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Abstract.—Any selective advantages of large body size may be counteracted by an increase in energetic costs associated with reproduction. In canids, larger female body size has been suggested to be associated with increasingly altricial young, larger litter sizes, and an increase in female pre- and postpartum energetic investment in offspring. It is hypothesized that the changing costs of reproduction with increasing body size result in a size-related diversity of canid reproductive life histories and social organization. Smaller canid species require less postpartum investment and thus tend toward polygyny and have a skewed dispersal ratio toward males. Larger species, with greater prepartum investment, require greater male investment in the rearing of offspring and thus tend to be group living. Using data on canid life histories, a phylogeny of the Canidae based on 383 base pairs of mitochondrial DNA, and an autoregressive comparative method, we found this hypothesis was not supported. Strong isometric relationships between neonate weight and female weight indicate that neonate size is constrained by female size directly or by parameters co-varying with female body size. Female weight accounted for only 26% of the variance in litter size, and no correlation was found between litter size and neonate weight. This result implies that female prenatal investment can be adjusted only by litter size (and not by neonate or litter weight), which in turn may be adjusted according to resource availability, an explanation supported by field and laboratory studies. In general, we hypothesize that much of canid interspecific and intraspecific variation in social structure may be explained by focusing on proximate environmental mechanisms, specifically resource availability.

Canids (family Canidae) are a diverse group of carnivores with a wide range of body weights (1–80 kg), dietary habits (omnivory to strict carnivory), and habitat preferences (from extreme deserts to ice fields to rain forests). The principal canid social system is monogamy (Kleiman 1977); however, widespread variation is observed in life-history traits (Gittleman 1986). Moehlman (1986, 1989) synthesized data on canid behavioral ecology and hypothesized that adult sex ratio, dispersal, mating, and neonate rearing systems are size related. In small canids (<6 kg), the adult sex ratio in social groups is biased toward females, young males tend to emigrate, and females stay in their natal ranges as helpers until a breeding opportunity arises. Medium-sized canids (6–13 kg) have an equal

adult sex ratio and an equal emigration rate, and both sexes may be helpers. Large-sized canids (>13 kg), excluding the maned wolf, *Chrysocyon brachyurus,* exhibit an adult sex ratio skewed toward males, female emigration, and male helpers. In this article, we reevaluate the hypothesis that the covariation of female body size and neonate size determines observed differences in social system among the three size classes of canids.

Previous comparative studies of canids have found significant allometric correlations between adult body weight and almost all life-history traits such as gestation length, birth weight, and litter weight (Bekoff et al. 1981, 1984; Gittleman 1986). Moehlman (1986) analyzed similar life-history data by examining the relative deviations of species values (residuals) from allometric regression lines and excluding outliers from the trends defined by the regression line. Her analysis indicated that neonate weight, litter size, litter weight, and gestation period were all correlated with female weight. Large canids have proportionally lighter neonates (regression slope of 0.76) but relatively larger litters (slope of 1.14). Therefore, females of large canids have larger litters of relatively smaller, more dependent neonates. As a consequence of these allometric patterns, the offspring of large canids have a longer period of dependency and require more male postpartum investment. Hence, in large canids, competition among females for males as helpers is more intense, which would drive the system toward polyandry. In contrast, the relatively heavy neonates of small canids constrain them to produce smaller litters of more precocial (relatively larger) neonates that require relatively less parental investment. This allows males to invest time and resources in additional females (polygyny) because competition for male parental investment is reduced (Fisher 1930; Trivers 1972). Consequently, canid mating systems and social organization are an outcome of the conflict between the effect of body size on reproductive traits and the constraints on females in obtaining resources for reproduction (Moehlman 1986).

These ideas raise several interesting problems. First, because large canids have a relatively longer gestation time (Gittleman 1986; Wayne 1986) but smaller young, prenatal growth rates are predicted to be relatively slower in large canids. The selective advantage of such reduced prenatal growth rates or smaller neonate size in large canids is unclear. Second, reproductive constraints of body size may also occur within species; thus, intraspecific shifts in social organization coinciding with litter size and body size should be observed. Although intraspecific variation in litter size, litter weight, and body size are documented for many canid species (see, e.g., Fuentes and Jaksič 1979; Gompper and Gittleman 1991), we are not aware of any study that reports intraspecific shifts in social organization consistent with observed variation in these traits. Finally, allometric correlations among body size, life-history traits, and social organization may not be phylogenetically independent; thus, evolutionary associations among taxa need to be considered (see Felsenstein 1985; Harvey and Pagel 1991; Gittleman and Luh 1992; Gittleman 1993). Also, related to comparative methodology, the exclusion of taxa should be based on criteria that are independent of the results of the analysis or have a precise statistical justification.

In this article, we assess the phylogenetic component of life-history variation

among canids using mitochondrial DNA sequence information and a phylogenetic autocorrelation analysis (Gittleman and Kot 1990; Gittleman and Luh 1992). Furthermore, in contrast to many other comparative studies, we directly estimate patristic distance among taxa from molecular data as an alternative to reconstructing distance based on taxonomic rank. Finally, we expand the comparative data originally synthesized by Moehlman (1986) and thus provide a more comprehensive test of hypotheses concerning the covariation of female body size and social organization in canids.

<div style="text-align:center">METHODS</div>

Moehlman's (1986) argument was based on allometric relationships between female body weight and four variables: mean gestation period, mean neonate weight, mean litter size, and litter weight (mean neonate weight × mean litter size). With the benefit of recent studies, we recompiled data for these traits from the literature and constructed a new data set for 24 canid species (table 1). To ensure appropriate species means, we used, whenever possible, several independent sources for each species. Additionally, to assess (indirectly) reproductive costs, we examined relative daily investment in individual neonates (neonate weight controlled for gestation time) and litters (litter weight controlled for gestation time) by regressing these parameters on female body weight.

