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Life-History Patterns and Sociality in Canids: Body Size, Reproduction, and Behavior

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Summary. Empirical associations among co-adapted traits such as body size and patterns of reproduction, development, and behavior are unknown for most animal species, despite numerous theories suggesting otherwise. One way to study these complex relationships is first to consider closely related species and then to generalize findings to other groups. In the present study, relationships among body size, reproductive patterns, development, and sociality were examined in 17 members of the family Canidae (canids). Large canids are more social than smaller species, and offspring of large species achieve independence and tend to breed first at a later age. Large females give birth to absolutely larger young, but relative to their own body weight they allocate fewer resources to bringing a large pup to term. Overall, sexual dimorphism in size is small to moderate, and this is associated with monogamous mating habits and paternal care of young.

Introduction

A life-history tactic is "a set of coadapted traits designed, by natural selection, to solve particular ecological problems" (Stearns 1976, p. 4). The importance of life-history phenomena to general evolutionary theory was stressed by Cole (1954) in his now classic paper, and recently, the significance of life-history patterns to furthering our understanding of behavioral and ecological adaptations has been emphasized by other biologists (Wiley 1974; Wilson 1975; Stearns 1977; Altmann and Altmann 1979; Mace 1979; Western 1979; Armitage 1981). However, theories have outstripped empirical data, and there are few comparative studies of life-history patterns among closely related species (Wiley 1974; Wilson 1975; Clutton-Brock and Harvey 1977; Mace 1979; Western 1979; Tuomi 1980; Armitage 1981), though such studies are necessary for elucidating precise relationships among life-history characters, social behavior, and demographic variables, and may also be useful for purposes of conservation (King and Moors 1979). Stearns (1980) has recently stressed that there is a need for studies in which life-history analyses are interfaced with various disciplines including physiology, genetics, management, and behavior.

To the best of our knowledge, there has been no previous attempt to compare, using multivariate analyses, life-history tactics and behavioral patterns in any carnivore group, though some suggestions about these relationships have been offered in general works (Ewer 1973; Kleiman and Eisenberg 1973; Wilson 1975; Kleiman 1977; Ralls 1977; Western 1979). Generalizations concerning patterns of association among life-history variables and behavior based on interspecific comparisons can be tested further and more rigorously by studying variation among closely related species (Tuomi 1980). The purpose of this study was to analyze patterns of association among body size, reproductive habits, physical and behavioral development, and social organization in members of the family Canidae (see von Gelder 1978 and references therein for reviews of canid classification).

Methods

Variables used in our analysis are listed in Table 1. Where possible, field data or information from captive animals living in "semi-natural" habitats were used. The complete list of references (about 200 sources) is too lengthy for inclusion but is available, along with the raw data, from M.B. Data were best-fit using species-typical patterns where nonquantifiable information was involved (type of pair-bound, hunting method, sociality, etc.). Mean-species estimated (Armitage 1981) were calculated for quantifiable characters (gestation period, litter size, weight and age measures, etc.). Three composite reproductive measures were also calculated (following Armitage's, 1981 example). The reproductive index (RI) was defined as the birth weight of 1 young/minimum female weight, and represents the effort by a single female to bring 1 young to term relative to her weight. Reproductive effort (RE) was derived by multiplying litter size × birth weight, and represents the total resources allocated to bringing a litter to term, irrespective of female weight. Lastly, specific reproductive effort (SRE) was calculated as [litter size × birth weight]/minimum female weight (=RE/minimum female weight), and represents the total resources allocated to reproduction relative to female weight.

Results

Data first were subjected to a principal components analysis (Fig. 1a) in order to summarize the relationships among the entire suite of characters by reducing the dimensionality of the data set (communality estimates are provided in Table 1). The variables loading highest (all positively) on the first prinicpal axis included gestation period (0.61), birth weight (0.93), adult weight (0.81), minimum female weight (0.91), age at independence and dispersal (0.89), age at which females (0.92) and males

