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Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology

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(With 1 figure in the text)

Sexual dimorphism in craniodental features is investigated in a sample of 45 carnivore species in relation to allometry, phylogeny, and behavioural ecology. Dimorphism is more pronounced in both upper and lower canine size and strength than in carnassial size, skull dimensions and biomechanical features, but all dimorphism indices covary. As with most morphological characters, differences in canine sexual dimorphism are significantly related to phylogeny, estimated from either taxonomic rankings or a limited matrix of molecular distances; in particular, mustelids, felids and procyonids are more dimorphic than other carnivore families. Thus, because of problems related to species dependence in comparative data, remaining analyses are based on phylogenetically transformed values using a spatial autoregressive method.

In contrast to other mammals, sexual dimorphism in carnivore canines is not correlated with differences in body weight, skull length or basicranial axis length. Nor is it correlated with categorical variables of activity pattern, habitat, or diet. In our carnivore sample, canine dimorphism is related only to breeding system: uni-male, group-living (harem) species have significantly greater canine dimorphism than multi-male, multi-female groups and monogamous pair-bonding species. By contrast, dimorphism in carnassial size is related to dietary differences, specifically greater dimorphism in meat-eating species, and not breeding patterns. Dimorphism in estimates of jaw muscle size suggest functional demands from both diet and breeding type. It is concluded that, befitting patterns of heterodont dentition, sexual selection influences variation in canine dimorphism while feeding ecology is related to carnassial dimorphism.

Introduction

Canine teeth in carnivores are conspicuous. Relatively large, sharp, placed anteriorly in the body, and used for display, fighting and predation, canines are extremely variable across carnivore taxa: small species such as the musteline weasels have canines around 3 mm in height, whereas the pantherine cats have canines ranging as large as 45 mm in height. As in other mammals, much variation is related to sexual dimorphism. For example, canines in male ermine (*Mustela erminea*) are almost twice as large as those in females. Despite extensive comparative work on the evolutionary significance of sexual dimorphism in canines across other mammals (especially primates), no systematic study has assessed variation in canine dimorphism among terrestrial carnivores.

Many studies have examined canine sexual dimorphism in primates (for review, see Martin, Willner & Dettling, 1994). Five factors and associated explanations are considered salient. (1) Size: sexual

dimorphism in canine size is a by-product of differences in body size which result from the same or different selective factors operating on teeth (Leutenegger, 1982; Leutenegger & Cheverud, 1982, 1985). (2) Sexual selection: polygynous species are more dimorphic than monogamous species owing to mechanisms of sexual selection, specifically increased competition for mates (Harvey, Kavanagh & Clutton-Brock, 1978; Kay *et al.*, 1988; Plavcan & van Schaik, 1992). (3) Phylogeny: owing to a lack of genetic variability, niche conservatism or common ancestry, canine dimorphism is similar in closely related taxa (Cheverud, Dow & Leutenegger, 1985; Lucas, Corlett & Luke, 1986). (4) Activity cycle: species which are primarily diurnal are more dimorphic than nocturnal species, reflecting the increased importance of a display function in dimorphic canines (Crook, 1972; Harvey, Kavanagh & Clutton-Brock, 1978). (5) Predation: terrestrial species are more dimorphic than arboreal forms because of increased predation pressure in terrestrial habitats (Leutenegger, 1982). These explanations are not mutually exclusive and hold, to varying degrees, across divergent taxa.

Carnivores as a group are ideal for an independent assessment of hypotheses generated from primate studies. In addition to the intrinsic variation of canine size and dimorphism, many of the biological characteristics associated with the above-mentioned factors and explanations are extremely diverse across carnivores. The overall range of body weight in carnivores is unsurpassed by any other mammalian order (Gittleman, 1985). Ecologically, carnivores are found in virtually all zonal gradients (from semi-aquatic to strictly terrestrial to exclusively arboreal), feed on a variety of diets (from exclusively herbivorous to exclusively meat-eating), and have activity patterns that cover all parts of the day (Ewer, 1973; Eisenberg, 1981; Gittleman 1989a, 1996). Likewise, behavioural diversity is reflected by the solitary living of most mustelids and felids, the flexible sociality of many canids and the spotted hyaena (*Crocuta crocuta*), and the stable nuclear or extended family groups observed in the coati (*Nasua narica*), European badger (*Meles meles*), dwarf mongoose (*Helogale parvula*), and African lion (*Panthera leo*) (see Kleiman & Eisenberg, 1973; Macdonald & Moehlman, 1982; Macdonald, 1983; Bekoff, Daniels & Gittleman, 1984; Rood, 1986; Gittleman, 1989b; Kruuk, 1989; Moehlman, 1989; Sandell, 1989; Creel & Macdonald, 1995; Geffen *et al.*, 1996; Gompper, Gittleman & Wayne, In press). Although carnivores span such morphological, behavioural and ecological variation, their phylogenetic relationships are reasonably well established (Wayne *et al.*, 1989; Wozencraft, 1989) so that phylogenetic patterns in canine dimorphism can be tested. In sum, the carnivores are an important test group for describing and analysing functional differences in canine sexual dimorphism.

