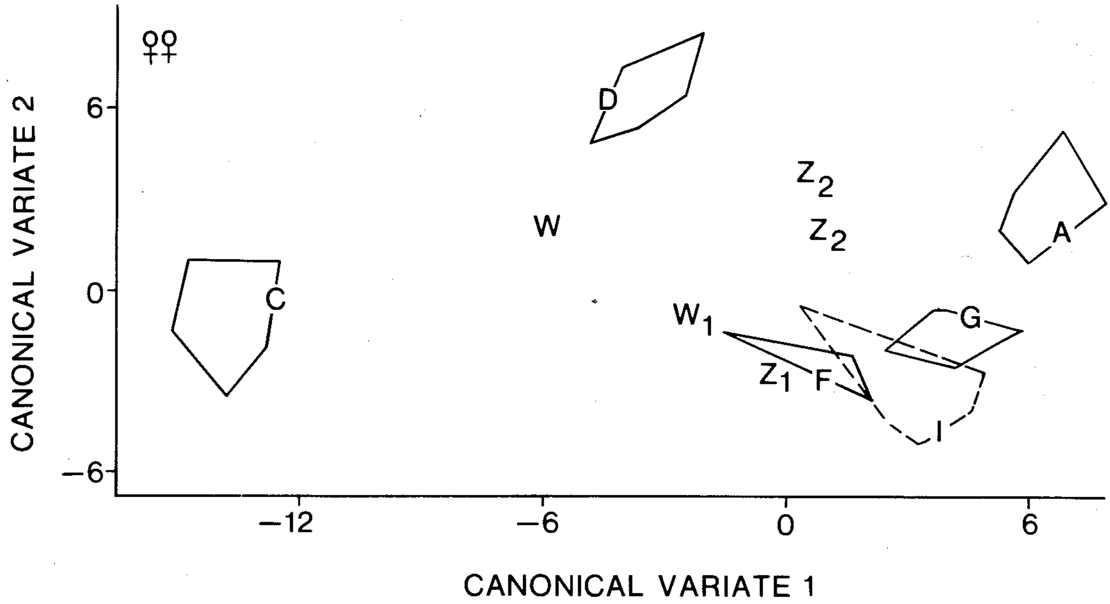

Fig. 9. Distribution of *Canis latrans* (C), *C. familiaris* (D), and four groups of female *C. lupus* (A, F, G, I) on the first two canonical variates. See Fig. 8 for explanation. The first canonical variate accounts for 72% of the variation, the second for 17%.

jective assessment of phenetic overlap among the specimens. Skeel and Carbyn (1977) found, as we did, that there was no clear separation among recognized taxonomic groups of wolves. They believed that this was not surprising because the groups were of low taxonomic rank (i.e., subspecies). Indeed, they (1977:746) stated that "The tremendous overlap of individuals in the PCA and MDA [Multiple Discriminant Analysis] illustrate [sic] the variability of the populations, and the poor probability of being able to identify to which population a single specimen would belong."

The ordination of the individuals on the first PC substantiated previous reports of size variation in wolves. Nowak's (1973) study supported earlier hypotheses of clines in size, with size increasing from south to north and from east to west. The largest animals in our study were specimens of *youngi* from northern New Mexico, and the smallest were specimens of *baileyi* from the southern portions of the range of *C. lupus*. Specimens from the eastern portions of our study area are smaller than *youngi* to the west, but not appreciably different from *baileyi*. The large proportion of variance accounted for by the first PC illustrates the importance of size variation in our sample. Although there was considerable overlap, the first PC indicated some separation between *youngi* and *baileyi*, and showed the intermediate nature of other samples. Plots of the individuals on PCs II and III revealed no obvious pattern of ordination and may indicate how little non–size variation exists. We believe that size differences are an important adaptive component of variation among wolves.