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Table 1. Life-history and behavioral traits of 17 canids as compiled from about 200 sources. *GP*=gestation period (days); *LS*=litter size; *EO*=age at eye-opening (days); *BW*=birth weight (gm); *AW*=adult weight (kg); *MW:FW*=ratio of male to female weight; *MFW*=minimum female weight (kg), equal to average of lowest reported weights; *W*=age at weaning (weeks); *DE*=age at den emergence (weeks); In/Disp=age at independence (individuals are self-sufficient and can hunt on their own) and/or earliest likelihood of dispersal (months) (the two are not always differentiated, and dispersal typically occurs a few months after the young become independent); *FB*=age at which females typically first breed (months): *MB*=age at which males typically first breed (months); *SM*=does scent-marking by females increase during breeding? 1=yes, 2=no; *PB*=nature of pair bond, 1=forms only during breeding, may be short-term, 2=long-term bond; *Soc*=sociality, 1=solitary, 2=pairs, 3=solitary, pairs, or small groups, 4=small groups, 5=large groups or packs; *AP*=activity pattern, 1=diurnal, 2=nocturnal, 3=both; *HM*=hunting method, 1=primarily a scavenger, 2=hunt small game singly or in pairs, 3=hunt medium size game singly, in pairs, or in small groups, 4=hunt medium size or large game in packs, 5=2+3. Adequate data on longevity and intrinsic rates of population growth were not available. Most canids produce 1 litter per year. Numbers in parentheses are communality estimates, which are percentages of variance accounted in each character. Communality estimates for RI, RE, and SRE (defined in the text) were 93%, 100%, and 100%, respectively

Species	GP (65)	LS (44)	EO (32)	BW (90)	AW (79)	MW:FW (50)	MFW (36)	W (17)	DE (29)	IN/DISP (81)	FB (51)	MB (61)	SM (61)	PB (44)	SOC (88)	AP (44)	HM (33)
Wolf, *Canis lupus*	63	6.4	11	400	51	1.2	23	5	3	8	20	20	1	2	5	3	4
Coyote, *C. latrans*	63	7.4	11.5	250	13	1.5	8	7	2.5	4	9	9	1	2	3	3	5
Dingo, *C. dingo*	63	5.2	11	300	16	1.5	10	6	3	4	12	12	1	2	3	2	2
Golden jackal, *C. aureus*	62	4.8	10	–	9	–	–	7	3	3	9	9	2	2	3	2	5
Side-striped jackal, *C. mesomelas*	62	5.2	8	159	10	1.6	8	8	2	3	7	6	2	2	3	2	5
Black-backed jackal, *C. adustus*	63	5.7	10	–	9	–	–	6	3	3	9	9	2	2	3	2	5
Raccoon dog, *Nyctereutes procyonoides*	62	7.2	9.5	75	8	1.5	5	7	2	5	10	10	1	2	3	2	2
Bushdog, *Speothos venaticus*	72	4.5	15.5	157	6	1.6	4	4	2.2	–	12	12	1	2	5	2	5
Dhole, *Cuon alpinus*	62	4.5	14	275	18	1.3	13	–	5.5	–	12	12	–	2	5	1	4
Cape hunting dog, *Lycaon pictus*	69	7.2	14	365	22	1.2	15	11	4	10	24	24	1	2	5	1	4
Bat-eared fox, *Octocyan megalotis*	63	3.7	–	–	4	–	–	15	4	4	–	–	1	2	3	2	2
Fennec fox, *Fennecus zerda*	53	3.5	8	28	2	1.5	1	9	–	–	9	9	–	2	4	2	2
Red fox, *Vulpes fulva*	52	5.1	8.7	100	5	1.3	3	8	4.5	3	10	10	1	1	2	3	2
Red fox, *V. vulpes*	53	5.7	12.2	107	6	1.3	3	7	4	3	10	10	1	1	1	3	2
Arctic fox, *Alopex lagopus*	53	6.9	15	70	4	1.7	3	–	3	4	9	9	1	2	1	3	2
Pampas fox, *Dusicyon gymnocercus*	58	4.5	–	–	4	–	–	–	2.5	–	–	–	–	–	–	3	2
Gray fox, *Urocyon cinereoargenteus*	63	3.9	–	115	5	1.3	3	12	5	5	12	12	–	2	3	2	2

(0.70) first breed, sociality (0.70), and RE (0.94). Thus, the first axis summarized variation in "size, maturity, reproduction, and sociality". Variables loading highest on axis II were RI (−0.54), SRE (−0.81), and female scent-marking during breeding (+0.58), all of which are associated with female reproductive behavior; those characters having highest loadings on the third axis were litter size (−0.54), SRE (−0.63), sociality (+0.61), and activity pattern (−0.56).