To estimate evolutionary divergence between taxa, we sequenced 383 base pairs (bp) of the mitochondrial cytochrome b gene in 24 canid species. This region was sequenced following the protocol outlined elsewhere (Geffen et al. 1992a) for 10 species of foxlike canids. Pairwise sequence divergence values were corrected for multiple substitutions and transition/transversion bias using a Kimura two-parameter model and assuming a transition/transversion ratio of 6.0 based on the average of pairwise comparisons between all taxa. To assess whether divergence values would change substantially if an additional sequence were obtained for each species, we compared our sequence divergences values to those based on 2,001 bp of protein-coding sequence (730 bp of cytochrome b, 588 bp of cytochrome oxidase I, and 684 bp of cytochrome oxidase II) obtained for a reduced subset of 20 taxa (Gottelli et al. 1994; R. K. Wayne, unpublished data). The correlation between these two distance measures is high and significant (Mantel's test, $r = 0.9228$, $P < .001$), which indicates our distance matrix is representative of that based on a much larger analysis of protein-coding sequence. Finally, we constructed a maximum-likelihood tree using the Macintosh program PHYLIP (DNAML version 3.5c; Felsenstein 1993), assuming a transition/transversion ratio of 6.0 and using the global rearrangement option (fig. 1).

All size and life-history data were log transformed prior to analysis (table 1). To estimate phylogenetic correlation in the data, we used the Moran's (1950) I statistic, a measure of autocorrelation. In applying this statistic to comparative problems, previous researchers (Gittleman and Kot 1990) provided an equation for the maximum I and suggested scaling I relative to the maximum value (i.e., observed values are scaled between -1 and 1). Moran's I may be taken to be normally or randomly distributed (Cliff and Ord 1971, 1981). Using randomiza-

TABLE 1

Original and Corrected (see text) Reproductive Traits for 24 Canids

Species	Size	Original Data					Corrected Data					Source
		FW	G	LS	NW	LW	FW	G	LS	NW	LW	
Alopex lagopus	S	2.9	51.5	6.3	75.0	472.5	-.125	-1.532	1.082	-.690	-.241	1-5
Canis adustus	M	8.3	63.5	3.4	...	...	-.214	.789	-.599	...	...	6-8
Canis aureus	M	9.0	63.0	5.5	...	...	-.131	.689	.712	...	...	6, 9
Canis latrans	M	11.6	61.5	5.3	274.0	1,452.2	.125	.434	.611	.604	.625	10-17
Canis lupus	L	37.4	63.0	6.0	400.0	2,400.0	1.562	.690	.950	1.098	1.141	18-20
Canis mesomelas	M	7.1	60.0	3.5	197.5	691.2	-.398	.153	-.518	.226	-.061	7-9, 21-23
Canis simensis	L	14.5	60.0	4.0	...	...	.275	.154	.072	...	...	24
Cerdocyon thous	S	6.0	56.0	3.5	140.0	490.0	.128	-.603	-.518	-.187	-.380	9, 25
Chrysocyon brachyurus	L	22.7	64.0	2.2	385.0	847.0	.993	.861	-1.785	1.072	.164	6, 26, 27
Cuon alpinus	L	11.5	61.5	7.7	275.0	2,117.5	.170	.433	1.628	.639	1.033	28-30
Dusicyon culpaeus	M	6.7	57.5	5.5	168.0	924.0	.283	-.297	.712	.040	.241	6, 31, 32
Dusicyon griseus	S	3.3	55.5	4.0	...	...	-.643	-.705	-.154	...	...	6, 32-34
Dusicyon gymnocercus	S	4.2	57.5	3.4	...	...	-.353	-.297	-.599	...	...	6, 32, 35
Fennecus zerda	S	1.3	51.0	3.5	28.0	98.0	-1.049	-1.588	-.518	-1.729	-1.567	18, 36
Lycaon pictus	L	25.0	72.4	10.1	365.0	3,686.5	1.087	2.240	2.368	.989	1.594	6, 37-40
Nyctereutes procyonoides	S	4.0	61.5	6.0	110.0	660.0	.673	.757	.950	.523	.705	41-43
Otocyon megalotis	S	3.3	63.5	4.1	123.5	506.3	.457	1.113	-.085	.666	.449	44-47
Speothos venaticus	M	5.6	67.0	3.8	170.0	646.0	-.729	1.373	-.292	.009	-.112	48-52
Urocyon cinereoargenteus	S	3.5	59.0	4.2	86.0	361.2	.520	.298	-.022	.222	.127	53-56
Vulpes cana	S	1.1	55.0	2.0	29.5	59.0	-1.270	-.769	-2.042	-1.660	-2.086	57, 58
Vulpes chama	S	2.7	51.5	3.5	...	...	-.191	-1.513	-.518	...	...	59, 60
Vulpes macrotis	S	1.9	52.0	4.5	39.9	179.6	-.655	-1.429	.166	-1.519	-1.231	61-63
Vulpes rueppelli	S	1.7	...	2.5	...	...	-.788	...	-1.434	...	...	6, 64
Vulpes vulpes	S	4.0	53.0	4.0	104.0	413.9	.273	-1.252	-.167	-.303	-.399	5, 66-69