Discriminant function analyses among a priori designated groups provide more separation among the groups than does PCA. Several investigators have used these techniques in studying interspecific relationships among canids, but we are aware of only three multivariate studies on infraspecific relationships in wolves. Kolenosky and Standfield (1975) found evidence for two "types" of *C. l. lycaon* in Ontario based in part upon multivariate analyses. Although they used no other reference groups in their analysis, they suggested that the larger Boreal type of *lycaon* was probably closest to *C. l. hudsonicus* or *C. l. nubilus*, whereas the smaller Algonquin type "admirably" fit Goldman's description of *C. l. lycaon*. They found that both types overlap in east–central Ontario with no conclusive evidence of interbreeding. They believed that the smaller type had followed deer into Ontario as a result of changing land–use patterns and was therefore a recent invader in Ontario. Pichette and Voight (1971) studied three populations of *C. l. lycaon* in Ontario and Quebec and found significant differences among the three groups. Skeel and Carbyn (1977), in a thorough study of wolves from central North America, found that *C. l. lycaon* and *C. l. hudsonicus* separated fairly distinctly but that there was less separation among other groups in the analysis, especially between *C. l. nubilus* and *C. l. irremotus*. Specimens from four national parks were ordered to one side of *nubilus* and *irremotus*. There was a size trend with the largest wolves from the boreal and subalpine forest areas of the parks and the smallest wolves from the grassland *(nubilus)* and Rocky Mountain *(irremotus)* areas. Wolves from the tundra *(hudsonicus)* and Great Lakes *(lycaon)* were intermediate in size.

We found the two most distinct southwestern subspecies to be *baileyi* and *youngi*. We believe that specimens of *mogollonensis* represent intergrades between *baileyi* and *youngi*. The intermediate nature of *mogollonensis* was confounded by the separate phenetic similarities shown by the sexes. The results of the DFAs, either by subspecies or by geographic group, indicated the affinities of male *mogollonensis* to be with *baileyi* whereas female *mogollonensis* were closer to female *youngi*. Female *youngi* and *mogollonensis* were similar because female *mogollonensis* were larger in size than would be predicted from the other samples. Our comparisons also indicated less sexual dimorphism between male and female *mogollonensis*. Reasons for this are unknown.

Goldman (1944:471) noted that in southeastern Arizona and southwestern New Mexico *baileyi* intergraded with *mogollonensis*, but that the transition from one to the other was "remarkably abrupt." Our analyses indicated no such sharp break, especially among the males. Given the extensive overlap among male *baileyi* and *mogollonensis*, we believe that *mogollonensis* is best synonymized with *baileyi*. Nowak (1973:34a, Fig. 8) also found considerable overlap among subspecies of *C. lupus*. We suspect that the addition of other groups of wolves would tend to compress the taxonomic distances among the southwestern groups of wolves. Our samples of *monstrabilis* are small and thus any conclusions are tentative. Nonetheless, we find no convincing evidence to support the recognition of *monstrabilis* as a subspecies separate from *baileyi*. In most of the analyses it exhibited considerable overlap not only with groups representing *baileyi* but also with wolves from the Mogollon Plateau.

We feel that the most parsimonious treatment of southwestern wolves is to recognize three subspecies, *youngi* in the north (southern Rocky Mountains), *nubilus* in the Great Plains, and *baileyi* in the Mogollon Plateau, southern New Mexico, Arizona, Texas, and in Mexico. The exact affinities of these wolves may never be known because available samples are small and the wolves are extirpated in most areas.

We suspect that males exhibited more phenetic overlap as a result of increased character variation. Males had larger CVs for 19 of the 25 variables, and although the increment of variability was slight for each character, the additive effect may have been sufficient to account for the poorer separation of the male OTUs. Because PCs are linear combinations of the old variables, the cumulative effect of slight increased variation in each character may be considerable. The greater male variability was also reflected in the lower correlations of the characters with the first PC. In the DFA, variables were weighted depending upon their ability to separate groups. When 19 of 25 variables are even slightly more variable, as in males, it seems reasonable to expect poorer discrimination of groups. The influence of environmental and behavioral factors on male and female wolf phenotypes also may be important. The demands of pregnancy and lactation on females may be severe, and females might be taking a smaller size of prey than males. These factors may affect the absolute size attained by adult females in a given geographic region. To the extent that males are freed from some of these energetic demands or that they are more mobile, they may be relatively more plastic in their adaptation to a given environment. In addition, the role of males in the social behavior of packs may lead to the development of larger size, as reflected in certain types of appositional growth (e.g., sagittal or occipital crests), that may obscure geographic patterns of variation.