Although many species were clustered on axis I, the most social canids [wolves (W) and cape hunting dogs (CHD)] were best separated from the other canids. Dholes (Dh) were also separated from the main cluster. Dholes are highly social, but are smaller than wolves or cape hunting dogs and typically breed at an earlier age. The clustering of the remaining species reflects a closer association among variables accounted on axes I and II, despite reported variations in weight, social organization (Kleiman and Eisenberg 1973; Bowen 1978; Camenzind 1978; Macdonald 1979; Bekoff and Wells 1980), age at first breeding [which can vary with the social environment (Kleiman 1977; Macdonald 1980; Packard 1980; Bekoff 1981)], and age at independence and dispersal (Zimen 1976; Bekoff 1977, 1981). For example, when large, clumped, and defendable food items are available, coyotes tend to live in packs (Bowen 1978; Camenzing 1978; Bekoff and Wells 1980). However, when coyotes are dependent on either a dispersed food source or small rodents, they tend to be less gregarious. Young coyotes also disperse and breed at different ages depending on the social environment and ecological conditions.

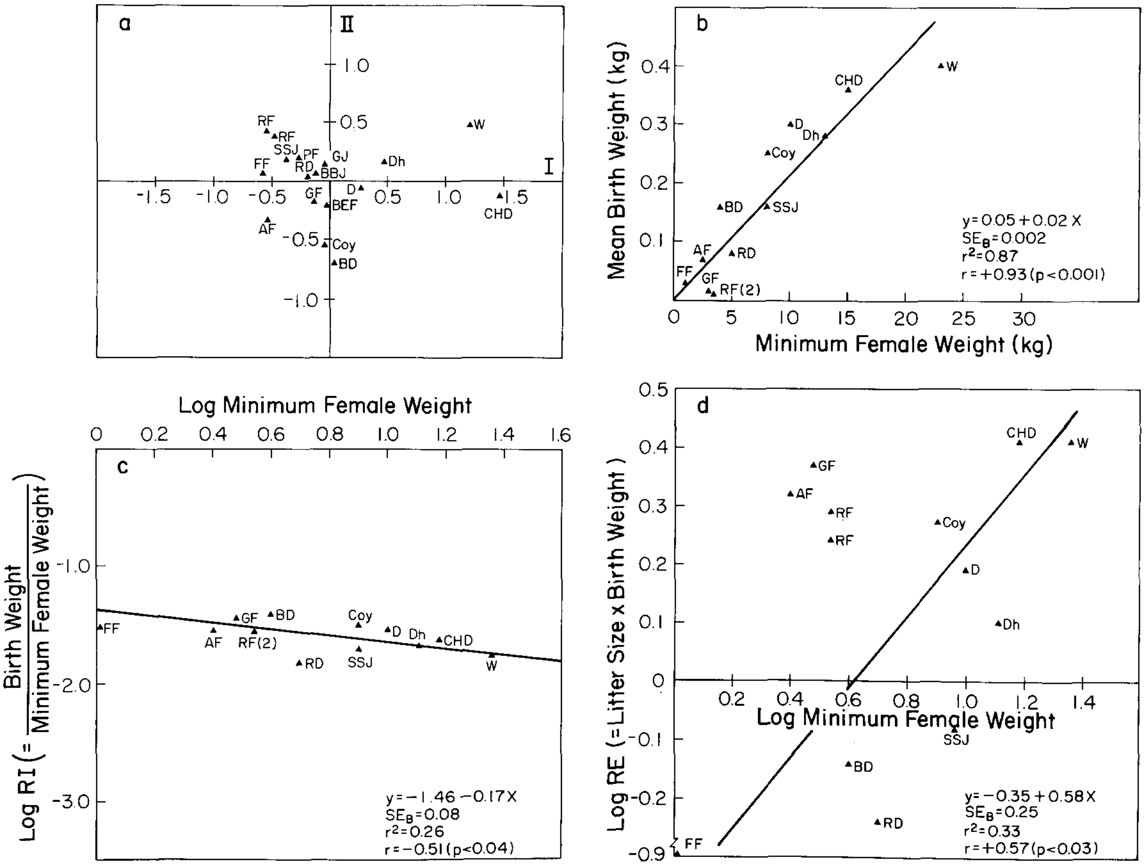

Fig. 1. a Projections of 17 canids on the first two principal axes of a principal components analysis of life-history traits and behavioral patterns. Axis I (accounting for 42.2% of the variance of the entire data set) summarizes variation in size, maturity, reproduction, and sociality and axis II (accounting for 13.2% of the variance) represents female reproductive behaviors (see text). Axis III (not shown) accounted for 11.7% of the variance (see text). *CHD*, cape hunting dog; *W*, wolf; *Dh*, dhole; *D*, dingo; *BEF*, bat-eared fox; *Coy*, coyote; *BD*, bushdog; *BBJ*, black-backed jackal; *GJ*, golden jackal; *GF*, gray fox; *RD*, raccoon dog; *PF*, pampas fox; *SSJ*, side-striped jackal; *RF*, red fox; *FF*, fennec fox; *AF*, arctic fox. **b** Relationship between mean birth weight and minimum female weight for 13 canids. Legend as in **a**; see text for discusion. **c** Relationship between reproductive index (*RI*) and minimum female weight plotted on a log scale. Legend as in **a**; see text for discussion. **d** Relationship between reproductive effort (*RE*) and minimum female weight plotted on a log scale. Legend as in **a**; see text for discussion