Note.—FW is mean female weight (kg), G is mean gestation time (d), LS is mean litter size, NW is mean neonate weight (g), and LW is litter weight (g). Size classes: S < 6 kg, M = 6–13 kg, and L > 13 kg. Sources: 1, Banfield 1974; 2, Chesemore 1975; 3, Eberhardt et al. 1983; 4, Garrott and Eberhardt 1987; 5, Novikov 1962; 6, Ginsberg and Macdonald 1990; 7, Kingdon 1977; 8, Skinner and Smithers 1990; 9, Moehlman 1986; 10, Andrews and Boggness 1978; 11, Bekoff 1977; 12, Berg and Chesness 1978; 13, Gier 1968; 14, Hawthorne 1971; 15, Kennelly 1978; 16, Knowlton 1972; 17, Nellis and Keith 1976; 18, Bekoff and Jameson 1975; 19, Mech 1970; 20, Mech 1974; 21, Moehlman 1979; 22, Rowe-Rowe 1978; 23, Stuart 1981; 24, Sillero-Zubiri and Gottelli 1994; 25, Brady and Ditton 1979; 26, Brady 1978; 27, Dietz 1985; 28, Cohen 1978; 29, Johnsingh 1982; 30, Sosnovskii 1967; 31, Crespo and Carlo 1963; 32, Crespo 1975; 33, Johnson 1992; 34, Redford and Eisenberg 1992; 35, Crespo 1971; 36, Koenig 1970; 37, Dekker 1968; 38, Frame and Frame 1976; 39, Frame et al. 1979; 40, Van Heerden and Kuhn 1985; 41, Ikeda 1983; 42, Valtonen et al. 1977; 43, Ward and Wurster-Hill 1990; 44, Lamprecht 1979; 45, Malcolm 1986; 46, Smithers 1971; 47, Smithers 1983; 48, Collier and Emmerson 1973; 49, Jantschke 1973; 50, Kitchner 1971; 51, Porten 1983; 52, Porten et al. 1987; 53, Fritzell and Haroldson 1982; 54, Fritzell 1987; 55, Samuel and Nelson 1982; 56, Sullivan 1956; 57, Geffen 1990; 58, Geffen et al. 1992; 59, Brand 1963; 60, Bester 1982 (in Skinner and Smithers 1990); 61, Egoscue 1962; 62, Grinnell et al. 1937; 63, Morrell 1972; 64, Mendelssohn et al. 1987; 65, Kilgore 1969; 66, Harris 1979; 67, Smith 1939 (in Sheldon 1949); 68, Storm and Ables 1966; 69, Storm et al. 1976.
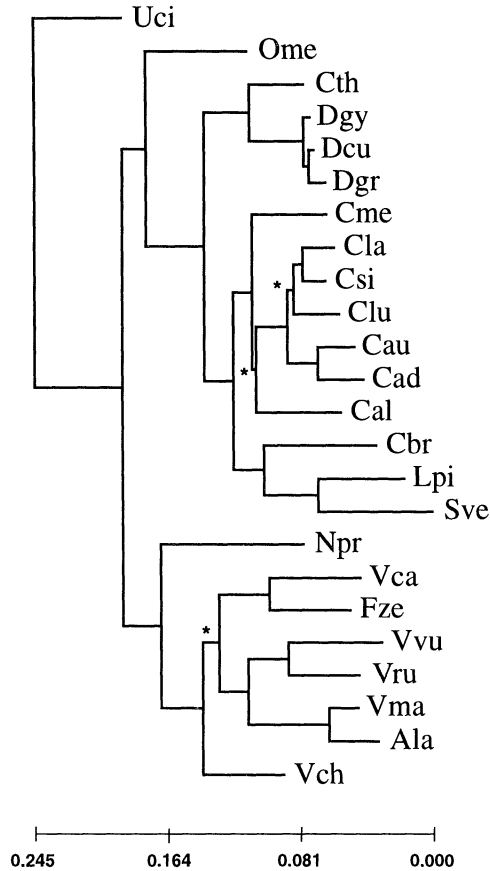
FIG. 1.—A maximum-likelihood tree for 24 species of canids based on 383 bp of cytochrome *b* sequence (transition/transversion ratio = 6.0, DNAML, PHYLIP; Felsenstein 1993). Ln likelihood = $-2,949.07$, and 8,160 trees were examined. Nodes that were not significantly different from zero are marked by an asterisk. Key to species: *Uci, Urocyon cinereoargenteus; Npr, Nyctereutes procyonoides; Ome, Otocyon megalotis; Fze, Fennecus zerda; Vca, Vulpes cana; Vru, Vulpes rueppelli; Vvu, Vulpes vulpes; Vma, Vulpes macrotis; Ala, Alopex lagopus; Vch, Vulpes chama; Sve, Speothos venaticus; Cbr, Chrysocyon brachyurus; Lpi, Lycaon pictus; Clu, Canis lupis; Cla, Canis latrans; Csi, Canis simensis; Cau, Canis aureus; Cme, Canis mesomelas; Cal, Cuon alpinus; Cad, Canis adustus; Cth, Cerdocyon thous; Dgr, Dusicyon griseus; Dcu, Dusicyon culpaeus; Dgy, Dusicyon gymnocercus.*

tion, we tested the null hypothesis of no phylogenetic autocorrelation at the 0.05 level by using a z-test to examine whether I varies from an expected value by more than 1.96 standard deviations (Gittleman and Kot 1990). Using a correlogram, which shows how autocorrelation (I/I_{max}) varies with phylogenetic (genetic) distance (fig. 2), we located where in the tree traits are phylogenetically correlated. Using molecular phylogenetic information, we averaged over all species within some fine interval of distance, set in accord with the distribution of values
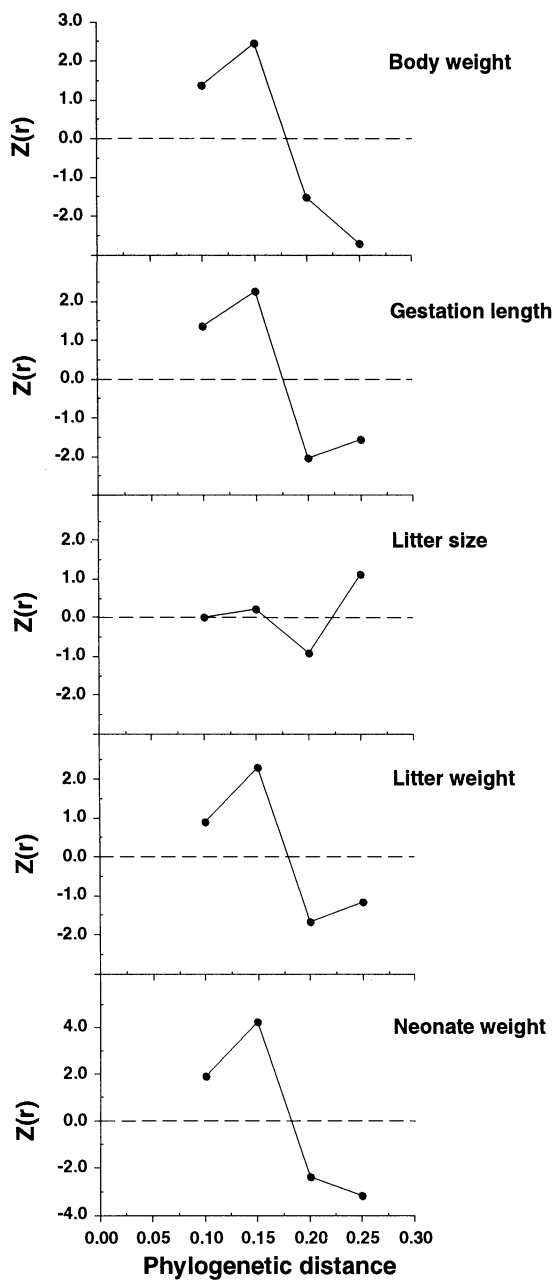
FIG. 2.—Correlograms for all five life-history traits examined. The null hypothesis of no phylogenetic autocorrelation at the 0.05 level is tested here by using a $Z(r)$-test to examine whether Moran's I varies from an expected value by more than 1.96 SDs. All traits, excluding litter size, show Z values higher than 1.96 (or lower than -1.96) at one or more phylogenetic distances.