Two other issues motivate our analysis of sexual dimorphism in carnivore canines. First, aside from behavioural and ecological factors, canine dimorphism may covary with other craniodental characters and associated mechanical functions. For example, as with absolute measures of canine size (see Radinsky, 1981; Van Valkenburgh, 1989; Van Valkenburgh & Ruff, 1987; Van Valkenburgh & Koepfli, 1993), canine dimorphism may relate to variation in postcanine teeth (carnassials in carnivores), geometrical differences in skull shape or size, or functional differences in canine strength and muscle mechanics. It is possible that the canine teeth of males might be much larger in one dimension, such as crown height, but not necessarily stronger if diameter has not kept pace with tooth length. The above-mentioned primate studies have not examined such morphological associations. Second, in a series of recent papers (Dayan *et al.*, 1989, 1990, 1992; Dayan & Simberloff, 1994) interspecific variation in sexual dimorphism of carnivore canine size was explained in terms of character displacement; these studies, however, have not examined alternative hypotheses related to other above-mentioned behavioural and ecological factors (see e.g. Pimm & Gittleman, 1990). We evaluate these ideas with an original comparative dataset on craniodental measures across carnivores.

Materials and methods

Teeth and skull measurements

Canine size and various components of the skull were measured from skulls housed at The Natural History Museum (London, UK), The Smithsonian Institution (Washington, DC, USA), and the American Museum of Natural History (New York, USA). Using digital callipers, we measured the length, width and crown height of the upper and lower canines. Measurements were also taken of: skull length, basicranial axis length, upper and lower carnassial length and width, and indices of the moment arm(s) of the temporalis muscle, masseter muscle and resistance for an object at the canines (see below, for detailed definitions). All measurements were in mm. Care was taken to sample only adult, wild-caught individuals from the same geographic area so that geographic effects would not confound differences due to sex. All craniodental measures were taken on a total of 45 terrestrial carnivore species, including a minimum of 5 (and up to 10 for well represented species, e.g. *Canis lupus*, *Mephitis mephitis*, *Ursus arctos*, *Crocota crocuta*, *Panthera leo*) individuals of each sex of each species (see Table I). The complete data set of all individual measures and statistical errors associated with each is available from the authors. The individual values were averaged for each sex before computation of dimorphism indices and statistical analysis.

The morphological variables used in the analysis are described below and the data are shown in Table I. All indices of dimorphism were calculated as the ratio of male to female measures.

1. Canine size: mediolateral breadth and anteroposterior length of upper and lower canines were measured at the tooth base (dentine-enamel junction) (mm). In addition, crown height of unworn canines was measured from the tip to the dentine-enamel junction (mm).

2. Carnassial size: anteroposterior length and mediolateral breadth of upper fourth premolar and lower first molar of adult males and females (mm). The breadth of the upper fourth premolar was measured at the notch between paracone and metacone (see Van Valkenburgh, 1988, 1989 for details).

3. Skull length: condylobasal length of adult males and females (mm), measured from the back of the occipital condyles to the anterior tip of the premaxilla.

4. Basicranial axis length: basicranial axis length of adult males and females (mm), measured from the midventral border of the foramen magnum to the basisphenoid-presphenoid suture (see Radinsky, 1984 for details).

5. Body weight: average species body weight of adult males and females (kg); data taken from Gittleman (1985).

6. Bite mechanics: the moment arms of the 2 primary jaw muscles, the masseter (MAM) and temporalis (MAT), were estimated from aspects of the mandibular ramus as in Emerson & Radinsky (1980). In addition, the moment arm of resistance (MAR) of a load placed at the canines was measured as the linear distance between the mandibular condyle and anterior border of the lower canines.

Several of the measures were combined to produce computed estimates of canine strength and muscle leverage, as follows (see Van Valkenburgh & Ruff, 1987 for details of each measure):

1. Upper canine basal area (UCarea): calculated as the product of the maximum anteroposterior length and mediolateral breadth measured at the dentine-enamel junction.

