

CARNIVORE LIFE HISTORY PATTERNS:  
ALLOMETRIC, PHYLOGENETIC, AND ECOLOGICAL ASSOCIATIONS

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Previous approaches to life history problems are considerably varied, and reviews may be found in Stearns (1976, 1977, 1980), Southwood (1976), Horn (1978), Horn and Rubenstein (1984), Western and Ssemakula (1982), and Calder (1984). In general, three factors have been shown to correlate with interspecific differences in life histories across mammals: size, phylogeny (taxonomy), and ecology.

Size (primarily body weight) appears as an important variable in analyzing life history variation because most life history traits correlate with the rate of physiological activity and consequently with size (Huggett and Widdas 1951; Leitch et al. 1959; Millar 1977, 1981; Western 1979; McNab 1980; Lindstedt and Calder 1981; Calder 1984). Assuming that size must be considered when analyzing life histories, two problems should be addressed. First, the allometric relationship of many life history variables is not constant (Gould 1966, 1971). Numerous studies (e.g., Sacher and Staffeldt 1974; Millar 1977, 1981; Case 1978) have drawn conclusions about mammalian life history evolution by combining taxa (e.g., rodents, ungulates) that are heterogeneous in slope and therefore have differences in scaling. Certainly, extreme care must be taken before comparing trends between variables that are different in form among taxa (see Clutton-Brock and Harvey 1984).

When allometric effects of life histories are considered, some index of size must be removed. Most studies have used body weight as the independent variable, arguing that weight reflects metabolic rate, which in turn regulates reproductive effort (Calder 1984). Sacher (1959) and Sacher and Staffeldt (1974), however, found that brain weight, rather than body weight, accounted for a greater proportion of the variance in life span and gestation time. They argued that the slow growth of neural tissue constrains somatic cell proliferation, thus slowing the reproductive rate of large-brained mammals. Support for this hypothesis has been

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mixed: comparative data reveal that brain weight correlates more highly than body weight with longevity in birds (Lindstedt and Calder 1976), primates (Harvey and Clutton-Brock 1985), and small mammals (Mace 1979), with weaning age and age of sexual maturity in small mammals (Mace 1979), and with gestation time and life span across mammals (Sacher 1959; Sacher and Staffeldt 1974). By contrast, body weight correlates more highly than brain weight with litter weight and estrous-cycle length in small mammals (Mace 1979). Other variables, such as inter-birth interval and neonatal weight, seem to correlate equally well with both morphological characters. Attempts to partition the relative amount of variance explained by brain weight or by body weight are hampered by the close interrelationship of the two variables (Gould 1966; Jerison 1973; Clutton-Brock and Harvey 1980; Gittleman 1986) and by the variation in body weight resulting from fat deposits (Lindstedt and Calder 1981). Furthermore, Martin (1981, 1983) has recently shown that of the two, brain size, not body size, may be more closely linked to maternal metabolic rate and that metabolism may consequently be the more relevant constraint on life histories (see Harvey and Bennett 1983). Additional empirical and theoretical work is required before any decisive statement can be made on this problem. For the present study I have retained both morphological characters as separate independent variables before attempting taxonomic or ecological comparisons of life histories.

After removing allometric effects, some studies have detected significant taxonomic effects, which have been (conservatively) interpreted as phylogenetic. In every comparative study that has considered variation in relative life histories between orders or between families within orders, significant differences were found (Mace 1979; Stearns 1983; Harvey and Clutton-Brock 1985). Such taxonomic effects present two problems. First, if taxonomic effects are detected at a taxonomic level below that at which the analysis is performed, then searching for ecological trends becomes meaningless unless these differences are accounted for; analyzing life history differences across species at various independent levels (e.g., family, order) is one method for simultaneously examining phylogenetic and ecological effects (see Harvey and Mace 1982; Clutton-Brock and Harvey 1984). Second, and more problematical, once phylogenetic relationships are inferred from comparative life history data, it is impossible to give an adequate phylogenetic explanation without an unusually complete knowledge of the taxonomy. Nevertheless, as Felsenstein eloquently stated, "efforts to cope with the effects of phylogeny will have to be made. Phylogenies are fundamental to comparative biology; there is no doing it without taking them into account." (1985, p. 14.)

Finally, once allometry and phylogeny have been considered, we can safely approach traditional questions of ecological (adaptive) patterns in life histories. Cross-species comparisons have revealed a multitude of environmental factors associated with mammalian life histories (e.g., Fleming 1977; Mace 1979; May and Rubenstein 1985). Generally, however, the availability and quality of food resources are considered the primary ecological variables influencing mammalian life histories (see Millar 1981). Increased food resources, it is argued, may allow for faster growth rates, larger litters, and frequent reproduction. Few comparative studies, though, have actually demonstrated dietetic effects, and even fewer

studies have shown ecological associations once size and phylogeny have been considered. I analyze comparative life history patterns across carnivores in relation to activity rhythm, habitat, zonation, and diet.

Cross-species comparisons of life history traits in the order Carnivora reveal extensive differences in the rates and modes of reproduction (Ewer 1973; Bekoff et al. 1984; Gittleman 1984), thus indicating considerable variation for studying allometric, phylogenetic, and ecological associations. Aside from a qualitative overview by Ewer (1973) and a quantitative analysis by Bekoff et al. (1981) on the Canidae, no study has examined life history patterns across the Carnivora. Here I analyze eight life history traits in carnivores in relation to allometric, phylogenetic, and ecological variation.

#### METHODS

##### *Data Sources*

Information on carnivore life histories and body weight were taken primarily from original published sources and, when these were unavailable, occasionally from review compilations; information from review volumes was verified against additional sources (table 1; abbreviated data-source references are listed in the Appendix). Data from natural populations were preferred over information from zoo or captive populations; however, life history data for most carnivores are available only for captive animals. These data were used when values for numerous individuals had been collected, on the grounds that for certain well-studied species (e.g., *Canis lupus*, *C. latrans*, *Vulpes vulpes*, *Procyon lotor*, *Panthera leo*) trends observed in captive animals were comparable to those seen in natural populations (particularly for the variables of gestation length, birth weight, and litter weight). Medians were calculated of data from geographically diverse populations. All analyses used values from "congeneric" species—species within a genus having similar ecological traits (see Clutton-Brock and Harvey 1977; Gittleman 1986)—to ensure greater independence of species points. Data on brain weight and ecology were taken from Gittleman (1984, 1985a, 1986).

##### *The Variables*

1. Litter size: average number of offspring at birth.
2. Gestation length: average time from conception to birth (days). The period of delayed implantation was excluded in those species having this characteristic (e.g., *Mustela americana*).
3. Birth weight: average weight of the young at birth (g).
4. Litter weight: litter size multiplied by birth weight (g).
5. Weaning age: length of time from birth to independence of the neonate from maternal milk (days). In cases in which a range was quoted to represent partial to complete weaning, the latter figure was used to more accurately reflect nutritional independence.
6. Age of independence: age when the juvenile disperses from its natal territory or, in group-living species, is independent of parental care (days).

7. Longevity: age of the oldest individual recorded in captivity (mo). Some data were analyzed of longevity records from natural populations, however, and these are distinguished in the Discussion section.

8. Age of sexual maturity: age at first conception (days). In some species (e.g., *Ursus americanus*, *M. frenata*), males and females reach sexual maturity at markedly different ages. Therefore, averages were calculated when data were available for each sex; otherwise, species were excluded so as not to introduce error.

9. Inter-birth interval: period between successive births (mo). It should be noted that inter-birth interval, as used here, is distinguished from other definitions that add the gestation period to the lactation period to equal inter-birth interval (Hayssen 1984). Such a definition is incorrect to use for species that typically have a resting period between successive births (e.g., ursids).

10. Ecological variables. Species were assigned to one type in each of the following ecological categories (for further discussion of the methodology of data collection, references, and definitions of variables, see Gittleman and Harvey 1982; Gittleman 1984, 1985a, 1986).

a. Diet: meat, insects, fruit/vegetation. Species were allocated to a dietetic type if one type of food constitutes at least 60% of the diet. Species not feeding predominantly on one food type were categorized as omnivores.

b. Zonation: terrestrial, terrestrial and occasionally arboreal (primarily terrestrial but also using trees when escaping from predators), terrestrial/arboreal (equal time spent on the ground and in trees), aquatic.

c. Habitat vegetation: open grassland, dense brush or scrub, forest, woodland, water. As in the categories of zonation, some species could not accurately be described as of one vegetational type; in these cases, vegetational types were combined.

d. Activity pattern: nocturnal, diurnal, crepuscular, arrhythmic (active at any part of the day), nocturnal and crepuscular.

### *Analysis*

Logarithmically transformed values were used for all statistical tests (Harvey 1982). Longevity and age of sexual maturity were analyzed using characteristics of average species size (table 1), whereas the remaining life history variables were analyzed using values for characteristics of average female size because of the direct energetic constraints imposed by maternal size. The lines of best fit between size and life history variables were established by major-axis analysis. A regression model was not used because independent variables (body weight and brain weight) were measured with some error, and since most correlation coefficients were less than 0.85, slopes based on a regression model would have been artificially shallow (Harvey and Mace 1982; Seim and Saether 1983; Clutton-Brock and Harvey 1984). Differences in slope (between families or ecological types) were examined by determining whether covariance matrices of each respective group were diagonal. A likelihood ratio, constructed from the observed correlation matrix, was used to produce a  $\chi^2$  statistic (see Harvey and Mace 1982).