of the original genetic distance matrix (table 2; see Purvis et al. 1994), and then calculated correlations at those distance intervals. The observed intervals are 0.1, 0.15, 0.2, and 0.25. Correlograms showing the correlation of each trait at these intervals are given in figure 2. We then used Cheverud et al.'s (1985) autoregressive model to remove the observed phylogenetic autocorrelation. The model takes the form

$$\mathbf{y} = r\mathbf{Wy} + e ,$$

where $\mathbf{y}$ is the vector of standardized trait values, $r\mathbf{Wy}$ is the phylogenetic component (i.e., the observed relation between phylogenetic distance and the trait values among taxa), and e the residual vector that is free of phylogenetic correlation. This technique uses a maximum-likelihood function to fit the observed trait values on the phylogenetic tree, as presented elsewhere (Gittleman and Kot 1990). Recent simulation studies indicate that the autoregressive approach is statistically robust when phylogenetic correlation is indeed observed in the comparative data and when phylogenetic information (genetic distance) is based on relatively small samples of less than 50 species (Gittleman and Luh 1992, 1994; Purvis et al. 1994). Both conditions are met in the present analysis.

After accounting for phylogenetic effects, the data were standardized to a mean of zero and standard deviation of one and then used to investigate associations of life histories with female body weight via least-squares linear regression. We controlled for the effect of gestation time on litter weight by using the residuals generated from the regression of these two traits as the dependent variable in the regression of litter weight on female body weight. Similarly, neonate weight was controlled for the effects of gestation time, and these were defined in this article as energetic daily investment in neonates and litters, respectively. Litter size and neonate weight were controlled for the effects of female weight in a similar manner. Finally, to test directly the Moehlman (1986) hypothesis, we classified all species into three size classes: small canids—species mean body weight < 6.0 kg; medium canids—species mean body weight of 6.0–13.0 kg; and large canids—species mean body weight > 13.0 kg (see table 1).

RESULTS

The phylogenetic tree generated by the maximum-likelihood algorithm showed all branch lengths, except three, were significantly different from zero ($P < .05$; fig. 1) and were largely consistent with past analyses based on molecular or karyological data (Wayne et al. 1987; Wayne 1993). We examined the degree of autocorrelation in five traits across the four specified intervals of phylogenetic distance and found that the Moran's I-test showed significant phylogenetic correlation in all the traits except for litter size (fig. 2; table 2) (see Gittleman and Kot 1990). For the four variables showing significant autocorrelation, we then examined the autoregressed data (table 1) through a Moran's I statistic and verified that the transformed comparative data were not phylogenetically correlated at any phylogenetic distance ($-1.96 < Z[r] < 1.96$ in all cases).

Using the autoregressed data, we analyzed relationships between mean female

TABLE 2

Divergence (above diagonal) and Number of Substitutions (below diagonal) among 24 Canids in 383 bp of Cytochrome *b* Sequence