2. Upper canine strength: using the canine size measures described above and modelling the canines as beams, strength in resisting forces applied to the tip in a mediolateral direction (S_x) was calculated as:

$$S_x = ab^3/4hb$$

where a is half the anteroposterior diameter, b is half the mediolateral diameter, and h is crown height of the upper canine. Similarly, S_y , or strength in resisting forces applied to the tip in an anteroposterior direction was calculated as:

$$S_y = a^3b/4ha$$

3. Muscle leverage: MAT divided by MAR was used as an estimate of the mechanical advantage of the temporalis muscle for a bite with the canines.

TABLE I
Mean values for the craniodental measures (see text)

Taxa	Sex	UCH	UCW	UCL	LCH	LCW	LCL	SL	BCAL	UCrL	UCrW	LCrL	LCrW	MAT	MAM	MAR	Sx	Sy
Canidae																		
<i>Canis lupus</i>	M	28.93	8.63	14.08	25.73	9.7	14.47	252.96	58.72	24.65	10.73	28.57	11.78	45.92	29.57	175.36	5.83	3.57
	F	27.11	8.02	13.3	24.3	8.58	13.35	230.32	53.58	23.41	10.22	27.33	11.11	40.82	28.11	161.18	5.19	3.13
<i>Canis latrans</i>	M	21.02	5.67	10.13	19.59	6.67	9.87	193.61	46.69	19.91	7.76	21.88	8.35	35.4	23.57	136.07	2.74	1.53
	F	21.2	5.63	9.45	19.12	6.09	9.63	192.49	46.57	19.7	7.74	21.81	7.68	33.61	22.91	134.72	2.35	1.40
<i>Canis mesomelas</i>	M	16.32	4.75	7.51	14.36	5.42	7.2	159.67	40.06	16.84	6.47	18.27	7.52	25.28	21.62	120.97	1.63	1.03
	F	14.74	3.93	6.95	13.73	4.69	7.49	149.27	37.71	15.99	5.83	18.2	7.04	23.63	18.14	112.20	1.27	0.72
<i>Vulpes velox</i>	M	13.26	3.38	5.39	10.72	3.44	6.1	116.07	33.94	10.54	3.84	12.05	4.34	16.71	10.44	82.90	0.73	0.46
	F	11.88	2.91	4.77	10.37	3.28	5.14	114.59	31.32	10.24	3.94	11.99	4.3	17.13	10.44	81.74	0.55	0.34
<i>Vulpes vulpes</i>	M	18.71	4.81	7.17	17.19	5.43	7.95	151.36	37.88	15.01	5.67	16.17	5.87	25.18	14.42	107.09	1.31	0.88
	F	18.3	4.45	6.95	16.21	5.17	7.76	144.41	37.12	14.41	5.29	15.73	5.69	23.05	13.66	101.50	1.16	0.74
<i>Alopex lagopus</i>	M	13.81	3.77	6.17	12.87	4.43	6.8	118.44	30.73	12.21	4.9	13.4	5.01	20.02	12.5	80.35	1.03	0.63
	F	13.35	3.73	6.31	12.06	4.37	6.69	119.58	30.69	11.6	4.78	12.44	4.66	20.56	12.23	82.25	1.10	0.65
<i>Urocyon cinereoargenteus</i>	M	11.85	3.37	5.26	10.2	3.52	5.68	125.25	34.19	10.75	4.37	11.9	4.73	19.9	12.59	87.60	0.78	0.50
	F	11.3	3.31	5.03	9.99	3.56	5.46	120.97	34.37	10.26	3.98	11.67	4.77	18.63	11.68	84.37	0.74	0.48
Procyonidae																		
<i>Procyon lotor</i>	M	13.08	4.53	6.18	12.24	4.35	6.28	114.58	21.95	8.63	8.74	10.03	6.03	20.81	11.54	75.80	1.32	0.97
	F	12.14	3.9	5.58	10.24	3.68	5.98	110.47	20.16	8.51	8.64	9.88	6.08	20.31	10.73	72.39	0.99	0.69
<i>Potos flavus</i>	M	9.72	3.7	5.68	11.4	4	6.3	87.79	28.27	4.08	5.29	5.37	3.91	18.95	21.34	54.90	1.21	0.79
	F	9.74	3.43	5.37	11.26	4.03	6.02	86.59	29.76	4.32	5.45	5.47	4.02	17.98	22.21	52.98	1.00	0.64
<i>Nasua nasua</i>	M	11.22	3.98	8.36	15.89	5.67	6.8	109.46	30.8	7.12	7	7.64	4.86	15.92	8.05	85.11	2.44	1.16
	F	9.38	3.13	6.33	9.83	3.78	4.67	107.50	28.51	6.71	6.7	7.42	4.97	15.53	8.15	84.11	1.34	0.66
Ursidae																		
<i>Ursus arctos</i>	M	37.93	16.44	21.88	34.88	16.37	22.68	385.64	90.77	22.93	17.85	25.4	15.6	69.02	34.79	230.56	20.84	15.59
	F	34.44	14.99	20.75	33.3	14.61	20.61	368.04	87.2	22.34	16.97	24.39	14.73	66.97	30.78	225.26	19.46	13.89
Mustelidae																		
<i>Mustela sibiricus</i>	M	7.34	2.6	3.43	6.35	2.64	3.12	58.11	27.63	6.51	4.68	6.96	2.85	13.76	5.45	33.16	0.41	0.31
	F	6.41	2.01	2.5	5.04	2.36	3.2	51.06	24.45	6.01	4.68	6.14	2.3	11.11	4.55	28.63	0.20	0.16
<i>Mustela frenata</i>	M	5.35	1.76	2.27	4.54	1.85	2.64	42.56	21.59	4.8	4.71	5.15	2.42	8.91	3.65	23.68	0.17	0.13
	F	4.11	1.41	1.75	3.37	1.63	2.35	36.70	18.88	4.21	3.49	4.5	1.76	7.03	3	19.45	0.11	0.08
<i>Mustela erminea</i>	M	5.27	1.72	2.12	4.46	2.03	2.81	41.77	20.59	4.78	4.74	4.94	2.37	8.53	3.92	22.11	0.15	0.12
	F	3.53	1.27	1.57	2.93	1.44	2.11	34.55	18.51	3.83	3.70	3.87	1.62	6.27	2.76	17.04	0.09	0.07
<i>Meles meles</i>	M	13.74	5.84	7.6	13.4	6.3	8.11	131.63	40.95	8.74	8.34	16.11	7.35	26.89	12.1	88.77	2.43	1.87
	F	12.52	5.17	6.87	11.78	5.43	7.66	128.81	40.55	8.71	8.00	16.06	7.62	26.9	10.64	87.04	1.93	1.45
<i>Taxidea taxus</i>	M	18.02	6.41	8.33	16.31	6.39	8.8	124.71	32.87	12.07	11.95	13.32	5.85	30.09	16.44	82.53	2.43	1.88
	F	16.05	5.7	7.5	15.41	5.76	7.86	120.68	29.65	11.64	11.59	13.22	5.79	28.31	15.15	79.49	1.98	1.50