Five skulls thought to be dog–wolf hybrids by

Nowak (1973) were also examined in this study. Unfortunately, we were not aware of Nowak's comments on these specimens until after we had examined them and included them in some analyses. Because the status of these specimens has been questioned we believe we should discuss them. Four of the five specimens have no sex recorded on the specimen label. Nowak identified the four animals as females. Our discriminant function analysis with animals of known sex from the appropriate geographic areas classified them as females. These five females were used as specimens in the five group (subspecies) analysis and all five plotted with their appropriate group on the canonical variates. The classification probabilities were: *C. l. baileyi:* USNM 15278, 100%, MCZ 10506, 95%; *C. l. monstrabilis:* USNM 159017, 74%, USNM 159019, 97%. We noted that one animal, MCZ 7023, had a small skull. Nonetheless, this animal had a 100% probability for *baileyi*. Although we did not run these animals as unknowns against other reference groups (dogs and coyotes) as Nowak did, the results of the classification procedure and the canonical variate plot indicated no reason for excluding them from the analysis. Specimen MCZ 7023, from Orizaba, Veracruz, (given as MCZ 2023 by Nowak) was not used in any of our geographic comparisons due to its extreme geographic position. No wolf specimens were listed for Veracruz by Hall and Dalquest (1963). Leopold (1959) plotted localities from points near the Valley of Mexico and Goldman referred to the range of *baileyi* extending at least to the Valley of Mexico; we found no museum specimens documenting these records. Dalquest (1953) reported wolves in San Luis Potosi and examined one young animal, but no specimens from there appear to be in museum collections. Specimen USNM 15278 from "Tanks, Arizona," was also excluded from the geographic comparisons as we were unable to find this locality. It may be Tanque in Graham County, Arizona.

One additional specimen has locality information that is suspect to us. This is USNM 1380, purportedly from Matamoros, Tamaulipas, and representing the easternmost locality for *C. lupus monstrabilis* or for any gray wolf from Mexico for that matter. This specimen was obtained by Lieutenant D.N. Couch, probably as part of a large collection of natural history specimens and manuscripts gathered by Jean Louis Berlandier who lived for many years in Matamoros (McKelvey, 1955). Berlandier's travels took him over a large part of Mexico and southern Texas (then a part of Mexico) and it seems likely that the wolf could have come from anywhere in this region. There is also the possibility that Couch himself obtained or purchased the animal in Matamoros. Given the paucity of documented records of gray wolves in eastern Texas and Mexico, wolves must have been extremely uncommon in this area.

In general, wolves taken since 1945 do not differ from those taken earlier. The two possible exceptions, one male from Sonora and one female from Durango, suggest hybridization with dogs, although both were classified with southern wolves with a high probability. Lawrence and Bossert (1967, 1969), using discriminant function analysis, found that F_1 hybrids between coyotes and dogs were more variable morphologically than either parental type, and fell between them with no overlap. There was considerable overlap, however, between F_2 hybrids and the parental types. Thus, it may not be possible to detect interbreeding in our sample of wolves.

Our analysis assumes that the correct parental population of each unknown individual is represented by one of the reference groups. If it is not, the classification may be inaccurate (Gipson et al., 1974; Rao, 1952). Thus, the two females taken recently from Durango may have been classified with the Mogollon Plateau and southern groups because there was no reference group of wolves from the Durango region. In any case, all recent specimens show closest affinities with southwestern wolves that we consider to represent *C. l. baileyi.*

Most captive individuals from both the ASDM and WCSRC lines showed affinities with the southern wolf groups (i.e., *C. l. baileyi*) rather than with coyotes, dogs, or wolves from northern New Mexico. Individuals of the ASDM line appeared to have relatively shorter, but not wider rostra than the wild wolves that we examined. The reasons for this are not certain. In a study comparing specimens of captive and wild–killed lions *(Felis leo)* from the same locality, Hollister (1924) found marked differences between them. He found the skulls of five captives (taken as young from the wild) to be shorter and broader, and the bones of the zygomatic arches thicker and more cylindrical. Thus, some morphological changes in captive carnivores are probably due to captivity, whether or not genetic influences such as inbreeding are also present. This conclusion has also been expressed by Devra Kleiman (pers. comm.). Scott (1968) referred to reports that captive breeding in wolves results in a shortening of the jaw; because the teeth are not similarly reduced in size, this results in a relative crowding of the teeth in captive wolves. Scott cited no references for these reports.