|	Uci	Npr	Ome	Vca	Vch	Vru	Ala	Fze	Vvu	Vma	Sve	Clu	Cla	Csi	Cal	Lpi	Cme	Cad	Cau	Cth	Dgr	Dcu	Dgy	Cbr
Uci		.179	.181	.196	.199	.184	.214	.196	.159	.207	.189	.186	.200	.196	.178	.201	.183	.168	.148	.200	.178	.189	.189	.218
Npr	58		.177	.194	.151	.169	.171	.184	.170	.160	.235	.204	.196	.196	.196	.183	.175	.184	.196	.215	.178	.189	.189	.199
Ome	59	58		.158	.137	.160	.198	.151	.160	.180	.222	.155	.165	.168	.141	.176	.145	.145	.142	.122	.145	.141	.138	.179
Vca	62	62	52		.128	.150	.172	.107	.118	.147	.191	.159	.152	.163	.180	.203	.195	.170	.164	.178	.166	.163	.170	.202
Vch	63	50	46	43		.115	.161	.126	.141	.136	.212	.147	.164	.154	.185	.178	.164	.161	.162	.179	.157	.154	.161	.200
Vru	57	54	51	48	38		.145	.152	.104	.130	.220	.199	.192	.207	.196	.197	.217	.181	.195	.193	.174	.163	.178	.215
Ala	66	55	62	55	52	47		.178	.164	.050	.238	.210	.184	.202	.206	.227	.192	.218	.204	.226	.199	.202	.202	.250
Fze	63	60	51	37	43	49	57		.142	.151	.136	.161	.148	.148	.161	.169	.170	.132	.143	.168	.151	.148	.155	.175
Vvu	52	56	53	40	47	35	53	48		.146	.179	.174	.154	.171	.150	.179	.168	.168	.155	.171	.154	.150	.164	.204
Vma	66	53	59	49	46	43	18	51	49		.192	.184	.143	.170	.170	.185	.178	.177	.175	.202	.167	.170	.170	.206
Sve	61	73	71	61	67	67	72	46	58	62		.146	.120	.123	.150	.121	.150	.137	.137	.150	.137	.140	.140	.146
Clu	60	65	52	52	49	62	65	54	57	60	50		.054	.046	.096	.149	.099	.078	.063	.096	.105	.102	.102	.129
Cla	64	63	55	50	54	60	58	50	51	48	42	20		.035	.102	.136	.099	.078	.066	.114	.111	.114	.108	.123
Csi	63	63	56	53	51	64	63	50	56	56	43	17	13		.099	.133	.078	.063	.069	.105	.096	.099	.093	.120
Cal	58	63	48	58	60	61	64	54	50	56	51	34	36	35		.117	.099	.097	.100	.124	.137	.140	.140	.130
Lpi	64	59	58	64	58	61	69	56	58	60	42	51	47	46	41		.127	.134	.134	.137	.124	.127	.134	.146
Cme	59	57	49	62	58	66	60	56	55	58	51	35	35	28	35	44		.097	.093	.125	.121	.118	.118	.140
Cad	55	60	48	55	53	57	67	45	55	58	51	28	28	23	34	46	34		.052	.115	.118	.121	.121	.124
Cau	49	63	42	53	53	60	63	48	51	57	47	23	25	24	35	46	33	19		.128	.109	.112	.112	.134
Cth	64	68	49	57	58	60	69	56	56	65	47	34	40	37	43	47	43	40	44		.078	.075	.069	.127
Dgr	58	58	48	54	52	55	62	51	51	55	51	37	39	34	47	43	42	41	38	28		.013	.018	.124
Dcu	61	61	61	53	51	52	63	51	50	56	48	36	40	35	48	44	41	42	39	27	5		.010	.140
Dgy	61	61	47	55	53	56	63	52	54	56	48	36	38	33	48	46	41	42	39	25	7	4		.140
Cbr	69	64	59	64	64	66	75	58	65	66	50	45	43	42	45	50	48	43	46	44	43	48	48	

Note.—For key to species, see fig. 1.
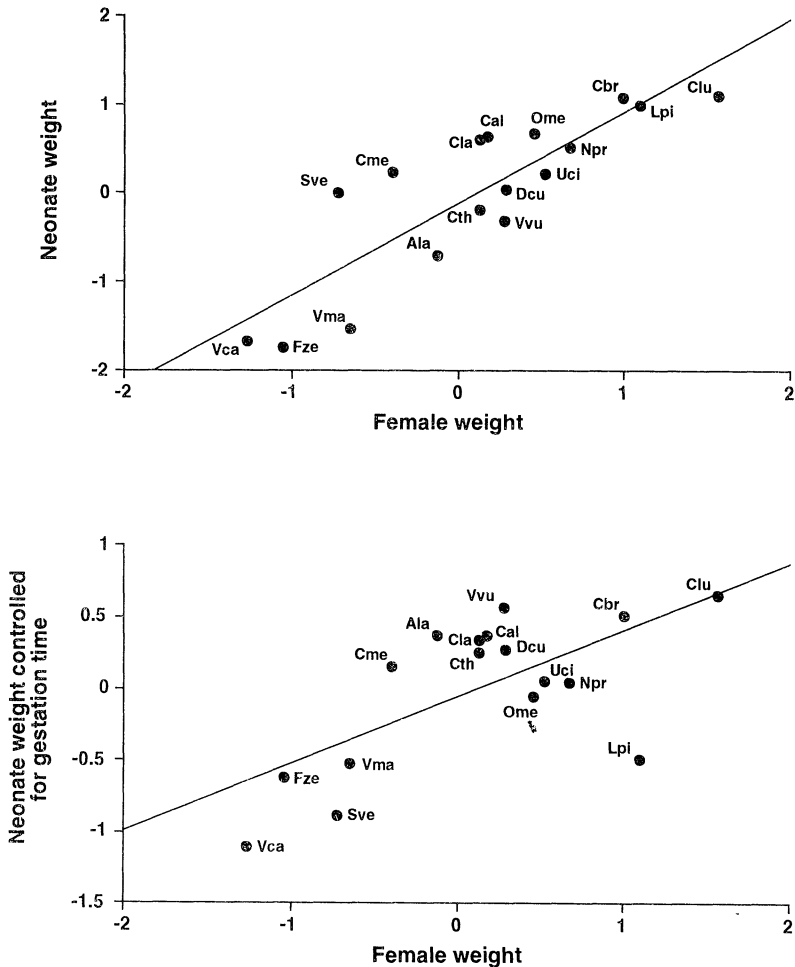
FIG. 3.—The relationship of mean female body weight with mean neonate weight (*top*, $y = 1.03x - 0.12$; $r^2 = 0.73$) and with mean neonate weight controlled for the effect of gestation time (*bottom*, $y = 0.47x - 0.06$, $r^2 = 0.45$). All traits are adjusted for phylogeny. For key to species, see fig. 1.