<i>Spilogale putorius</i>	M	6.48	2.35	3.07	5.81	2.48	3.54	50.73	27.43	6.14	5.30	6.87	3.26	11.64	6.16	33.89	0.34	0.26
	F	5.25	1.98	2.39	4.76	2.02	2.7	43.79	22.86	5.69	5.01	6.62	2.89	9.16	4.66	29.39	0.21	0.18
<i>Mephitis mephitis</i>	M	9.43	3.12	4.14	8.57	3.27	4.63	62.17	30.42	7.09	6.19	9.25	4.09	14.22	7.09	45.74	0.57	0.43
	F	7.38	2.65	3.5	5.92	2.76	3.87	58.80	28.24	7.04	5.72	9.03	4.07	13.39	7.72	43.27	0.43	0.33
<i>Conepatus humboldtii</i>	M	9.56	3.26	4.52	8.05	3.58	4.99	65.37	29.8	7.33	6.48	9.1	5.04	13.87	9.21	46.04	0.69	0.50
	F	7.2	2.83	4.14	5.51	2.89	3.5	61.31	28.41	7.27	6.26	8.8	4.87	13.64	9.27	43.35	0.66	0.45
<i>Ictonyx striatus</i>	M	9.2	2.71	4.1	7.39	2.95	4.37	62.36	26.84	7.44	7.56	7.49	3.81	14.3	6.54	41.51	0.49	0.32
	F	7.72	2.18	3.22	6.11	2.77	3.52	59.83	26.01	6.88	7.78	7.44	3.53	13.07	6.39	39.18	0.29	0.20
<i>Martes americana</i>	M	12.15	3.41	4.62	10.73	3.97	4.84	85.01	17.80	8.14	3.19	9.4	3.6	19.44	6.31	55.28	0.59	0.43
	F	9.84	2.95	3.85	8.7	3.55	4.23	75.47	16.66	6.95	2.73	8.03	3.25	16.03	5.61	47.33	0.44	0.34
<i>Eira barbara</i>	M	16.77	6.13	8.42	15.93	6.78	9.21	116.34	43.02	9.69	7.63	9.67	5.33	27.24	12.74	75.16	2.55	1.87
	F	15.27	5.53	7.85	15.21	5.95	8.61	110.29	41.6	9.56	9.32	9.65	5.79	24.83	12.64	70.84	2.20	1.56
<i>Lutra lutra</i>	M	12.96	5.28	5.91	10.84	5.21	6.62	111.75	30.27	10.42	8.49	13.49	6.11	25.39	9.89	74.18	1.40	1.25
	F	12.12	4.94	5.3	9.81	4.64	6.11	104.05	28.77	10.28	8.17	12.58	5.62	23.89	10.2	68.22	1.12	1.05
Viverridae																		
<i>Mungos mungo</i>	M	7.26	2.3	3.49	7.07	2.58	3.62	68.44	13.01	3.3	5.52	4.17	3.26	10.76	6.4	46.15	0.38	0.25
	F	6.9	2.37	3.37	6.47	2.51	3.14	67.56	12.87	3.29	5.59	4.12	3.26	10.64	6.06	46.01	0.39	0.27
<i>Herpestes edwardsi</i>	M	8.76	2.48	3.48	7.94	2.74	4.01	73.97	22.07	7.16	2.68	6.65	3.69	13.62	7.31	50.82	0.34	0.25
	F	8.13	2.49	3.43	7.51	2.72	3.55	73.21	20.65	7.35	2.7	6.65	3.6	12.74	7.68	50.49	0.35	0.26
<i>Herpestes pulverulentus</i>	M	7.64	2.52	3.42	7.55	2.87	4.00	70.29	25.37	7.32	2.77	5.86	3.57	11.58	7.81	47.85	0.38	0.28
	F	6.63	2.1	2.82	6.86	2.28	3.15	66.81	23.59	7.08	2.6	6.09	3.4	11.18	7.41	44.76	0.25	0.19