The sire of the WCSRC line appeared to be closely associated with southern wolves whereas the dam was much less so. Predictably, the two progeny fell between their parents with respect to their affinities. The actual affinities of the dam of the WCSRC line may be with a wolf population not examined in this investigation. The fact that her coordinates on the first canonical variable were not within the area encompassing our sample of dogs suggests that the correct reference group may be something other than dogs. No dog characters, as defined by Howard (1949) and Curtis Carley (pers. comm.), were evident in the skull.

Because of the extensive phenetic overlap among the reference groups of males, except those from northern New Mexico, captive males showed affinities with several groups. The F–tests indicated that the males from the Mogollon Plateau, the Sacramento Mountains, and each of the three southern male groups did not differ significantly from one another. The classification of any captive individual into one of these groups does not necessarily mean, then, that it has affinities for only that group. Female captives showed stronger affinities to the Mogollon Plateau and Sacramento Mountains group, wolves we also consider to represent *C. l. baileyi;* these two geographic groups do not differ significantly from one another, but both are significantly different from each of the three groups of southern wolves. Because there is an apparent relationship between captive rearing and, at least, a shortening of the skull, we are unable to discern whether the deviations of captive individuals from the groups of southern wolves are due to their captive rearing or the presence of genes from animals that are not southern wolves. Electrophoretic comparisons of captive animals compared with other samples of wolves, dogs, and coyotes might shed some light on this question.

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SPECIMENS EXAMINED

Complete names for collections in which specimens are housed are given in the Acknowledgments. When no collection is listed, that specimen is housed in the National Museum of Natural History. Single capital letters in parentheses designate the Geographic Group to which the specimens were assigned (see Figs. 6 and 7). Not all specimens were assigned to a geographic group.