Table 2. Patterns of significant correlation (Pearson's product-moment correlation, r) among variables representing size, reproduction, and sociality for 17 canid species (see Table 1 for legend). (The matrix from which these data were extracted included all variables listed in Table 1 plus RI, RE, and SRE; $r=0.43, p<0.05$; $r=0.52, p<0.02$; $r=0.56, p<0.01$; $r=0.68, p<0.001$)

Variables	Correlation coefficients										
AW	0.85										
MFW	0.93	0.96									
MW:FW	−0.50	−0.52	−0.52								
GP	0.59		0.46								
FB	0.75	0.75	0.74	−0.63	0.49						
MB	0.73	0.45	0.72	−0.62		0.64					
RI		−0.51	−0.55								
RE	0.96	0.84		−0.47	0.54	0.78					
IN/DISP	0.66	0.62	0.68	−0.61	0.53	0.95	0.54		0.72		
SOC	0.56	0.48	0.55		0.75	0.58			0.48	0.71	
	BW	AW	MFW	MW:FW	GP	FB	MB	RI	RE	IN/DISP	SOC
	Size				Reproduction					Sociality	

The way in which different characters varied together was studied using correlational analysis (Sokal and Rohlf 1969). Statistically significant correlations among variables representing size, reproduction, and sociality are presented in Table 2. Almost all cells are filled, indicating close associations among the variables. Length of gestation period was correlated with birth weight and minimum female weight (see also Kihlström 1972 and Kleiman et al. 1979). Litter size was not correlated with any weight measure, though for some mammals these variables are correlated (Kleiman et al. 1979; Western 1979; Tuomi 1980), with the sign of the correlation coefficient related to the size of the species under consideration (Tuomi 1980). In small mammals (less than 1 kg) litter size is positively correlated with body weight; in large mammals (greater than 1 kg) the correlation is negative. The lack of association between litter size and weight measures in the present analysis might be due to the use of a more extensive data base than that used in studies in which different groups are being compared. Significant correlations not listed in Table 2 were found for RI and SRE (+0.56; see also Bekoff and Jamieson 1975), sociality and the type of pairbond (+0.63; more social species tend to establish more permanent bonds), and hunting method and sociality (+0.47; more social species hunt as a group). Activity patterns and sociality were negatively correlated (−0.50), suggesting that social species tend to be diurnal whereas less social species are more nocturnal (in agreement with data reported in Rautenbach and Nel (1978).