<i>Herpestes sanguineus</i>	M	5.62	1.82	2.57	5.77	2.09	2.80	58.53	21.47	5.59	2.21	4.65	2.78	9.88	5.63	38.04	0.22	0.15
	F	6.04	1.9	2.54	5.71	2.01	3.00	63.06	21.86	5.93	2.09	5.17	2.87	10.28	7.1	40.71	0.20	0.15
<i>Helogale parvula</i>	M	5.66	1.72	2.69	5.23	2.07	2.62	48.45	9.42	2.58	4.72	3.14	2.62	9.12	4.88	31.92	0.22	0.14
	F	5.63	1.75	2.7	5	1.9	2.76	48.77	9.37	2.86	4.79	3.5	2.64	8.79	4.83	31.88	0.22	0.14
<i>Suricata suricata</i>	M	7.9	2.62	3.84	8.22	2.86	3.91	65.73	12.60	3.35	5.58	4.19	3.1	10.73	6.5	44.56	0.50	0.34
	F	7.76	2.37	3.37	7.57	2.59	3.57	62.69	12.25	3.46	5.68	4.25	3.12	9.56	5.68	41.77	0.34	0.24
<i>Ichneumia albicauda</i>	M	10.48	3.67	4.95	10.39	3.91	5.6	107.56	34.77	7.91	3.86	8.14	4.63	18.74	10.58	78.05	0.84	0.63
	F	10.28	3.27	4.56	9.8	3.6	4.75	101.69	32.48	7.47	4.94	7.57	4.5	18.87	10.33	76.22	0.65	0.47
<i>Cynictis penicillata</i>	M	8.59	2.3	3.43	8.05	2.65	4.03	67.68	22.65	6.16	2.48	5.42	3.12	11.11	6.68	46.32	0.31	0.21
	F	8.31	2.2	3.04	7.65	2.36	3.59	66.35	21.92	5.92	2.63	5.23	3.03	10.33	6.67	44.76	0.24	0.18
<i>Genetta genetta</i>	M	8.18	2.4	3.39	7.68	2.52	3.19	83.74	27.86	7.35	2.45	6.39	3.31	12.73	8.58	58.41	0.34	0.24
	F	7.7	2.22	3.05	7.22	2.35	3.41	79.62	26.07	7.12	2.43	6.11	3.12	12.36	8.11	53.84	0.27	0.19
<i>Genetta servalina</i>	M	8.65	2.16	2.92	7.78	2.2	3.41	81.82	28.00	6.83	2.26	6.05	2.79	13.01	8.09	55.89	0.21	0.16
	F	7.73	2.02	2.6	7.36	2.02	3.12	80.43	27.49	6.95	2.29	6.01	2.92	12.08	8.26	55.08	0.17	0.14
<i>Paradoxurus hermaphroditus</i>	M	9.96	3.16	4.56	8.83	3.46	4.46	92.01	29.20	7.14	6.51	8.14	5.27	16.84	10.9	69.24	0.67	0.47
	F	9.1	3.23	4.27	7.89	2.99	4.37	94.54	28.84	7.36	6.31	8.13	5.3	17.6	11.11	70.05	0.65	0.51
Hyaenidae																		
<i>Hyaena hyaena</i>	M	28.49	9.79	13.62	26.17	9.77	13.11	226.74	61.66	28.5	10.37	19.54	9.44	44.73	23.17	167.62	6.26	4.52
	F	29.15	11.02	15.1	26.49	10.76	14.54	237.07	61.98	29.32	11.51	20.3	10.39	46.19	24.15	168.93	8.47	6.19
<i>Crocuta crocuta</i>	M	29.47	11.11	15.05	27.48	12.01	13.95	256.64	69.14	34.1	10.35	25.88	10.95	50.44	27.39	182.48	8.40	6.20
	F	29.63	11.38	15.24	27.5	12.44	14.01	257.82	69.49	34.26	10.60	26.46	10.78	49.7	27.00	184.26	8.80	6.56