A one-way ANOVA was employed to compare mean deviations of ecological

TABLE 1

SPECIES AND DATA USED FOR ANALYSES\*

SPECIES	FW	SW	FB	SB	LS	GL	BW	WA	AI	LY	AM	IB
CANIDAE												
<i>Canis lupus</i>	31.1	33.1	130.0	132.3	5.5	63.0	425.0	35	—	177	913	12
<i>Canis latrans</i>	9.7	10.6	84.5	88.3	6.2	61.5	225.0	98	—	—	365	12
<i>Canis adustus</i>	10.6	11.3	53.5	51.8	4.3	63.3	—	—	—	127	—	—
<i>Canis mesomelas</i>	7.2	7.7	52.0	56.8	3.8	60.0	—	61	270	—	392	—
<i>Lycan pictus</i>	22.2	22.0	128.0	129.0	8.8	70.5	365.0	77	390	132	1132	13
<i>Cuon alpinus</i>	13.8	15.8	95.0	95.0	4.3	62.0	275.0	—	—	186	—	—
<i>Alopex lagopus</i>	2.9	3.2	37.0	35.5	7.1	53.3	66.0	21	165	108	293	12
<i>Vulpes vulpes</i>	3.9	4.1	43.0	43.5	4.8	54.5	105.0	56	225	144	—	12
<i>Vulpes bengalensis</i>	1.8	2.4	24.5	25.8	3.5	52.0	—	—	—	—	—	—
<i>Vulpes chamia</i>	3.1	3.1	33.0	33.5	4.0	—	—	—	—	—	—	—
<i>Fennecus zerda</i>	1.5	1.5	17.5	17.3	2.8	54.3	34.8	66	—	141	—	12
<i>Otocyon megalotis</i>	3.9	3.9	24.5	26.8	3.5	62.5	—	105	—	—	—	—
<i>Urocyon cinereoargenteus</i>	3.3	3.7	39.5	40.8	3.8	63.0	107.5	—	—	—	365	12
<i>Dusicyon culpaes</i>	6.7	7.4	51.0	51.5	5.0	57.5	168.0	—	—	—	365	12
<i>Dusicyon gymnocercus</i>	4.2	4.4	40.0	40.0	4.0	58.0	—	—	—	—	—	12
<i>Cerdocyon thous</i>	6.0	6.0	40.5	41.8	3.1	56.0	140.0	90	195	—	365	8
<i>Chrysocyon brachyurus</i>	23.0	23.0	116.0	120.0	1.8	63.3	360.0	—	—	162	—	—
<i>Speothos venaticus</i>	8.0	8.0	41.5	40.5	3.5	65.0	—	—	—	—	—	—
URSIDAE												
<i>Ursus arctos</i>	298.5	298.5	339.0	338.3	2.0	63.0	1000.0	730	648	304	1338	30
<i>Ursus americanus</i>	97.0	110.5	228.0	259.0	2.5	91.0	285.0	168	483	270	1834	27
<i>Thalarcctos maritimus</i>	320.0	365.0	365.0	459.5	1.9	—	641.6	—	821	408	1734	24
<i>Selenarctos thibetanus</i>	77.5	103.8	298.0	312.5	2.0	—	—	119	913	396	1186	—
PROCYONIDAE												
<i>Bassariscus astutus</i>	0.87	0.95	16.0	16.5	3.0	52.0	28.0	120	—	96	300	—
<i>Potos flavus</i>	2.0	2.1	24.0	25.5	1.5	106.5	170.5	—	—	228	—	—
<i>Nasua narica</i>	5.0	5.0	37.0	37.0	4.0	73.5	140.0	—	—	—	—	12
<i>Procyon lotor</i>	6.7	6.4	39.0	40.0	3.8	64.7	105.9	119	—	120	540	12
AILURIDAE												
<i>Ailuropoda melanoleuca</i>	120.0	135.0	205.0	234.3	1.5	—	104.8	180	180	216	2312	12
MUSTELIDAE												
<i>Mustela erminea</i>	0.62	0.95	3.0	4.0	4.5	70.0	1.7	—	—	—	336	12

<i>Mustela nivalis</i>	0.06	0.08	2.0	2.0	5.8	42.0	3.0	32	—	—	—	6
<i>Mustela rixosa</i>	0.05	0.05	1.0	1.0	4.8	37.0	0.01	24	—	—	—	6
<i>Mustela frenata</i>	0.23	2.33	4.0	4.0	6.0	23.5	3.1	30	84	—	252	12
<i>Mustela altaica</i>	0.13	0.19	4.5	4.5	4.0	40.0	—	56	56	—	—	—
<i>Mustela sibirica</i>	0.40	0.57	6.0	6.75	5.0	29.0	—	56	—	—	365	—
<i>Mustela lutreola</i>	0.44	0.59	8.0	8.5	4.5	38.5	—	70	—	—	420	—
<i>Mustela vison</i>	0.61	0.91	7.0	8.5	5.0	29.0	—	—	70	—	—	12
<i>Mustela putorius</i>	0.80	1.03	7.0	8.3	6.0	41.0	—	—	—	—	—	12
<i>Vormela peregusna</i>	0.53	0.60	4.0	4.8	6.0	61.5	—	—	—	—	—	—
<i>Martes martes</i>	1.2	1.2	18.0	20.0	3.3	30.0	—	—	—	—	—	—
<i>Martes americana</i>	0.77	0.87	14.5	15.8	2.6	26.5	28.0	46	—	150	365	12
<i>Martes pennanti</i>	2.25	3.75	29.0	31.8	2.7	77.0	28.0	46	—	—	730	—
<i>Martes zibellina</i>	1.03	1.18	17.0	18.5	3.0	28.0	32.5	49	—	—	600	—
<i>Gulo gulo</i>	10.35	11.6	72.5	78.5	2.8	35.0	99.2	70	639	186	630	27
<i>Tayra barbara</i>	4.4	4.4	35.0	35.8	3.5	64.0	—	—	—	144	—	—
<i>Grison vittatus</i>	1.8	2.6	23.5	24.3	2.0	—	—	—	—	—	—	—
<i>Ichonyx striatus</i>	0.63	0.77	8.5	9.8	2.3	36.0	15.0	56	—	—	—	—
<i>Poecilogale albinucha</i>	0.25	0.30	4.5	4.8	2.0	32.0	4.0	77	—	—	—	—
<i>Mellivora capensis</i>	7.59	8.08	64.0	72.8	2.5	168.0	—	—	—	288	—	6
<i>Meles meles</i>	10.9	11.6	45.5	50.5	3.0	42.0	103.5	95	210	180	525	12
<i>Taxidea taxus</i>	4.1	4.05	48.5	49.0	4.0	42.0	—	42	—	156	395	—
<i>Mephitis mephitis</i>	2.0	2.40	10.0	10.3	6.0	63.0	33.0	46	84	120	308	12
<i>Spilogale putorius</i>	0.43	0.55	5.0	5.0	4.3	30.0	15.9	56	—	—	—	8
<i>Lutra lutra</i>	7.1	8.9	39.0	42.0	2.5	66.5	285.0	112	238	—	913	—
<i>Lutra canadensis</i>	7.8	8.2	50.5	52.8	3.0	112.0	—	93	—	—	730	—
<i>Lutra maculicollis</i>	3.5	4.04	33.0	40.0	3.0	56.0	—	—	—	—	730	—
<i>Lutrogale perspicillata</i>	7.3	8.78	61.0	65.0	1.5	62.0	—	126	—	180	—	—
<i>Aonyx capensis</i>	18.0	19.0	93.0	95.0	3.0	63.0	—	—	—	—	—	—
<i>Enhydra lutris</i>	24.4	28.3	119.0	125.5	1.0	120.0	210.0	364	—	—	1095	12
VIVERRIDAE												
<i>Viverra zibetha</i>	9.0	9.3	36.5	37.0	2.8	77.0	—	—	—	—	—	—
<i>Civettictis civetta</i>	12.24	12.02	39.0	37.0	3.0	68.5	—	140	—	—	—	9
<i>Viverricula indica</i>	2.49	2.66	17.0	16.8	3.8	—	—	—	—	102	—	—
<i>Genetta genetta</i>	1.8	1.9	14.0	14.0	3.5	71.8	—	175	—	—	—	6
<i>Genetta tigrina</i>	2.02	2.06	15.5	15.3	2.5	70.0	—	56	—	180	—	—
<i>Pitonodon linsang</i>	0.72	0.67	8.0	8.5	—	—	40.0	—	—	102	—	—
<i>Nandihia binotata</i>	3.2	3.2	17.0	17.3	1.8	64.0	56.0	—	—	—	720	6
<i>Arctogalidia trivirgata</i>	2.4	2.4	21.0	22.0	2.8	45.0	—	—	—	132	—	6