Canis lupus baileyi Nelson and Goldman

MEXICO. CHIHUAHUA (I): Casas Grandes, 7 (UNAM, ENCB, FMNH, 1); Colonia Garcia, 12 (MCZ, 1); Colonia Garcia, near, 1; Colonia Garcia, 6 mi. SW, Gavilan River, 1 (MVZ); Colonia Juarez, 1; Gallego, 1; Sierra de la Tuna Mts., 30 km. NW Chihuahua, 1; Sierra Madres, near Guadalupe y Calvo, 1; Sierra Azul, 12 mi. W Pacheo, 1 (MVZ); Sierra del Nido, Arroyo Mesteno, 23 mi. E Sta. Clara, 1 (MVZ); Nuevo Casas Grandes, 1 (UNAM); San Buenaventura, Rancho El Arco, 1 (UNAM); San Buenaventura, Rancho Sr. Hector Nava, 1 (UNAM); San Buenaventura, Valle, 1 (UNAM); San Buenaventura, 11 km. S, 5 km. E, 1 (UNAM). DURANGO: El Salto, 1; Rancho San Juan, 38 mi. S, 1 (MSU); Rancho Las Margaritas, Vicente Guerrero, 28 mi. S, 17 mi. W, 1 (MSU); Vicente Guerrero, 45 km. S, 28 km. W, 1 (MSU). SONORA (F): Santa Cruz 1; Sierra Pinito (=Los Pintos?) Mts., 1. TAMAULIPAS: Matamoros, 1. VERACRUZ: Orizaba, Coyotera, 1 (MCZ). STATE UNSPECIFIED: Probably from NW Chihuahua, NE Sonora, or corner of NM or AZ, 2. UNITED STATES. ARIZONA: *APACHE CO.*(B): Concho, SW, 1; Escudilla Mts., 3; Escudilla Mts., near, 1; Escudilla Mts., 10 mi. E Springerville, 1; *COCHISE CO.*(G): Apache, Peloncillo Mts., 1; Chiricahua, 1; Chiricahua Mts., 1 mi. E Old Camp Rucker Ranch, Hampe, 1 (MVZ); Chiricahua Mts., 3.5 mi. E Old Camp Rucker Ranch, Hampe, 3 (MVZ); Chiricahua Mts., 5 mi. NE Old Camp Rucker Ranch, 1 (MVZ); Chiricahua Mts., Whitetail Canyon, 1 (MVZ); Dos Cabezos, 15 mi. N, Sulphur Springs Valley, Riggs Home Ranch, 1 (MVZ); Ft. Bowie, 1; Ft. Huachuca, 1; Parker Cañon, 18 mi. E, 1; Seep Springs, 35 mi. E Douglas, 1; *COCONINO CO.*(B): Kendrick Peak, 1; Williams, 6 mi. E, 1 (UA); *GRAHAM CO.:* Galiuro Mts., E slope, 1; *GREENLEE CO.*(B): Clifton, 3; *MARICOPA CO.:* Aguila, 1; *NAVAJO CO.*(B): Cibicue, 1; Heber, 1; *PIMA CO.*(F): Arivaca, 1 (MVZ); Arivaca, 5 mi. SE, 1; Helvetia, 1; Helvetia, 5 mi. SE, 1; Tucson, 20 mi. SE, 1 (UA); Tucson, 30 mi. S, Sta. Rita Experimental Range, 1 (UA); *SANTA CRUZ CO.*(F): Arivaca, 15 mi. SE, 2; Canilla, Canelo Hills, 1; Sta. Rita Mts., 1; Sta. Rita Mts., Parker Ranch, 2; *COUNTY UNSPECIFIED:* Tanks (=Tanque? Graham Co.), 1. NEW MEXICO: *CATRON CO.*(B): Alma, 15 mi. SW, Morgan's Ranch, 1; Datil Mts., 1; Diamond Creek, 1; Gila Forest Reserve, 3; Gila Forest Reserve, Mule Spring, 2; Gila National Forest, Upper Gila River Valley, 1; Luna, 1; Negrita Creek, Gila National Forest, 1; Reserve, 15 mi. SE, 1; Spur Lake, 0.25 mi. E, 1; *DOÑA ANA CO.:* Ft. Fillmore, 40 mi. from El Paso, 1; Hatch, 1; *GRANT CO.*(B): Hurley, 1; Mimbres River, Head, 2; Silver City, 2; *GUADALUPE CO.*(E): Santa Rosa, 18 mi. S, Hicks Ranch, 1; *HIDALGO CO.*(G): Animas, 1; Animas, 30 mi. SE, 1; Animas, 30 mi. S, OK Ranch, 1; Animas, 30 mi. SE, OK Ranch, 1; Animas, 35 mi. SE, 1; Animas Mts., 1; Animas Mts. Area, 1 (MSB); Animas Valley, Cloverdale Ranch, 1; Cloverdale, 4; Hachita, 8; OK Bar Ranch, NE of Animas Peak, 1 (KU); Locality unspecified, 1 (TCWC); *LINCOLN CO.:* Capitan Mts., Summit of Ridge, W end, 2(H); Gallo Canyon, 40 mi. E Corona, 1(E); *OTERO CO.*(H): Alamo National Forest, Sacramento Mts., 7; Elk, 2; Mayhill, 1; Mescalero, 1; *SIERRA CO.*(B): Black Range, 1; Chloride, 6; Chloride, 20 mi. NW, 1; E Diamond Creek, 1; Fairview, 2; Fairview, 15 mi. NW Burnt Calvin Flat, 1; Gila National Forest, Black Range, 3; Monticello, 1; *SOCORRO CO.*(E): Carthage, 4; Magdalena, 3; Locality unspecified, 1; *TORRANCE CO.*(E): Mountainair, 1; *COUNTY UNSPECIFIED:* Datil National Forest(B), 1; Diamond A Ranch, 1; Gila National Forest(B), 5. TEXAS (males J, females L): *BREWSTER CO.:* Cathedral Mt. Ranch, 17 mi. S Alpine, 1 (SRSU); *CROCKETT CO.:* Ozona, Cat. N.H. Ranch, 2; *EDWARDS CO.:* Nueces River, 1; *HUDSPETH CO.:* Guadalupe Mts., Summit near NM Line, 1; *JEFF DAVIS CO.:* Ft. Davis, 1; *KIMBLE CO.:* Locality unspecified, 1; *LLANO CO.:* Llano, 15 mi. E, 1; *PRESIDIO CO.:* Marfa, 20 mi. SW, 1; *UPTON CO.:* Rankin, 3; *COUNTY UNSPECIFIED:* Neutral Strip, 1 (AMNH); Corner of Pecos, Brewster, and Terrell Counties, 1 (SRSU).