Table I (cont.)

Taxa	Sex	UCH	UCW	UCL	LCH	LCW	LCL	SL	BCAL	UCL	UC+W	LCHL	LC+W	MAT	MAM	MAR	Sx	Sy
<i>Proteles cristatus</i>	M	14.21	4.52	6.46	12.52	4.64	5.86	133.11	39.22	3.09	2.06	3.16	1.93	15.93	11.52	93.02	1.31	0.92
	F	13.55	4.52	6.67	11.25	4.38	5.83	133.74	40.46	3.38	1.92	3.45	1.86	15.38	12.06	93.74	1.46	0.99
Felidae																		
<i>Felis silvestris</i>	M	13.18	4.01	5.19	10.29	3.56	4.76	96.99	31.13	10.51	3.74	7.88	3.8	18.12	11.58	66.52	0.81	0.62
	F	11.93	3.54	4.54	8.79	3.4	4.19	87.95	28.06	9.86	3.54	7.31	3.45	15.11	10.18	58.48	0.60	0.47
<i>Felis chaus</i>	M	13.88	4.49	5.57	11.56	4.04	4.86	107.68	31.59	11.73	4.41	9.84	4.14	19.75	11.45	72.03	0.99	0.80
	F	12.36	3.92	4.81	9.25	3.23	4.23	100.91	30.15	11.22	3.94	8.95	3.83	17.31	9.88	67.10	0.73	0.59
<i>Felis serval</i>	M	13.77	5.15	6.47	12.27	4.6	5.94	120.98	36.49	13.52	4.65	9.74	4.73	22.37	14.26	83.13	1.55	1.23
	F	12.28	4.53	5.91	11	4.1	5.57	111.96	34.80	12.56	4.34	9.03	4.45	19.76	11.19	75.85	1.28	0.98
<i>Felis caracal</i>	M	13.89	5.55	7.09	12.59	5.16	6.52	127.79	39.18	15.02	5.05	10.66	5.23	24.67	16.78	86.82	1.98	1.55
	F	13.43	5.42	6.72	11.16	4.65	6.07	121.33	36.65	15.04	4.89	10.98	5.25	23.03	14.47	81.10	1.81	1.46
<i>Lynx rufus</i>	M	16.8	5.69	6.68	14.35	5.25	6.55	121.4	36.86	14.14	5.56	10.14	4.92	21.84	12.31	74.88	1.51	1.28
	F	16.39	5.12	6.26	13.79	4.78	6.13	113.53	33.5	13.26	5.26	9.8	4.98	20.13	10.97	69.31	1.21	0.99
<i>Panthera leo</i>	M	49.32	18.38	25.67	41.19	16.69	23.68	367.35	89.89	37.7	14.09	30.04	14.96	70.76	44.2	233.23	24.26	17.39
	F	40.87	15.01	20.5	33.48	13.31	19.03	300.89	76.96	33.87	12.41	24.39	12.07	58.16	36.47	194.96	17.39	11.26
<i>Panthera pardus</i>	M	33.66	12.38	15.64	29.54	11.14	14.25	238.91	66.63	25.18	9.03	18.5	9.14	45.27	28.03	149.60	8.94	7.06
	F	27.9	9.82	12.24	24	8.87	11.68	194.17	53.71	23.39	8.08	15.68	7.92	34.69	20.95	127.31	7.07	4.20
<i>Panthera tigris</i>	M	53.15	19.52	25.44	44.28	16.69	22.86	356.09	86.00	32.63	11.91	25.49	12.46	68.95	48.51	221.74	23.48	18.01
	F	47.27	17.14	22.42	39.84	14.88	19.66	320.11	79.76	31.18	11.46	23.08	12.04	59.81	40.92	198.13	18.09	13.82

Teeth measures: UCH-upper canine height; UCW- upper canine width; UCL- upper canine length; UCLH- lower canine height; LCH- lower canine length; LCL- lower canine length; SL- skull length; BCAL- basicranial axis length; UCLH- upper carnassial length; UCW- upper carnassial width; LCHL- lower carnassial length; LCW- lower carnassial width; MAT- moment arm of temporalis; MAM- moment arm of masseter; MAR- moment arm of resistance; Sx- upper canine strength in resisting forces applied in a mediolateral direction; Sy- upper canine strength in resisting forces applied in an anteroposterior direction

Behavioural and ecological categories

Species were assigned to one type in each of the following categories (species categorization, original data sources and further discussion of categories are given in the citations listed for each variable).