(continued)

TABLE 1 (Continued)

SPECIES	FW	SW	FB	SB	LS	GL	BW	WA	AI	LY	AM	IB
<b>VIVERRIDAE (continued)</b>												
<i>Paradoxurus hermaphroditus</i>	2.7	3.0	18.5	18.5	3.3	—	95.5	—	—	168	—	6
<i>Paradoxurus zeylonensis</i>	2.3	2.8	17.5	17.8	2.5	—	—	—	—	—	—	—
<i>Paguma larvata</i>	5.0	4.7	29.5	30.8	3.0	—	—	—	—	180	—	—
<i>Arctictis binturong</i>	13.0	13.0	38.0	40.8	3.0	90.3	319.0	56	—	216	—	—
<i>Hemigalus derbyanus</i>	0.86	0.83	16.0	19.0	—	—	125.0	70	—	—	—	12
<i>Fossa fossa</i>	1.6	1.8	18.0	19.8	1.0	85.0	—	52	365	—	—	—
<i>Eupleres goudoti</i>	2.10	2.10	17.0	17.0	1.5	—	150.0	63	—	—	—	12
<i>Galidea elegans</i>	0.81	0.81	10.0	10.8	1.0	83.0	—	56	—	—	730	—
<i>Herpestes ichneumon</i>	2.90	3.05	23.0	23.3	2.5	63.0	—	—	—	156	—	—
<i>Herpestes sanguineus</i>	0.44	0.49	9.0	8.75	2.5	—	—	—	—	—	365	6
<i>Herpestes auropunctatus</i>	0.53	0.78	7.0	7.25	3.2	46.0	—	32	—	120	365	6
<i>Herpestes edwardsi</i>	1.04	1.28	10.0	10.5	3.0	60.5	—	—	—	—	270	5
<i>Herpestes smithi</i>	1.25	1.70	13.5	13.8	2.5	—	—	—	—	—	—	—
<i>Herpestes fuscus</i>	0.79	1.19	11.0	12.5	3.5	—	—	—	—	—	—	—
<i>Herpestes vitticollis</i>	1.70	2.38	26.0	25.8	3.0	—	—	—	—	—	—	—
<i>Herpestes urva</i>	2.04	2.38	20.0	21.0	3.0	63.0	—	—	—	120	—	—
<i>Mungos mungo</i>	1.23	1.26	10.0	10.5	3.8	59.0	20.0	—	—	108	323	—
<i>Crossarchus obscurus</i>	1.31	1.31	9.5	9.8	4.0	70.0	—	—	—	—	450	4
<i>Helogale parvula</i>	0.27	0.27	5.0	4.75	3.6	51.0	—	—	—	—	—	4
<i>Ichneumia albicauda</i>	3.53	3.89	22.5	24.3	2.5	—	—	—	—	—	—	—
<i>Atilax paludinosus</i>	3.30	3.70	27.0	28.5	2.5	—	—	—	—	—	—	6
<i>Cynictus penicillata</i>	0.60	0.60	10.0	10.5	2.5	54.5	—	42	—	—	—	12
<i>Paracynictis selousi</i>	1.64	1.70	15.5	15.8	1.5	—	—	—	—	—	—	—
<i>Suricata suricatta</i>	0.72	0.73	10.0	10.3	4.0	77.0	30.5	56	—	—	—	—
<b>HYAENIDAE</b>												
<i>Hyaena hyaena</i>	26.6	26.8	98.0	97.8	2.5	87.0	—	60	—	282	821	—
<i>Hyaena brunnea</i>	43.9	43.3	110.0	107.0	2.3	—	693.0	360	900	150	—	—
<i>Crocuta crocuta</i>	55.3	52.0	153.0	143.5	2.0	110.0	1500.0	390	913	276	913	17
<i>Proteles cristatus</i>	8.36	8.34	36.5	35.3	2.8	100.0	—	—	—	144	—	—
<b>FELIDAE</b>												
<i>Felis silvestris</i>	4.33	4.67	35.5	37.5	3.3	67.0	137.0	84	140	—	313	6
<i>Felis libyca</i>	3.85	4.30	33.5	36.3	2.8	57.0	—	—	140	180	280	—
<i>Felis chaus</i>	6.65	6.65	37.0	39.3	2.9	65.0	135.5	102	—	144	330	6

<i>Leptailurus serval</i>	10.4	11.7	57.0	56.8	2.4	71.0	143.5	—	—	180	—	6
<i>Prionailurus bengalensis</i>	3.3	5.5	28.5	29.3	2.5	67.3	83.0	25	—	150	750	12
<i>Prionailurus rubiginosa</i>	1.25	1.43	19.0	19.0	2.5	—	—	—	—	—	—	—
<i>Prionailurus viverrinus</i>	6.3	8.8	45.5	46.5	2.5	92.5	92.5	53	—	—	—	—
<i>Caracal caracal</i>	9.68	11.59	53.5	55.3	3.0	73.5	—	123	365	204	450	12
<i>Puma concolor</i>	39.6	51.8	119.0	125.5	2.5	90.0	400.0	—	420	—	913	19
<i>Leopardus pardalis</i>	10.75	11.88	60.0	63.8	2.5	72.5	250.0	49	—	—	653	—
<i>Leopardus geoffroyi</i>	2.2	2.2	35.5	34.0	2.0	69.5	65.0	63	—	—	480	12
<i>Lynx lynx</i>	17.8	19.3	68.5	70.0	2.3	67.8	70.0	113	240	162	690	12
<i>Lynx rufus</i>	5.2	6.2	58.5	58.3	3.2	63.0	311.5	60	365	156	593	12
<i>Panthera leo</i>	135.5	155.8	219.0	223.5	2.6	105.5	1650.0	150.0	1080	216	1620	25
<i>Panthera tigris</i>	131.0	161.0	247.0	279.3	2.5	104.1	1255.0	165	570	207	1643	32
<i>Panthera pardus</i>	39.3	52.4	112.0	125.5	2.6	98.0	549.3	139.0	600	264	1187	24
<i>Panthera onca</i>	77.6	86.2	149.0	151.5	2.5	104.5	816.6	115.0	—	—	1110	—
<i>Panthera uncia</i>	32.5	32.5	98.0	102.0	2.8	96.8	442.6	—	—	—	730	—
<i>Acinonyx jubatus</i>	60.0	58.8	106.0	111.0	3.8	91.0	287.5	109	465	—	645	18

SOURCES.—See the Appendix for short-form listings, by species.

\* FW, female body weight (kg); SW, average body weight of adult male and adult female (kg); FB, female brain weight (g); SB, average brain weight of adult male and adult female (g); LS, litter size; GL, gestation length (days); BW, birth weight (g); WA, weaning age (days); AI, age of independence (days); LY, longevity (mo); AM, age of sexual maturity (days); IB, inter-birth interval (mo).

Taxonomy follows Ewer (1973), except for placement of *Ailuropoda melanoleuca* (see Bekoff et al. 1984; Schaller et al. 1985).



TABLE 2  
 STATISTICAL RELATIONSHIPS BETWEEN EIGHT LIFE HISTORY TRAITS AND ADULT BODY WEIGHT AND BRAIN WEIGHT FOR THE ORDER CARNIVORA

Life History Trait	Morphological Variable	No. of Genera	No. of Families	Correlation Coefficient (r)	$\chi^2$	Coefficient of Determination ( $r^2$ )	Intercepts	Slope of Major-Axis Line across Order	Heterogeneity across Families	
									F	(df)
Gestation length	Body	92	7	0.84	7.75	0.71	4.02	0.11	2.7	(6,85)**
	Brain	92	7	0.80	11.61	0.64	3.65	0.14	1.4	(6,85)
Birth weight	Body	62	6	0.87	1.45	0.75	3.25	0.81	5.7	(6,54)***
	Brain	62	6	0.91	7.38	0.83	-0.19	1.35	10.45	(6,54)***
Litter weight	Body	59	6	0.84	1.68	0.71	4.18	0.86	6.1	(6,52)***
	Brain	59	6	0.88	7.61	0.78	-0.16	1.63	6.3	(6,52)***
Weaning age	Body	62	6	0.62	3.41	0.38	3.99	0.23	2.5	(6,55)*
	Brain	62	6	0.58	3.86	0.34	3.05	0.37	2.4	(6,55)*
Age of independence	Body	26	4	0.84	0.91	0.71	4.62	0.41	1.6	(4,23)***
	Brain	26	4	0.88	1.78	0.77	2.59	0.76	6.7	(4,23)***
Age of sexual maturity	Body	54	7	0.81	0.01	0.65	5.62	0.37	5.8	(6,47)***
	Brain	54	7	0.77	11.87	0.60	4.23	0.58	9.4	(6,47)***
Inter-birth interval	Body	54	5	0.67	8.48	0.45	2.17	0.10	4.9	(5,49)**
	Brain	54	5	0.64	9.37	0.41	1.89	0.13	5.2	(5,49)***
Longevity	Body	48	7	0.75	3.85	0.57	4.88	0.12	2.4	(6,41)*
	Brain	48	7	0.76	4.55	0.58	4.29	0.22	2.2	(6,41)*

NOTE.— $\chi^2$  represents levels of significance for differences in slope between families (see text).