body weight and five variables: mean neonate weight, litter weight, mean litter size, and energetic daily investment per neonate (mean neonate weight controlled for gestation time) and per litter (mean litter weight controlled for gestation time). Mean neonate weight and daily investment per neonate were significantly and positively correlated with mean female body weight ($r = 0.853$, $P < .0001$; and $r = 0.673$, $P = .003$, respectively; fig. 3). Litter size was significantly and positively correlated with mean female body weight ($r = 0.508$, $P = .01$; fig. 4). Litter weight, and litter weight controlled for the effect of gestation period, were significantly correlated with mean female body weight ($r = 0.835$, $P < .0001$; and $r = .678$, $P = .008$, respectively; fig 4). Both neonate weight and mean litter
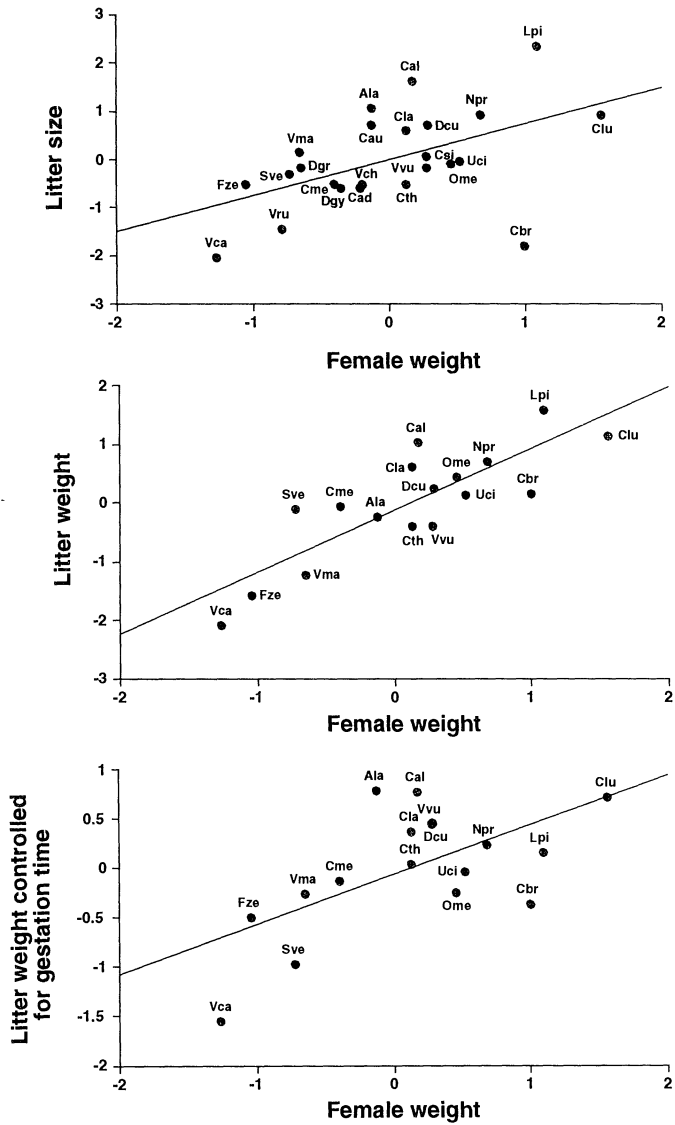
FIG. 4.—The relationship of mean female body weight with mean litter size (*top*, $y = 0.75x + 0.00003$; $r^2 = 0.26$), mean litter weight (*middle*, $y = 1.05x - 0.13$, $r^2 = 0.70$), and mean litter weight controlled for the effect of gestation time (*bottom*, $y = 0.51x - 0.06$, $r^2 = 0.38$). All traits are adjusted for phylogeny. For key to species, see fig. 1.
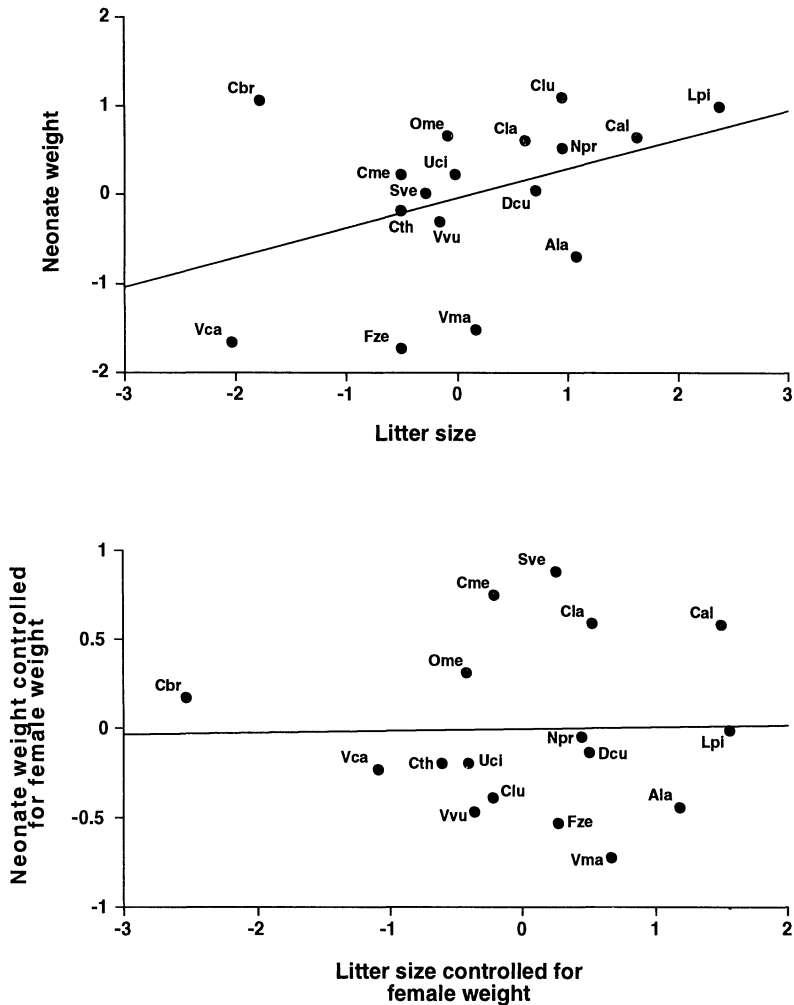
FIG. 5.—The relationship of mean neonate weight with mean litter size (*top*, $y = 0.33x - 0.05$, $r^2 = 0.16$) and mean nenonate weight controlled for female body weight with mean litter size controlled for female body weight (*bottom*, $y = 0.01x + 0.0004$, $r^2 = 0.0004$). All traits are adjusted for phylogeny. For key to species, see fig. 1.

weight are a constant proportion of female body weight (isometric regression slopes of 1.03 and 1.05, respectively). In contrast, all other significant allometric relationships scale with slopes of less than one. Finally, nonsignificant correlations were observed between neonate weight and litter size ($r = 0.404$, $P = .108$; fig. 5) and between these traits when both were controlled for female body weight ($r = 0.02$, $P = .938$; fig. 5). That is, residuals for litter size showed no correlation with the residuals for neonate weight.