- (a) Activity pattern: nocturnal, diurnal, crepuscular, arrhythmic, nocturnal and crepuscular (Gittleman, 1985, 1986).
- (b) Diet: flesh eaters (vertebrates), insectivores, frugivores, herbivores, omnivores (Gittleman, 1985, 1986).
- (c) Zonation: terrestrial, arboreal, terrestrial and arboreal, aquatic (Gittleman, 1985, 1986).
- (d) Breeding type: social or nonsocial breeding according to criteria defined by Creel & Macdonald (1995).
- (e) Mating system: single-male, multi-female groups; multi-male, multi-female groups; and monogamous pairs (Gittleman, 1986). This classification follows types defined in previous primate studies (see Harvey *et al.*, 1978).
- (f) Population group size: the number of adult male(s) and females that regularly associate and share a common home range (Gittleman, 1989b; Creel & Macdonald, 1995).

Data analysis

All craniodental data were logarithmically transformed prior to analyses in order to examine linear relations. Before assessing functional relationships it is necessary to assess the extent and direction of phylogenetic patterning with dimorphism. We use an autocorrelation technique to detect correlation between phylogenetic distance (or taxonomic ranks) and phenotypic trait variation (see Gittleman & Kot, 1990). If phylogenetic correlation is found, comparative trait values cannot be analysed as independent data points and therefore some statistical method is needed to incorporate phylogenetic pattern into a comparative test. Many comparative statistical methods are available for doing so (see Harvey & Pagel, 1991). We have selected the 'phylogenetic autoregressive' method (Gittleman & Kot, 1990) because simulation studies (see Gittleman & Luh, 1992, 1994; Purvis, Gittleman & Luh, 1994) indicate that the method is statistically appropriate when: (1) phylogenetic correlation is indeed observed in the comparative data; (2) comparative tests involve samples of greater than 10 and less than 50 taxa; and (3) phylogenetic trends are generally autoregressive whereby closely related taxa are more similar phenotypically than distantly related taxa. These conditions are met in the present analysis. Details of the phylogenetic autoregressive method are given in Gittleman & Kot (1990), Gittleman & Luh (1992, 1994) and Purvis *et al.* (1994); a computer version is available in Luh (1994).

The phylogenetic autoregressive method was applied to 2 types of systematic information. One employed taxonomic rank information from Wozencraft (1989) and was inclusive of all species for which trait data were available; the primary results on sexual dimorphism were based on this approach. The other employed molecular phylogenetic distance data from Wayne *et al.* (1989) which only encompassed 17 out of the 45 species included in Table I; phylogenetic information is based on pairwise distances between all species in relation to hybridization of unique sequence DNA. The molecular tree was used primarily to verify if indeed there were phylogenetic patterns in carnivore canine dimorphism as suggested by the taxonomic rank analysis. Generally, we proceed cautiously in using taxonomic rank information to estimate phylogenetic patterns. At the outset, estimates of phylogeny based on taxonomic rank are compared against molecular distance information. Results of comparative tests are reported with and without using taxonomic rank information in the autoregressive method. In addition, other empirical work suggests that, in some cases, taxonomic rank information reveals similar comparative trends across carnivores as phylogenetic distance data (Gittleman & Kot, 1990) and that the phylogenetic autoregressive method is statistically robust in using taxonomic rank information (Gittleman & Luh, 1994).

Results

Examination of mean values of sexual dimorphism among the various craniodental characters by family reveals that the canine dimensions are generally more dimorphic than other teeth, skull or

TABLE II
Mean sexual dimorphism by family of craniodental variables (see Table I and text for variable codes)