\*  $P < .05$ .

\*\*  $P < .025$ .

\*\*\*  $P < .001$ .

types from a common major-axis line calculated among congeneric species within families and placed across the order. When significant differences were observed, pairwise comparisons were performed using a *t*-test (variances not assumed equal) to determine direction.

Interrelationships between life history variables were examined with and without subtracting size effects: correlation coefficients were calculated for all pairs of absolute life history variables. Correlations between all variables were also calculated using generic deviations from the common major-axis line established for each body weight and brain weight.

## RESULTS

All life history variables increased significantly with body weight and brain weight (table 2). No differences in slope were observed among families, though differences in elevation (on the *y*-axis) were apparent (see, e.g., fig. 1). Therefore, in examining ecological factors it was assumed, a priori, that phylogenetic effects were significant at the family level and that the appropriate level of analysis was the family (Harvey and Mace 1982; Harvey, pers. comm.). Below are summaries (from pairwise comparisons) of the phylogenetic effects between families and the ecological effects within families for each life history variable. The results of taxonomic effects include each body weight and brain weight unless otherwise noted. For ecological analyses, all results are described for each examined family, but statistical values are quoted only for significant tests.

1. *Gestation length*.—Ursidae have shorter gestation lengths than Felidae; Felidae have longer gestation lengths than Canidae and Mustelidae. In Canidae, omnivores have longer gestation lengths than strict carnivores (body,  $t_{10} = 3.35$ ,  $P < .01$ ; brain,  $t_{10} = 2.89$ ,  $P < .02$ ); dietetic effects were not found in Mustelidae or Viverridae. In Viverridae, nocturnal species have shorter gestation lengths than diurnal ones (body,  $t_{15} = 2.21$ ,  $P < .05$ ); activity pattern was not influential in Canidae, Mustelidae, or Felidae. Terrestrial felids have shorter gestation lengths than felids that are terrestrial and occasionally arboreal (body,  $t_7 = 2.78$ ,  $P < .05$ ) and those that are both terrestrial and arboreal species (body,  $t_{14} = 6.84$ ,  $P < .001$ ); Mustelidae and Viverridae revealed no zonal patterns. Differences in gestation length were not detected between vegetational types in Canidae, Mustelidae, Viverridae, or Felidae.

2. *Birth weight*.—Canidae have heavier neonates than Ursidae and Mustelidae; Ursidae have lighter neonates than all other families. In Canidae, open-grassland forms have lighter neonates than open-grassland/woodland species (body,  $t_3 = 4.46$ ,  $P < .05$ ; brain,  $t_4 = 3.10$ ,  $P < .05$ ); no vegetational effects were found in Mustelidae or Felidae. Omnivorous canids have heavier neonates than strict carnivores (brain,  $t_9 = 3.15$ ,  $P < .02$ ); dietetic effects were not observed in Mustelidae and Viverridae. No differences in birth weight were found in any family with respect to zonation or activity patterns.

3. *Litter weight*.—Canidae have heavier litters than Ursidae, Mustelidae, and Felidae; Ursidae have heavier litters than the remaining families; Procyonidae have heavier litters than Felidae. In Felidae, forest-living species have heavier



litters than woodland species (body,  $t_6 = 3.43$ ,  $P < .02$ ; brain,  $t_6 = 2.57$ ,  $P < .05$ ). There were no ecological effects detected in any other family.

4. *Weaning age*.—Procyonidae take longer to wean their young than Canidae and Felidae. In Canidae, omnivores wean their young later than strict carnivores (body,  $t_7 = 3.07$ ,  $P < .02$ ; brain,  $t_7 = 2.84$ ,  $P < .05$ ); dietetic effects were not observed in Mustelidae or Viverridae. Sample sizes were too small to allow any conclusions about the effects of activity patterns or vegetation.

5. *Age of independence*.—After the effects of female body weight were removed, there were no differences among families. But with female brain weight there were significant differences: Hyaenidae are older at the age of independence than Canidae and Ursidae (data on the age of independence were not available for most Procyonidae and Viverridae). There were no ecological effects detected in any family.

6. *Longevity*.—Ursidae have longer life spans than Felidae. In Canidae, forest-living species have longer life spans than open-grassland species (body,  $t_2 = 4.50$ ,  $P < .05$ ; brain,  $t_2 = 4.99$ ,  $P < .05$ ; data for this analysis were taken from individuals in natural populations); differences with respect to vegetation were not found in Felidae. Differences in longevity were not related to any other ecological variable.

7. *Age of sexual maturity*.—Canidae reach sexual maturity earlier than Mustelidae, Viverridae, and Procyonidae; Mustelidae and Viverridae reach sexual maturity later than Hyaenidae and Felidae. In Mustelidae, forest-living species reach sexual maturity later than open-grassland/woodland species (body,  $t_3 = 4.48$ ,  $P < .05$ ) and open-grassland/forest species (body,  $t_3 = 3.19$ ,  $P < .05$ ); no vegetational effects were found in Felidae. No other ecological types were associated with differences in age of sexual maturity within Mustelidae, Viverridae, or Felidae.

8. *Inter-birth interval*.—Canidae have longer inter-birth intervals than Viverridae; Ursidae have longer inter-birth intervals than the remaining families; Viverridae have shorter inter-birth intervals than Procyonidae, Mustelidae, and Felidae. No ecological effects were detected in any family.

#### *Interrelationships of Life History Variables*

All absolute life history variables, with the exception of litter size, correlate with one another (table 3). Gestation length, birth weight, weaning age, age of independence, age of sexual maturity, longevity, inter-birth interval, and litter weight are positively correlated; litter size is negatively correlated with gestation length, age of independence, and age of sexual maturity.

In order to standardize for size, an analysis similar to that performed for absolute variables was performed using congeneric species (mean) deviations from the common major-axis lines of body or brain weight on each life history variable (table 4). With the effects of body weight removed, there are positive correlations between litter weight and birth weight, and inter-birth interval and longevity. With brain weight removed, there are positive correlations between litter weight and birth weight, longevity and inter-birth interval, and weaning age and gestation length, and a negative correlation between litter weight and inter-birth interval.

TABLE 3  
CORRELATION MATRIX OF ABSOLUTE LIFE HISTORY VARIABLES

Life History Trait	Litter Size	Gestation Length	Birth Weight	Weaning Age	Age of Independence	Longevity	Age of Maturity	Inter-Birth Interval
Litter weight	+ .032 (60)	+ .533 (58)***	+ .957 (60)***	+ .449 (46)**	+ .794 (23)***	+ .496 (31)**	+ .514 (41)***	+ .530 (42)***
Litter size		-.445 (94)***	-.261 (59)*	-.243 (62)	-.543 (29)**	-.055 (48)	-.505 (55)***	-.141 (57)
Gestation length			+ .643 (57)***	+ .567 (60)***	+ .665 (28)***	+ .762 (44)***	+ .693 (54)***	+ .383 (54)**
Birth weight				+ .563 (47)***	+ .861 (23)***	+ .518 (32)**	+ .623 (42)***	+ .516 (42)***
Weaning age					+ .581 (25)**	+ .469 (30)**	+ .465 (41)**	+ .387 (37)*
Age of independence						+ .608 (20)**	+ .715 (25)***	+ .728 (22)***
Longevity							+ .731 (28)***	+ .468 (25)*
Age of maturity								+ .653 (39)***

NOTE.—The correlation coefficient is given with sample size in parentheses.

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

TABLE 4

CORRELATION MATRIX OF RELATIVE LIFE HISTORY VARIABLES AFTER REMOVING THE EFFECTS OF BRAIN WEIGHT AND BODY WEIGHT

Life History Trait	Gestation Length	Birth Weight	Litter Weight	Weaning Age	Longevity	Age of Maturity
BRAIN WEIGHT						
Inter-birth interval	+ .232	-.281	-.498*	+.110	+.458*	+.286
Gestation length		+.190	+.164	+.484*	+.217	+.032
Birth weight			+.737***	+.010	+.170	+.014
Litter weight				+.028	-.310	-.077
Weaning age					+.351	-.148
Longevity						+.195
BODY WEIGHT						
Inter-birth interval	+.190	-.259	-.400	+.045	+.465*	+.161
Gestation length		+.241	+.396	+.333	+.326	+.164
Birth weight			+.845***	-.155	+.070	+.230
Litter weight				-.382	-.432	-.105
Weaning age					+.425	+.270
Longevity						+.075

\*  $P < .05$ .\*\*  $P < .01$ .\*\*\*  $P < .001$ .

## DISCUSSION

The emerging life history patterns across carnivores highlight the importance of adopting a more pluralistic approach to analyzing the evolution of life history traits (see Gould 1977; Bonner and Horn 1982; Horn 1982). Toward this end, the following discussion centers on the relationships of size, phylogeny, and ecology to carnivore life histories. It should be mentioned, however, that the overall conclusions are constrained by an emphasis on bivariate analysis, in that multivariate techniques are required to partition relative effects of the three general factors considered. At this time, such an analysis is not possible because of insufficient ecological data for the Carnivora as a whole (see Bekoff et al. 1984; Gittleman 1984).