While correlational analyses estimate the degree to which two measures vary together (Sokal and Rohlf 1969), more detailed functional relationships between two variables can be estimated using regression analyses. This allows a prediction of what values of one variable correspond to given values of the other (Sokal and Rohlf 1969). Regression analyses (Figs. 1b–d) showed that females of larger species tend to (i) give birth to absolutely larger young [Fig. 1b; but total litter weight is less relative to the female's weight (see also Leitch et al. 1959, Bekoff and Jamieson 1975, and Robbins and Robbins 1979)], (ii) put fewer resources into bringing 1 (large) pup to term relative to body weight (Fig. 1c), and (iii) put more resources into bringing a full litter to term, regardless of body weight (Fig. 1d). However, there was no relationship between SRE and minimum female weight ($y=-0.82-0.03x$, $SE_b=0.09$, $r^2=0.01$, $r=+0.11$, $p=0.36$). Patterns similar to those shown in Figs. 1b–d were found for North American Ground squirrels (Armitage 1981) in which body size also appeared to be an important factor explaining variations in RE.

General Discussion

Life-History Patterns, Behavior, and Ecology of Canids

The above analyses demonstrated that life-history tactics and behavioral patterns are closely related in the canids considered. Though mechanisms underlying the evolution of sociality still are not well understood, this area is currently receiving a great deal of attention (Kleiman and Eisenberg 1973; Wilson 1975; Armitage 1981; and references therein). Body size appears to be an important variable accociated with species-typical behavioral profiles (Western 1979; Tuomi 1980; Armitage 1981). For canids, birth weight, minimum female weight, and adult weight were positively correlated with almost all measures of sociality and reproduction. Large size, group-living, and group hunting undoubtedly are adaptations for procuring large prey (Kleiman and Eisenberg 1973; Rautenbach and Nel 1978).

The data presented here also suggest a relationship between delayed dispersal and increased sociality, namely, the young of more social (and larger) species tend to become independent and disperse at a later age (see also Barash 1974 and Armitage 1981). Delayed breeding may also be an important factor leading to increased sociality. Although the mechanisms responsible are not well known, and cause and effect are difficult to untangle, a delay in breeding often occurs in young adults (that supposedly should be reproductively active) if they remain with older individuals (parents, older siblings; Wilson 1975; Kleiman 1977; Bekoff and Wells 1980 and unpub. data; Macdonald 1980; Packard 1980). We found strong relationships between delayed independence and dispersal and the age at which females and males first breed. In canids and other species, sociality (and group cohesion) may be increased by having individuals who do not disperse serve as "helpers" (alloparents; Wilson 1975) who provide postnatal care to young (other than their own) born to parents, older siblings, or other group members.

Prenatal and postnatal parental reproductive investments also can be influenced by the size of offspring (Western 1979), as well as by different behavioral patterns. Generally, requirements for parental care tend to increase with body size (Western 1979; this study). One way that a large female canid can reduce both prenatal and postnatal energy allocations is to produce litters who total weight is low relative to her own (which they do). Another way to reduce postnatal care would be to expide independence and/or dispersal by some pups after weaning, even though early dispersal may be more risky than a delayed departure (Bekoff 1977). Furthermore, "helpers" assistance in rearing young might also reduce parental postnatal investments.

Sexual dimorphism and breeding and care-giving patterns also were interrelated. The canids used in the present analysis demonstrated small to moderate sexual dimorphism (using Ralls' 1977 criteria). Furthermore, 9 of 13 (69%) species we considered would be classified as being monogamous (Kleiman 1977) with male provisioning of young occurring in many of these monogamous species (Kleiman 1977). Monogamy and paternal care are usually associated with a reduction in sexual dimorphism (Kleiman 1977; Ralls 1977). Dimorphism was also negatively correlated with age at independence and/or dispersal and age at first breeding; delayed dispersal and delayed breeding also are associated with monogamy (Kleiman 1977). Small to moderate sexual dimorphism in size may also be related to the fact that there does not appear to be intense competition for mates among male canids.

Although there will be exceptions to the generalizations derived from this study, and more comparative data are needed, an appreciation for some of the "ground rules of mammalian adaptation" will enable us to ask informed questions about these exceptions (Clutton-Brock and Harvey 1978), and to make predictions about relationships among body size, reproduction, development, and sociality in other animal taxa. General theories and comprehensive explanations must be tested empirically.

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