In sum, among canids, neonate weight and litter weight are positively correlated with female weight. However, larger canids do not have relatively smaller

young. Further, although the correlation between maternal weight and litter size is significant, it explains only 26% of the observed variance, and the regression slope is less than one. Last, after controlling for phylogeny, neonate weight is independent of litter size.

<center>DISCUSSION</center>

Size and Life-History Patterns

An analysis of data corrected for phylogenetic correlations indicates that neonate weight and litter size, controlled for female body weight, are not correlated. Moreover, the correlation between litter size and female body weight is weak, with only 26% of the variance explained by the regression. Therefore, our results do not support the idea that body size imposes different energetic constraints on reproduction in small and large canids and influences their social organization. Differences in the results of this study and previous analyses (Bekoff et al. 1981; Gittleman 1986; Moehlman 1986) highlight the power of modern comparative methods using molecular phylogenetic data and suggest a reinterpretation of the relationships between canid life histories and social organization.

The high correlation and isometric relationship between neonatal weight and female body weight (r = 0.85) implies that the size of young is constrained directly by female size or possibly by indirect allometric parameters that parallel those constraining female size. One such parameter might be female pelvic width, which, as suggested for primates, limits neonate size (Leutenegger 1982); unfortunately, data on pelvic width across most canids are currently unavailable. In contrast, litter size is weakly and nonisometrically correlated with female body weight (r = 0.51), which suggests a greater potential to respond to differing selective pressures. Litter weight showed a significant relationship with female body size but explained only 38% of the observed variance when controlled for gestation time. Thus, body size allometry alone is not enough to explain variance in litter size. Moehlman (1986) found significant allometric correlations in litter size and litter weight when outliers were excluded from the analysis, a posteriori. In general, large sample sizes can reveal weak but significant correlations, and correlations can be improved by excluding outliers a posteriori. The combination of both should be used with caution. Indeed, as often pointed out in comparative allometric studies (see Schmidt-Nielsen 1984; Harvey and Pagel 1991), outliers are especially instructive for revealing functional relationships, and their exclusion may disguise empirical relationships.

Two general aspects of the allometry of mammalian life histories are relevant to our discussion. First, based on many comparative studies of phylogenetically independent groups, body size alone is a poor explanatory factor of variation in life-history traits (Harvey et al. 1989; Gittleman 1993): species with different body sizes (e.g., the giant panda and the long-tailed weasel) often have similar life histories (e.g., small neonate weights and slow growth rates). Second, Charnov's (1991, 1993) unified model of mammal life histories shows that, independent of size, life-history traits (particularly age at sexual maturity and growth rate) are

determined by adult mortality rate so as to maximize lifetime reproductive success. Empirical support for the model is found across eutherian mammals as a whole (Harvey et al. 1989; Berrigan et al. 1993) and carnivores in particular (Gittleman 1993). The key variable for testing the model is mortality rate, preferably measured when populations across species are at equilibrium. A previous review (see Gittleman 1993) of the literature on carnivore mortality schedules revealed information on mortality rates for only four canid species (*Canis lupus, Canis latrans, Vulpes vulpes, Urocyon cinererargenteus*). Thus, the present analysis cannot incorporate this life-history model.

Moehlman (1986) suggests that litter size and litter weight determine the social organization of a species by constraining a female's ability to provision her offspring, as implied by Fisher's (1930) theory on parental investment. She argues that females with large litters require greater nutritional investment and consequently the assistance of other adults (perhaps males) to help provision the pups. By contrast, in species with small litters, less parental investment is required, which allows the male to invest in more than one female. Moehlman argues that neonates are more altricial (relatively smaller) in species with large litters and more precocial (relatively larger) in species with small litters. This observation leads to the prediction that as litter size increases, neonates will be relatively smaller. Our analyses indicate that large canids do not have relatively smaller neonates (fig. 3). In addition, the lack of correlation between relative litter size and relative neonate weight implies that no general energetic linkage exists between these variables. In fact, because neonatal weight is tightly linked with and perhaps narrowly constrained by body size, the variance in female prebirth investment can only be adjusted by litter size. This interpretation is supported by intraspecific empirical studies. Intraspecific studies can help explain causal relationships of comparative interspecific patterns (Moehlman 1986, 1989; Gompper and Gittleman 1991). A series of elegant field experiments demonstrated that food given to Arctic foxes (*Alopex lagopus*) during the winter increased reproductive success as indicated by larger litters and more breeding pairs (Angerbjörn et al. 1991). More generally, in five of eight studies involving food supplementation to different mammal species, there was an increase in litter size (Boutin 1990). Last, canids show declines in litter size with decreases in prey abundance (Macpherson 1969; Harrington et al. 1983; Lindström 1989; Hersteinsson and Macdonald 1992). From these comparative trends, both intra- and interspecific, we therefore hypothesize that litter size has intrinsic variability, which permits females to adjust their investment according to the availability of resources.

In general, a positive relationship exists within species between body size and food abundance (Gittleman 1985; Geist 1987; Gompper and Gittleman 1991). Changes in body size, litter size, and social organization within the Canidae may be attributed as a response to food availability. Body size co-varies to some degree with availability of food in different geographical localities. Very small canids (e.g., *Fennecus zerda*) are usually associated with arid and poor habitats in which only a small body mass can be supported year-round. In contrast, large canids (e.g., *Canis simensis, Lycaon pictus*) are often associated with habitats in which prey is abundant. Litter size and group size exhibit similar patterns (Bekoff

et al. 1984; Nel et al. 1984; Angerbjörn et al. 1991). Carnivore species living in areas with low food availability have small litters and live in pairs or small groups, whereas species inhabiting areas where food is abundant have large litters and live in large groups (Kruuk and Parish 1982; Carr and Macdonald 1986).