*Allometry*

The close relationship between adult body size or brain size with life histories is pervasive in mammals (Millar 1977, 1981; Western 1979; Eisenberg 1981; Stearns 1983). In carnivores, all life history variables commonly scaled with size; no heterogeneity of slope was detected among taxa within the order (table 2). This result is consistent with other allometric studies of mammalian life histories. The only exception to this generality is Millar's (1981) calculation that weaning age does not scale with body weight. Many of the values in Millar's study were multiples of seven, indicating that they had originally been measured in weeks. Undoubtedly, considerable measurement error was introduced and consequently the lack of correlation was probably due to this problem (Clutton-Brock and Harvey 1984; for further discussion of problems with measurement error in

analyzing life histories, see also Vitt and Seigel 1985). In carnivores, even though termination of suckling by young is difficult to determine (see Schaller 1972), weaning age is positively correlated with adult body weight, although the correlation is lower than with other variables. As Eisenberg (1981) pointed out, lactation time is strongly constrained by maternal size and should scale accordingly.

Many of the calculated slopes of relative life histories in carnivores are similar to other mammalian orders and across eutherians as a whole. The slope for gestation length on body weight for 93 carnivore genera is 0.11, which is similar to Western's (1979) figures for artiodactyls (0.16), primates (0.14), and carnivores (0.12) and to Kihlström's (1972) calculations for 208 species of eutherian mammals (0.17). The slope for relative birth weight in carnivores (0.81) is similar to that calculated by Leitch et al. (1959), Millar (1977), and Harvey and Clutton-Brock (1985). Although it is tempting to infer biological laws from such exponential scaling, it would be premature to do so without precise causal explanations. At present it is meaningful and necessary, however, to use such scaling as a means for subtracting allometric effects from life histories (see Clutton-Brock and Harvey 1984; Schmidt-Nielson 1984; Smith 1984).

The percent of variance accounted for by either body weight or brain weight is difficult to assess, even with large sample sizes. In carnivores, both morphological characters are significantly correlated with each life history variable. As in other mammalian taxa (Jerison 1973; Clutton-Brock and Harvey 1980; Eisenberg 1981), brain weight and body weight in carnivores are closely related (Gittleman 1986), and it is perhaps unsurprising that one variable does not reveal a more significant correlation than the other. In the present analysis it does appear that birth weight, litter weight, and age of independence are more closely related to brain weight, whereas gestation length, weaning age, age of sexual maturity, and inter-birth interval are closely related to body weight. Further comparative work must establish the relationship between maternal metabolic rate with brain weight and body weight (as suggested in Martin 1981, 1983), in order to account for physiological expenditure, and specifically measure those structural and physiological characters that directly impinge on particular life history traits (i.e., determine what characteristics are represented by variables of size).

### *Phylogeny*

This study, as well as those by Mace (1979) on small mammals, by Harvey and Clutton-Brock (1985) on primates, and by Stearns (1983) on eutherians in general, indicates significant differences at the family level for most carnivore life histories. For example, Procyonidae and Viverridae have significantly heavier relative litter weights than the other carnivore families. Therefore, comparisons of life histories between carnivores and other mammalian orders, as exemplified in other studies (e.g., Millar 1977, 1981; Calder 1984; Hayssen 1984), are meaningless without prior analysis at lower taxonomic levels (see Harvey and Mace 1982; Clutton-Brock and Harvey 1984). For this methodological reason, the following discussion of phylogeny concentrates on intra- and interfamilial variation.

Comparisons of families within some taxonomic groups reveal fairly consistent differences in life histories. In small mammals, families with relatively long

gestation lengths (Chinchillidae, Echimyidae, Ctenodactylidae) tend to have extended lactation periods and long life spans, whereas Cricetidae tend to develop quickly according to all temporal measures (Mace 1979). Although differences between carnivore families are apparent for all life histories, they do not reveal consistent trends: variation in one life history variable is not associated with change in another. For example, in the Ursidae, a family that appears at extremes for most life history variables, an examination of temporal measures indicates that inter-birth interval and lactation are long, whereas age of independence and age of sexual maturity are reached quickly (see table 5). Likewise, no consistent trends are observed among life histories in other carnivore families. It is therefore difficult to establish phylogenetic statements regarding the entire suite of life histories among carnivore families.

Nevertheless, it would be premature and misleading to say that phylogeny is unimportant. Deviations from the ordinal major-axis line for each life history variable indicate that families cluster together in accord with carnivore taxonomy despite considerable variation (Ewer 1973; Radinsky 1981*a,b*). In this regard, it is particularly interesting that the Viverridae, the only family to receive suggested major taxonomic revisions (see Eisenberg 1981), seems relatively homogeneous. On the basis of work by various taxonomic authorities, Eisenberg (1981) suggested dividing the family into three groups: Viverridae (the civets); Herpestidae (the mongooses); and Cryptoproctidae (the fossa). Eisenberg noted that "Ecologically [Viverridae] show more diversification in trophic specialization and substrate use than any other carnivore family" (1981, p. 126). For life histories, however, the Viverridae show clear trends that establish their unity: heavy birth and litter weights (see fig. 1), brief inter-birth intervals, average (for their size) gestation lengths, and delayed sexual maturity. This is not to say that no differences occur. For example, interesting exceptions stand out from the trends just mentioned: *Arctogalidia trivirgata*, an arboreal species inhabiting dense forests, has a comparatively short gestation length; *Herpestes edwardsi* reproduces for the first time at a comparatively early age; and *Civettictis civetta* weans its young relatively late. Explanations for such exceptions are difficult to test because of a lack of detailed ecological information; at this stage, it is only fruitful to search for adaptive explanations in well-studied groups in which numerous species deviate from familial life history trends.

### Ecology

With the exception of diet, most ecological information concerning the order Carnivora is based on descriptive summaries of species' characteristics (Gittleman and Harvey 1982; Bekoff et al. 1984; Gittleman 1984). It is therefore expected that considerable error was incorporated into testing for ecological trends and perhaps is partly responsible for so few ecological effects being detected for carnivore life histories, even though similar negative patterns have been found in primates (Harvey and Clutton-Brock 1985). Furthermore, because analyses were restricted to the family level, sample sizes were often small and life history and ecological variation were reduced.

Carnivores are well known for their widespread dietetic differences (see Ewer



TABLE 5  
COMPARATIVE FAMILY LIFE HISTORY VARIABLES: MEAN CONGENERIC DEVIATIONS FROM MAJOR-AXIS LINE

Family	Gestation Length	Birth Weight	Litter Weight	Weaning Age	Age of Independence	Longevity	Age of Maturity	Inter-birth Interval
Canidae	-.21	-.11	+.65	-.30	+.07	-.14	-.27	+.10
Ursidae	-.64	-1.22	-1.70	+.41	-.24	+.31	-.22	+.59
Procyonidae	+.15	+.45	+.42	+.60	—	-.06	+.13	+.14
Mustelidae	-.37	-.50	-.27	+.09	-.05	+.07	+.19	+.16
Viverridae	+.10	+.59	+.22	+.15	—	-.04	+.47	-.31
Hyaenidae	+.26	+.54	+.14	+.50	+.54	+.03	-.18	—
Felidae	+.33	+.01	-.11	-.25	-.02	+.02	-.18	+.13
				BODY WEIGHT				
Canidae	-.23	-.24	+.08	-.39	-.14	-.19	-.44	+.06
Ursidae	-.31	-1.26	-2.14	+.35	-.45	+.27	-.21	+.66
Procyonidae	+.12	+.24	+.25	+.55	—	-.07	-.07	+.13
Mustelidae	-.29	-.16	+.31	+.07	+.28	+.05	+.24	+.16
Viverridae	+.31	+.82	+.69	+.10	—	+.02	+.56	-.32
Hyaenidae	+.28	+.78	-.08	+.50	+.53	+.05	-.17	—
Felidae	+.02	-.08	-.34	-.26	-.06	-.02	-.17	+.14
				BRAIN WEIGHT				

1973; Eisenberg 1981; Bekoff et al. 1984; Gittleman 1984). Fortunately, diet is the one ecological variable that has received quantitative measurement, and examples from intraspecific studies showing dietetic effects on reproduction are legion: significant decreases in reproductive success and litter size with a decline of the primary food in the diet are observed in coyotes (Todd et al. 1981), wolves (Harrington et al. 1983), stoats (Erlinge 1981), weasels (King 1983), and black bears (Rogers 1977). For the Canidae, diet is associated with differences in three life history characteristics: compared to carnivorous species (e.g., *Canis lupus*, *C. latrans*, *Lycaon pictus*, *Alopex lagopus*, *Dusicyon culpaeus*), omnivorous species (*Urocyon cinereoargenteus*, *Fennecus zerda*, *Cerdocyon thous*) have heavier birth weights, longer gestation lengths, and longer lactation periods. There is also a weak (not statistically significant) trend indicating that omnivores reach sexual maturity earlier than carnivores.