Canis lupus nubilus Say

KANSAS: *SHERMAN CO.:* Locality unspecified, 1 (KU); *TREGO CO.:* Castle Rock, near, 1 (KU). OKLAHOMA (males K, females L): *COMANCHE CO.:* Wichita Forest Reserve, 1; Wichita Mts. Mt. Tarbone, 1; *OTTAWA CO.:* Afton, 2 (AMNH); *COUNTY UNSPECIFIED:* Neutral Strip, Indian Territory, Beaver Creek, 1 (AMNH); No Man's Land, 3 (KU).

Canis lupus youngi Goldman

NEW MEXICO: *RIO ARRIBA CO.*(A): Abiquiu, 2 (FMNH, 1); Abiquiu, 18 mi. SW, 1; Cajalone (=Canjilon?), 3; Dulce, 1; Dulce, 35 mi. SW, 1; El Rito, 2; El Vado, 2; Tusas, 2; *SANDOVAL CO.*(A): Cuba, 3; Jemez, 1; Senorita, 2; Senorito, 20 mi. E Cebollo Creek, 1 (FMNH); *SAN JUAN CO.*(A): Haynes, 4; La Plata, 1; *SAN MIGUEL CO.*(A): Pecos Pueblo, 1 (AMNH); *SANTA FE CO.*(A): Lamy, 3.5 mi. NW, 1; Lamy, 15 mi. S, 1; *VALENCIA CO.*(A): San Mateo, 2; San Mateo Mts., 1. COLORADO: *COSTILLA CO.*(A): Ft. Massachusetts, 2.

Captive *Canis lupus*

ASDM Line. ARIZONA: *PIMA CO.:* Arizona Sonoran Desert Museum, 1 (Hankins). NEW MEXICO: *EDDY CO.:* Living Desert State Park, 6 (1, Ames); *RIO ARRIBA CO.:* Abiquiu, Ghost Ranch Museum, 2; *BERNALILLO CO.:* Rio Grande Zoo, 2 (Ames). TEXAS: *PRESIDIO CO.:* Alpine, Sul Ross State University (lineage unconfirmed), 1 (SRSU). WCSRC Line. MISSOURI: *ST. LOUIS CO.:* Wild Canid Survival and Research Center, 4 (WCSRC).

Canis latrans

MEXICO. CHIHUAHUA: Colonia Diaz, 1; Ojo Laguna, 1 (MVZ); SONORA: Sierra de Pinacate, Tinajas de los Papagos, 1 (MVZ). UNITED STATES. NEW MEXICO: *CATRON CO.:* Gila National Forest, 2; Quemado, 10 mi. SW, 1; *EDDY CO.:* Carlsbad, 30 mi. SE, 1.

Canis familiaris

MEXICO. CHIHUAHUA: Sierra Madre near Guadalupe y Calvo, 1. UNITED STATES. ARIZONA: *COUNTY UNSPECIFIED:* Big Smokey Creek, 1. NEW MEXICO: *CATRON CO.:* Locality unspecified, 1 (MSB); *OTERO CO.:* Sacramento Mts., 1; *SANDOVAL CO.:* Bernalillo, 5 mi. S, 1 (MSB); *SAN JUAN CO.:* Locality unspecified, 1 (Cole); *COUNTY UNSPECIFIED:* 1 (MSB).

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