For example, the maned wolf, *Chrysocyon brachyurus,* is a large canid that occupies South American savannas and feeds largely on rodents and fruit (Dietz 1985). During the Pleistocene, four other large canids (genus *Canis* and *Protocyon*) inhabited these savannas, which were rich in large prey (Berta 1987). At the end of the Pleistocene, all the large South American canids except *Chrysocyon* went extinct as a probable result of a sharp decline in large herbivorous prey (Berta 1987; Pascual and Jaureguizar 1990). Today, low food availability in this habitat relative to the large body size of maned wolves probably constrains litter size to a mean of 2.2 pups. If body size in the maned wolf is inflexible (e.g., as a result of interspecific competition; Fuentes and Jaksič 1979; Dayan et al. 1989), then only group and litter sizes could have been reduced to accommodate the present level of food abundance.

Alternative Hypotheses Regarding Social Organization

Within and among species, canid societies are characterized by three potentially interrelated attributes: mating or social system, sex ratio, and helping behavior (the extent of helping and the sex of helpers). The intra- and interspecific variation in these traits may be explained by shifting attention from solely allometric explanatory mechanisms to environmental mechanisms (Geffen and Macdonald 1992). For example, empirical studies on primates and rodents have shown that social organization may change as a result of fluctuations in food abundance and habitat patchiness (see, e.g., Milton and May 1976; Travis and Slobodchikoff 1993). Moreover, recent quantitative analysis across 53 primates and 39 carnivore species suggests that variation in group size is constrained by feeding competition (Wrangham et al. 1993). A compelling example of a shift in canid social organization in response to a change in food availability is provided by a study of a small population of red foxes (*V. vulpes*) on Round Island, Alaska (Zabel and Taggart 1989). This study documented a shift from 71% polygyny when food was superabundant to 100% monogamy when prey abundance decreased dramatically, with a concomitant decrease in litter size. If an increase in food availability permits an increase in litter size, then males could afford to invest in more than one female only when prey is especially abundant. On the other hand, if litter size determines social organization in canids, then within species like the arctic fox, in which litter size ranges from three to nine, females with large litters might be expected to tend toward polyandry, and females with small litters might be expected to shift toward polygyny. The published intraspecific canid field studies do not support such a trend (see, e.g., Angerbjörn et al. 1991).

The example of the red foxes on Round Island may be extended to help explain differences in social organization among other canid species. It has been demonstrated that helpers in canid societies may contribute to the survival of the pups (Macdonald 1979; Moehlman 1979; Malcolm and Marten 1982; Harrington et al. 1983). In small canids, adult sex ratio is biased toward females, males generally

emigrate, and females stay in their natal ranges as helpers (e.g., *V. vulpes:* Macdonald 1979). In large canids, adult sex ratio is biased toward males, females emigrate, and males stay as helpers (e.g., *L. pictus:* Malcolm and Marten 1982). Midsized canids have an approximate 1:1 sex ratio and equal probability of having a male or a female helper (e.g., *Canis mesomelas:* Moehlman 1986). Moehlman hypothesizes that in large canids, females require more male investment because of their large altricial litters, and in small canids females require less paternal investment, which thus reduces competition among females for males. Why are male helpers better than female helpers in the societies of large canids? Helpers contribute to pup survival by providing food (regurgitating or carrying it to the den), guarding, and grooming and playing with pups. There is little evidence that female helpers allosuckle the dominant female's pups except when two females give birth at the same or neighboring dens (Macdonald 1979; Malcolm and Marten 1982; Zabel and Taggart 1989). In the African hunting dog (*L. pictus*), in which intragroup sex ratio is usually male biased, dimorphism is small and females are known to participate in and successfully to lead hunts (Malcolm and Marten 1982; Fanshawe and FitzGibbon 1993). On the other hand, observational data on gray wolves, *C. lupus,* suggest an equal sex ratio in many populations (Mech 1970; Gese and Mech 1991). In sexually dimorphic canid species that hunt communally, male helpers may be able to handle larger prey and return more food to the pups. Thus, females might increase the contribution of helpers to their litter by producing more males. One factor that might affect the sex ratio of helpers is that male bias in adulthood could arise from selection operating on sex ratio at birth. A skewed sex ratio within litters could result from intense competition within litters, siblicide, or genetic determination (Malcolm and Marten 1982). In the red fox, for which adult sex ratio is biased toward females, the sex ratio at birth favors females in at least one large sample (94 males:100 females, $n = 4,551$; Layne and McKeon 1956). Complete or partial dominance in mating by the alpha male has been observed in all canid species studied. Therefore, if a skewed birth sex ratio in a population persists to adulthood, then unpaired individuals of the majority sex would have no choice but to wait in their natal pack until a breeding opportunity arises. Such a scenario would suggest that in the Canidae, sex ratio among adults within social groups could be determined by birth sex ratio, which in turn is determined by selective pressures to maximize reproductive success.

   In small canids, what selective pressures might favor a female-biased sex ratio at birth? Small canids tend to be sexually dimorphic with females being the smaller sex. Females of small canids may thus require less parental investment to reach adulthood. Conceivably, birth sex ratio in the Canidae may be related to food availability; limited food resources during pregnancy may select for female-biased litters (Trivers and Willard 1973). Experimental studies on white mice and golden hamsters have demonstrated that low-fat diets produce litters skewed considerably toward females, whereas balanced diets produced equal sex ratios (Rivers and Crawford 1974; Labov et al. 1986). If this relationship exists in canids, then a change in birth sex ratio across species may co-vary with habitat quality, as was previously suggested for body size and litter size covariance.

In conclusion, shifts in the sex ratio, composition of helpers, and social system among canids of different body size cannot be explained solely as a result of differences in litter size and female body size. Data on the effect of food availability on birth sex ratio in canids, and experimental field data on the contribution of helpers in different species, are essential for resolving the causes underlying differences in sex ratios of helpers among canid societies.

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