There are two possible explanations for these differences. First, omnivores have a wider food base to choose from, and therefore reproduction (in terms of nutritional requirements) may be less demanding energetically. Unlike a carnivore, a species like *Canis mesomelas*, which feeds on a wide range of foodstuffs including beetles, termites, fallen fruits, berries, snakes, and various birds and mammals (see Moehlman 1983, 1986), is better able to maintain itself during prey fluctuations. Thus, depending on digestive efficiency during reproduction (see Oftedal 1984; Sampson and Jansen 1984), an omnivore may endure the energetic costs of an extended gestation length, followed by a long lactation period for large offspring. By contrast, carnivorous species have brief developmental periods, at least early in the ontogenetic sequence, and give birth to lighter young so as to minimize the maternal energetic cost of feeding young and the vulnerability to prey fluctuations. Similar explanations have been given for parallel findings in lizards, where "sit and wait" species have heavier clutch masses than widely foraging predatory lizards (Vitt and Congdon 1978; Huey and Pianka 1981).

Second, post-weaning experience in omnivores and carnivores is markedly different: carnivores progress toward the age of independence (natal dispersal or, in social species, the cessation of maternal care) more slowly than omnivores in the Canidae, possibly so that the young can acquire necessary predatory skills to hunt independently on an exclusively carnivorous diet (see Ewer 1973).

The Canidae is an unusually diverse family in which specific ecological trends have been well studied relative to other carnivore taxa (Ewer 1973; Kleiman and Eisenberg 1973; Bekoff et al. 1984). Patterns detected in the remaining carnivore families suggest that life history trends observed in canids may not be similar for the order as a whole. For example, in the Hyaenidae, *Crocuta crocuta* is extremely carnivorous, but its life history sequence is more aligned with an omnivorous canid: this species has a relatively long gestation, heavy births, and heavy litters, depends entirely on milk for around 8 mo, and may not be completely weaned until 16 mo (Kruuk 1972; Kingdon 1977). Thus, although diet may be a very influential factor in shaping some carnivore life histories, caution must be used in assuming that diet may select for parallel trends in divergently evolved taxa, as this comparison illustrates.

Some comparative studies have suggested that in addition to diet, habitat

vegetation may be an important variable related to life histories. In an early comparative study of carnivores, Kleiman and Eisenberg (1973) qualitatively asserted that life history differences in Canidae and Felidae resulted from phylogenetic consequences of felids evolving from forest environments and canids from open-grassland habitats. Observing that felids have smaller litter sizes (for their body size) than canids, Kleiman and Eisenberg postulated that this difference has two causes: felids are polyestrous, thus having the potential to breed throughout the year, and they live in forest habitats, which provide a broader food base (including both arboreal and terrestrial prey species) and thus sufficient food to rear offspring for a longer period during the year. In addition, larger litters may be expected in the Canidae because of a tendency for paternal or communal rearing (Kleiman and Malcolm 1981; Gittleman 1985*b*; Moehlman 1986). In the present work, Canidae were observed to have relatively heavier litter weights than Felidae (body,  $t_{26} = 3.15$ ,  $P < .01$ ; brain,  $t_{26} = 2.25$ ,  $P < .05$ ), which supports Kleiman and Eisenberg's statement. Nevertheless, ecological heterogeneity within each taxonomic family is so great that analyses must be performed at the family level in order to adequately examine the hypothesis (in relation to vegetational effects).

In Canidae, open-grassland species (*L. pictus*, *A. lagopus*) have lighter birth weights than open-grassland/woodland species (*D. culpaeus*, *Cerdocyon thous*) and forest dwellers (*Cuon alpinus*, *Vulpes vulpes*), though similar differences in litter weight, the variable more relevant to energetics, are not observed. Significant differences in relative litter weight are observed in Felidae: forest-living species (e.g., *Prionailurus bengalensis*, *Leopardus pardalis*, *Panthera tigris*) have heavier litters than woodland species (*Puma concolor*, *L. geoffroyi*, *Panthera pardus*). Therefore, the quantitative data analyzed here are consistent with Kleiman and Eisenberg's assertion that vegetational effects selected for divergence in canid and felid life histories.

The previous discussion emphasizes differences in nutritive content and seasonality of vegetational types. Spatial heterogeneity is also reflected in contrasting environments: forest habitats may present more perceptual and ranging complexity than open-grassland or savannah areas (see Eisenberg 1981). Such environmental complexity may underlie differences in life histories observed across the Mustelidae. Forest-living species (congeneric groupings of *Mustela* and *Martes*), and to a lesser extent aquatic forms (*Lutra lutra*, *Enhydra lutris*), reach sexual maturity later than open-grassland/woodland species (*Mustela frenata*, *Meles meles*) and open-grassland/forest species (*Gulo gulo*, *Mephitis mephitis*). Unfortunately, information is not available on the behavioral stages leading toward maturity in these species. Nevertheless, it seems likely that reproduction is delayed in those species living in harsher environments (forest, aquatic) so that a female at first reproduction is familiar enough with the environment to successfully rear a litter. Late sexual maturity may also be promoted by slow development in an environment that is nutritively limiting (Oftedal 1984; Gittleman and Oftedal 1986).

Although the remaining ecological variables, zonation and activity cycle, are both ecologically important (see Cartmill 1972; Charles-Dominique 1975; Clutton-

Brock and Harvey 1977), no study has established that either variable is an influential factor independent of other ecological and behavioral attributes. Certainly any adaptive explanations concerning zonation and activity cycle would be hard to envisage without considering such factors as habitat and food resources.

#### CONCLUSIONS AND SUMMARY

This study examined interspecific variation in eight life history traits of the order Carnivora in relation to size, phylogeny, and ecology. Each life history trait scales according to body weight and brain weight across the order, although it is difficult to partition the relative effects to either independent variable because the allometry of each correlates so highly. After size effects were removed, significant differences between taxonomic families were found for most life history traits. It is assumed that such variation represents phylogenetic history and that familial differences must therefore be considered before searching for ecological associations with relative histories. At the family level, most life histories do not correlate with ecological factors; some differences do exist, however: in Canidae, dietetic differences are associated with the variation in birth weight, gestation length, and weaning age; in Canidae and Felidae, vegetational effects are observed with litter weight and, in the Mustelidae, with the onset of sexual maturity. Although few significant ecological associations are observed compared with the total number of examined trends, they perhaps represent trends that should be considered in further studies of life histories in carnivores and other mammals.

In contrasting these cross-species findings with intraspecific variation across carnivores, there appear to be some consistent associations of life histories with particular ecological factors at both taxonomic levels. Many authors (e.g., Macdonald 1979; Lott 1984) have emphasized the opposing nature of observed trends of intraspecific and interspecific differences, stating that variation within species rules out species-specific values used in comparative study. As first suggested by Darwin (1859) and subsequently by others (see Clutton-Brock and Harvey 1979; Jarman 1982), however, ecological adaptations may occur at many levels, thus representing potentially similar biological trends. For example, for comparative carnivore life histories—as for home-range movements (Gittleman and Harvey 1982), group living (Bekoff et al. 1984; Gittleman 1984), parental care (Gittleman 1985*b*), body size (Gittleman 1985*a*), and growth patterns (Gittleman and Oftedal 1986)—ecological associations often suggest functional explanations that parallel ecological effects within species. Future studies should use comparative analyses not only for generating evolutionary hypotheses and testing them (see Harvey and Mace 1982; Clutton-Brock and Harvey 1984), but also for suggesting the kinds of variables and relationships (e.g., dietetic influences on birth weight) that may prove helpful for within-species study.

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## APPENDIX

ABBREVIATED DATA-SOURCE REFERENCES FOR "SPECIES AND DATA USED FOR ANALYSES"  
(TABLE 1)

The taxonomy follows Ewer (1973), except for the placement of *Ailuropoda melano-leuca* (see Bekoff et al. 1984; Schaller et al. 1985). The sequence of the references is random.

Full citations for the sources cited below are available in Gittleman (1984, pp. 382–440), from the office of *The American Naturalist*, and from the National Auxiliary Publications Service.\*

## CANIDAE

*Canis lupus*: Mech 1966, 1970; Ballenbergh 1975; Pimlott 1967; Peterson 1977; Rausch 1967; Novikov 1956; Jordan et al. 1967

*Canis latrans*: Bekoff 1978; Grinnell et al. 1937; Fichter et al. 1955; Berg and Chessness 1978; Andrews and Boggess 1978; Bekoff and Wells 1980; Gier 1975; Andelt et al. 1979; Kennelly 1978

*Canis adustus*: Bekoff 1975; Smithers 1966, 1971; Bothma 1971; Kingdon 1977; Merwe 1953; Rosevear 1974

*Canis mesomelas*: Smithers 1971; Moehlman 1979; Rowe-Rowe 1976, 1978; Bothma 1971; Bekoff 1975; Merwe 1953; Kingdon 1977; Kruuk 1972; Wyman 1967

*Lycyon pictus*: Frame et al. 1979; Malcolm and Marten 1982; Smithers 1971; Pienaar 1969; Schaller 1972; Estes and Goddard 1967; Kruuk and Turner 1967; Mitchell et al. 1965; Rosevear 1974; Kingdon 1977

*Cuon alpinus*: Davidar 1975; Sosnovskii 1967; Lekagul and McNeely 1977; Tweedie 1978; Johnsingh 1982

*Alopex lagopus*: Chesemore 1975; Banfield 1974; Brom et al. 1948; Stroganov 1969; Novikov 1956

*Vulpes vulpes*: Leitch et al. 1959; Amores 1975; Macgregor 1942; Eadie 1943; Heitt 1944; Ables 1975; Stanley 1963; Stroganov 1969; Tembrock 1957; Ognev 1962; Macdonald 1977, 1980

*Vulpes bengalensis*: Roberts 1977; Johnsingh 1978

*Vulpes chama*: Bekoff 1975; Rowe-Rowe 1978a

*Fennecus zerda*: Dorst and Dandelot 1969; Bekoff 1975; Weiher 1976; Gauthier-Pilters 1965; Koenig 1970; Morris 1965; Rosevear 1974

*Otocyon megalotis*: Smithers 1971; Berry 1978; Viljoen and Davis 1978; Bothma 1971; Lamprecht 1979; Kingdon 1977

*Urocyon cinereoargenteus*: Grinnell et al. 1937; Trapp and Hallberg 1975; Hatfield 1939; Ewer 1973; Wood 1958; Banfield 1974

\* See NAPS document no. 04385 for 60 pages of citations in full for the references in this appendix. Order from NAPS, Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, NY 10163. Remit in advance \$4.00 for microfiche copy or \$19.75 for photocopy. Outside the United States and Canada, add \$1.50 for postage of microfiche orders or \$4.50 for postage and handling for the first 20 pages plus \$1.00 for each additional 10 pages of material.

- Dusicyon culpaeus*: Crespo 1975; Crespo and DeCarlo 1963; Jaksić et al. 1980  
*Dusicyon gymnocercus*: Crespo 1975; Crespo and DeCarlo 1963; Cabrera and Yepes 1950  
*Cerdocyon thous*: Brady 1978; Kleiman and Brady 1978  
*Chrysocyon brachyurus*: Kleiman 1967, 1972; Morris 1965; Langguth 1975; Cabrera and Yepes 1960; Brady and Ditton 1979; Da Salvaera 1968; Acosta 1972  
*Speothos venaticus*: Hershkovitz 1969; Ewer 1973; Jantschike 1973; Morris 1965; Cabrera and Yepes 1960; Kleiman 1972; Husson 1978

## URSIDAE

- Ursus arctos*: Martinka 1972, 1974; Bromlei 1973; Banfield 1974; Pearson 1972; Stroganov 1969; Craighead and Craighead 1972; Craighead et al. 1969; Dittrich and Kronberger 1962; Heisel et al. 1969; Ognev 1962; Curry-Lindahl 1972; Herrero 1972  
*Ursus americanus*: Rogers 1976, 1977; Amstrud and Beecham 1968; Grinnell et al. 1937; Jonkel and McT. Cowan 1971; Banfield 1974; Erikson et al. 1964; Cottam et al. 1939; Butterworth 1969; Herrero 1972; Ewer 1973; Eisenberg 1981  
*Thalarcos maritimus*: Erdbrink 1953; Flyger and Townsend 1968; Stirling et al. 1977; Tsackin 1936; Novikov 1956; Michalowski 1971; Jonkel et al. 1972; Banfield 1974  
*Selenarctos thibetanus*: Stroganov 1969; Schaller 1969; Bromlei 1956, 1973; Lekagul and McNeely 1977

## PROCYONIDAE

- Bassariscus astutus*: Poglayen-Neuwall and Poglayen-Neuwall 1980; Richardson 1914; Grinnell et al. 1937; Trapp 1978; Toweill and Teer 1977; Taylor 1954; Ingles 1965  
*Potos flavus*: Cabrera and Yepes 1960; Poglayen-Neuwall 1962; Husson 1978; Clift 1967; Bhatia and Desai 1972  
*Nasua narica*: Cabrera and Yepes 1960; Kaufmann 1962; Asdell 1964; Russell 1979  
*Procyon lotor*: Stains 1956; Banfield 1974; Stuewer 1943; Grinnell et al. 1937; Yeager and Rennels 1943; Hamilton 1944; Schneider et al. 1971

## AILURIDAE

- Ailuropoda melanoleuca*: Schaller et al. 1985; Sung and Chang-Kun 1973; Brambell 1976; Sheldon 1937; Morris and Morris 1966; Kleiman 1983

## MUSTELIDAE

- Mustela erminea*: Hamilton 1933; Erlinge 1977*a,b*, 1979; Ingles 1965; Southern 1964; Stroganov 1969; Hall 1951; Day 1968; Deansy 1941; Asdell 1964  
*Mustela nivalis*: Southern 1964; Harrison 1968; Stroganov 1969; Easterla 1970; Erlinge 1979; Day 1968; Parouschikov 1975; King 1975  
*Mustela rixosa*: Heidt et al. 1968; Banfield 1974; Asdell 1964; Hall 1951  
*Mustela frenata*: Banfield 1974; Glover 1943; Hamilton 1933; Hall 1951; Polderboer et al. 1941; Foresman and Mead 1973; Heidt et al. 1968; Ingles 1965; Wright 1947  
*Mustela altaica*: Stroganov 1969; Ognev 1962; Fetisoff 1936  
*Mustela sibirica*: Stroganov 1969; Ognev 1962; Fetisoff 1936  
*Mustela lutreola*: Stroganov 1969; Novikov 1956  
*Mustela vison*: Asdell 1964; Suihla 1931; Grinnell et al. 1937; Hamilton 1940; Sealander 1943; Gerrell 1967; Banfield 1974; Heidt et al. 1968; Enders 1952  
*Mustela putorius*: Stroganov 1969; Southern 1964; Zuerov 1931; Novikov 1956; Ognev 1962  
*Vormela peregusna*: Stroganov 1969; Novikov 1956; Roberts 1977  
*Martes martes*: Southern 1964; Novikov 1956; Stroganov 1969; Balharry 1978; Schmidt 1934; Landowski 1961  
*Martes americana*: Mech and Peters 1977; Grinnell et al. 1937; Lensink et al. 1955; Newby 1951; Banfield 1974; Ewer 1973  
*Martes pennanti*: Ingles 1965; Banfield 1974; Powell 1982  
*Martes zibellina*: Stroganov 1969; Novikov 1956; Ewer 1973  
*Gulo gulo*: Asdell 1964; Krott 1960; Grinnell et al. 1937; Rausch and Pearson 1972; Myhre and Myrderget 1975; Haglund 1966; Banfield 1974; Mehrer 1976; Woods 1944  
*Tayra barbaru*: Asdell 1964; Morris 1965; Poglayen-Neuwall 1975

- Grison vittatus*: Dalquest and Roberts 1951; Cabrera and Yepes 1960; Kaufmann and Kaufmann 1965
- Ictonyx striatus*: Ball 1978; Rowe-Rowe 1978*a,b*; Smithers 1971; Lamprecht 1978; Kingdon 1977
- Poecilogale albinucha*: Rowe-Rowe 1978*a,b*; Kingdon 1977; Dorst and Dandelot 1969
- Mellivora capensis*: Kingdon 1977; Wilson 1968; Smithers 1971; Dorst and Dandelot 1969; Rosevear 1974; Harrison 1968; Rowe-Rowe 1978*a*; Johnstone-Scott 1965
- Meles meles*: Neal 1948, 1977; Stroganov 1969; Kruuk 1978*a,b*; Kruuk et al. 1979
- Taxidea taxus*: Grinnell et al. 1937; Snead and Hendrickson 1942; Ingles 1965; Long 1973; Banfield 1974; Ewer 1973; Wright 1969
- Mephitis mephitis*: Verts 1967; Selko 1937; Banfield 1974; Asdell 1964
- Spilogale putorius*: Banfield 1974; Grinnell et al. 1937; Crabb 1941, 1948; Selko 1936; Mead 1968*a,b*
- Lutra lutra*: Harris 1968; Southern 1964; Erlinge 1967; Novikov 1956
- Lutra canadensis*: Ewer 1973; Harris 1968; Sheldon and Toll 1964; Lagler and Ostenson 1942; Liers 1966; Hamilton and Eadie 1964
- Lutra maculicollis*: Kingdon 1977; Smithers 1966, 1977; Rowe-Rowe 1977, 1978*a*; Prochter 1963; Mortimer 1963
- Lutrogale perspicillata*: Yadav 1967; Roberts 1977; Lekagul and McNeely 1977
- Aonyx capensis*: Rowe-Rowe 1977, 1978; Harris 1968; Kingdon 1977; Smithers 1971; Rosevear 1974
- Enhydra lutris*: Stroganov 1969; Harris 1968; Kenyon 1969; Barabash-Nikiforov 1935, 1962; Novikov 1956
- VIVERRIDAE
- Viverra zibetha*: Medway 1969; Van Peenan 1969; Pocock 1933; Lekagul and McNeely 1977; David 1967
- Civettictis civetta*: Ewer 1973; Rosevear 1974; Wilson 1968; Smithers 1971; Bothma 1971; Kingdon 1977; Dorst and Dandelot 1969; Ewer and Wemmer 1974; Roberts 1977; Eisenberg and Lockhart 1972
- Viverricula indica*: Phillips 1935; Asdell 1964; Lekagul and McNeely 1977; Krishnan 1972; Roberts 1977
- Genetta genetta*: Smithers 1971; Stuart 1977; Kingdon 1977; Volf 1965; Roeder 1979; Wemmer 1977
- Genetta tigrina*: Kingdon 1977; Smithers 1971; Rowe-Rowe 1978*a*; Bearder 1972; Wemmer 1977; Morris 1965
- Prionodon linsang*: Lekagul and McNeely 1977; Ewer 1973; Medway 1969; Louwman 1970
- Nandinia binotata*: Taylor 1970; Kingdon 1977; Dorst and Dandelot 1969; Charles-Dominique 1978; Rosevear 1974
- Arctogalidia trivirgata*: Medway 1969; Batten 1966; Lekagul and McNeely 1977
- Paradoxurus hermaphroditis*: Asdell 1964; Phillips 1935; Medway 1969; Acharjyo and Mohapatra 1978; Lekagul and McNeely 1977; Pocock 1933
- Paradoxurus zeylonensis*: Phillips 1935; Eisenberg and Lockhart 1972; Asdell 1964
- Paguma larvata*: Pocock 1934; Lekagul and McNeely 1977; Roberts 1977; Medway 1969
- Arctictis binturong*: Lekagul and McNeely 1977; Ewer 1973; Gensch 1962; Xanten et al. 1976; Aquilina and Deyer 1979
- Hemigalus derbyanus*: Liat 1973; Louwman 1970; Lekagul and McNeely 1977; Medway 1969
- Fossa fossa*: Alagnac 1972, 1973; Eisenberg and Gould 1970
- Eupleres goudoti*: Alagnac 1972, 1973, 1974
- Galidia elegans*: Alagnac 1972, 1973; Eisenberg and Gould 1970
- Herpestes ichneumon*: Wilson 1968; Smithers 1971; Rowe-Rowe 1978*a*; Rosevear 1974; Harrison 1968; Hinton and Dunn 1967; Kingdon 1977
- Herpestes sanguineus*: Smithers 1971; Rood and Waser 1978; Rowe-Rowe 1978*a*; Kingdon 1977; Hinton and Dunn 1967; Taylor 1970; Rosevear 1974

- Herpestes auropunctatus*: Acharjyo and Mohapatra 1976; Gorman 1976, 1979; Ewer 1973; Baldwin et al. 1952; Hinton and Dunn 1967; Pimentel 1955; Harrison 1968; Pearson and Baldwin 1953; Powell 1913
- Herpestes edwardsi*: Asdell 1964; Hinton and Dunn 1967; Pocock 1937; Krishnan 1972; Medway 1969; Harrison 1968; Frere 1928
- Herpestes smithi*: Phillips 1935; Hinton and Dunn 1967; Eisenberg and Lockhart 1972
- Herpestes fuscus*: Hinton and Dunn 1967; Phillips 1935
- Herpestes vitticollis*: Hinton and Dunn 1967; Phillips 1935; Krishnan 1972
- Herpestes urva*: Hinton and Dunn 1967; Pocock 1937; Ewer 1973; Lekagul and McNeely 1977
- Mungos mungo*: Rood 1975; Smithers 1971; Ewer 1973; Neal 1970; Rosevear 1974; Kingdon 1977
- Crossarchus obscurus*: Hinton and Dunn 1967; Rosevear 1974; Kingdon 1977; Dorst and Dandelot 1969; Booth 1960
- Helogale parvula*: Hinton and Dunn 1967; Rood 1978, 1980; Kingdon 1977
- Ichneumia albicauda*: Wilson 1968; Rowe-Rowe 1978a; Bothma 1971; Harrison 1968; Kingdon 1977; Taylor 1972; Rosevear 1974
- Atilax paludinosus*: Taylor 1970; Rowe-Rowe 1977, 1978; Dorst and Dandelot 1969; Booth 1960; Kingdon 1977; Hinton and Dunn 1967
- Cynictis penicillata*: Rowe-Rowe 1978; Smithers 1971; Herzig-Straschil 1977; Viljoen and Davis 1973; Dorst and Dandelot 1969; Ewer 1973
- Paracynictis selousi*: Wilson 1968; Smithers 1968, 1971; Dorst and Dandelot 1969
- Suricata suricatta*: Smithers 1971; Viljoen and Davis 1973; Ewer 1963; Hinton and Dunn 1967

## HYAENIDAE

- Hyaena hyaena*: Rieger 1979; Novikov 1956; Kruuk 1976; Van Peenan 1969; Kingdon 1977
- Hyaena brunnea*: Skinner 1976; Owens and Owens 1978, 1979, 1980; Smithers 1971; Mills 1976, 1982; Mills and Mills 1978; Schulz 1966
- Crocuta crocuta*: Kruuk 1972; Smithers 1971; Wilson 1968; Bearder 1977
- Proteles cristatus*: Kingdon 1977; Smithers 1971; Rowe-Rowe 1978a; Bothma 1971; Kruuk and Sands 1972

## FELIDAE

- Felis silvestris*: Matthews 1941; Kingdon 1977; Guggisburg 1975; Novikov 1956; Corbett 1978; Southern 1964; Meyer-Holzappel 1968
- Felis libyca*: Wilson 1968; Smithers 1971; Rowe-Rowe 1978a; Stuart 1977; Roberts 1977; Guggisburg 1975; Kingdon 1977
- Felis chaus*: Phillips 1935; Guggisburg 1975; Schauenberg 1978, 1979; Ishunin 1965; Roberts 1977; Acharjyo and Mohapatra 1977
- Leptailurus serval*: Kingdon 1977; Smithers 1971, 1978; Geertsema 1976; Guggisburg 1975; Rowe-Rowe 1978a
- Prionailurus bengalensis*: Stroganov 1969; Hemmer 1976; Guggisburg 1975; Lekagul and McNeely 1977; Roberts 1977; Pohle 1973; Dathe 1968
- Prionailurus rubiginosa*: Stroganov 1969; Hemmer 1976; Guggisburg 1975
- Prionailurus viverrinus*: Fagen and Wiley 1978; Guggisburg 1975; Roberts 1977; Lekagul and McNeely 1977
- Caracal caracal*: Kingdon 1977; Smithers 1971; Viljoen and Davis 1973; Rosevear 1974; Guggisburg 1975; Kralik 1967
- Puma concolor*: Hornocker 1970; Grinnell et al. 1937; Young and Goldman 1946; Robinette et al. 1959, 1961; Pfeifer 1980; Cabrera and Yepes 1960; Seidensticker et al. 1973
- Leopardus pardalis*: Guggisburg 1975; Husson 1978; Cabrera and Yepes 1960; Morris 1965; Hershkovitz 1969; Hemmer 1976; Fagen and Wiley 1978
- Leopardus geoffroyi*: Fagen and Wiley 1978; Cabrera and Yepes 1960; Ximenez 1975; Anderson 1977; Scheffel and Hemmer 1975



- Lynx lynx*: Ewer 1973; Stroganov 1969; Saunders 1963, 1964; Haglund 1966; Nellis and Keith 1968; Guggisburg 1975; Hemmer 1976; Koehler et al. 1979
- Lynx rufus*: Stanley 1958; Hamilton and Hunter 1939; Rollings 1945; Pollack 1951; Bailey 1974; Guggisburg 1975; Provost et al. 1973; Gashweiler et al. 1961; Crowe 1975
- Panthera leo*: Schaller 1972; Bertram 1975*a,b*; Eloff 1973; Kruuk and Turner 1967; Elliot and Cowan 1978; Adamson 1968
- Panthera tigris*: Schaller 1967; Sunquist 1981; Guggisburg 1975; Sankhala 1967; Medway 1969; Singh 1973
- Panthera pardus*: Bertram 1974; Schaller 1972; Kingdon 1977; Phillips 1935; Krüuk and Turner 1967; Smith 1978; Grober and Wilson 1972; Pienaar 1969; Adamson 1968; Muckhenhahn and Eisenberg 1973; Eisenberg and Lockhart 1972; Guggisburg 1975
- Panthera onca*: Schaller and Vasconcelos 1978; Cabrera and Yepes 1960; Guggisburg 1975; Ewer 1973; Hemmer 1976
- Panthera uncia*: Stroganov 1969; Schaposchnikov 1956; Hemmer 1972; Schaller 1977; Marma and Yunchis 1968; Guggisburg 1975
- Acinonyx jubatus*: Eaton 1974; Kruuk and Turner 1967; Bertram 1979; Schaller 1972; Kingdon 1977; Guggisburg 1975

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