Family (#species)	UCH	UCW	UCL	LCH	LCW	LCL	SL	BCAL	UCrL	UCrW	LCrL	LCrW	MAT	MAM	MAR	M/MAR	UCarea	Sx	Sy
Canidae (7)	1.05	1.08	1.06	1.04	1.07	1.05	1.05	1.04	1.04	1.04	1.03	1.04	1.05	1.06	1.04	1.01	1.14	1.15	1.17
Procyonidae (3)	1.09	1.17	1.16	1.29	1.22	1.18	1.02	1.04	1.01	1.01	1.01	0.98	1.03	1.01	1.03	1.00	1.36	1.46	1.47
Ursidae (1)	1.10	1.10	1.06	1.08	1.13	1.10	1.05	1.04	1.03	1.05	1.04	1.06	1.03	1.13	1.02	1.00	1.17	1.07	1.12
Mustelidae (12)	1.24	1.21	1.23	1.28	1.19	1.2	1.12	1.1	1.08	1.08	1.10	1.14	1.17	1.14	1.14	1.02	1.52	1.43	1.41
Viverridae (11)	1.05	1.05	1.08	1.07	1.10	1.08	1.00	1.03	0.99	0.99	1.00	1.01	1.04	1.00	1.02	1.01	1.14	1.20	1.15
Hyaenidae (3)	1.01	0.96	0.95	0.95	0.98	0.97	0.98	0.99	0.96	0.99	0.95	0.99	1.01	0.98	0.99	1.01	0.91	0.86	0.87
Felidae (8)	1.12	1.14	1.15	1.16	1.16	1.14	1.12	1.1	1.06	1.08	1.1	1.07	1.16	1.2	1.12	1.04	1.32	1.28	1.35
All groups (45)	1.11	1.12	1.13	1.15	1.13	1.12	1.06	1.06	1.04	1.04	1.04	1.06	1.09	1.09	1.07	1.02	1.28	1.26	1.26
ANOVA (F)	3.79	3.88	3.87	3.66	2.15	2.03	3.57	2.84	2.81	1.30	2.12	1.39	2.80	2.55	2.52	0.61	3.24	4.19	4.25
Significance	0.005	0.004	0.004	0.006	0.07*	0.09*	0.007	0.02	0.02	0.28*	0.07*	0.25*	0.02	0.04	0.04	0.71*	0.01	0.003	0.002

* = non significance

M/MAR = MAT/MAR

strength indices (Table II). Among the raw measurements, mean male/female values for the entire sample span 1.04–1.15, with canine dimensions ranging from 1.11–1.15 compared with a range of 1.04–1.09 for skull size, carnassial size and muscle moment arms. In part, because strength values are computed with the cube of half the relevant diameter, canine strength tends to show even greater dimorphism, with an overall mean of 1.26.

Phylogeny

Using the phylogenetic autocorrelation method, significant correlations are found between sexual dimorphism of all craniodental characters and taxonomic rank, as well as (molecular) phylogenetic distance (Table III); the only exceptions are for *Sy* and the mechanical advantage of the temporalis muscle (MAT/MAR). Relative correlational values are similar between molecular and taxonomic information for the various craniodental characters. However, in the taxonomic analysis, there are significant differences among families with respect to absolute values of sexual dimorphism (Table II). Generally, family comparisons reveal that mustelids, felids and procyonids are more dimorphic than canids, viverrids, hyaenids and the single ursid. Therefore, the remaining analyses of allometric, behavioural and ecological variables mainly use data that have been transformed using the phylogenetic autoregressive method.

Allometry

Three allometric variables were examined. Body weight is a general representation of changes in overall size. Skull length also reflects changes in size while minimizing possible allometric effects due

TABLE III

Correlation (r^2) with taxonomic rank and phylogenetic (molecular) distance of dimorphism in carnivore craniodental characters. All correlations are significant at the 0.01 level of significance except those denoted by an asterisk. Sample sizes with taxonomy are 45 species and with phylogeny 17 species. See Table I and text for variable codes

Character	Taxonomy r^2	Phylogeny r^2
UCH	0.45	0.45
UCW	0.48	0.45
UCL	0.58	0.57
LCH	0.41	0.43
LCW	0.44	0.41
LCL	0.54	0.52
UCarea	0.55	0.48
<i>Sx</i>	0.32	0.47
<i>Sy</i>	0.15*	0.10*
SL	0.49	0.49
BCAL	0.40	0.41
UCrL	0.44	0.43
UCrW	0.43	0.47
LCrL	0.41	0.42
LCrW	0.37	0.39
MAT/MAR	0.21*	0.17*

TABLE IV
Correlation coefficients (r) of allometric variables and carnivore teeth dimorphism using absolute species values and phylogenetic autoregressive residuals⁺

Teeth	Species values			Phylogenetic residuals		
	BW	SL	BCAL	BW	SL	BCAL
UCH	0.14	0.27	0.14	0.04	0.26	0.16
UCW	0.13	0.22	0.12	0.04	0.21	0.17
UCL	0.22	0.24	0.20	0.19	0.29	0.19
LCH	0.14	0.28	0.20	0.16	0.24	0.21
LCW	0.02	0.15	0.12	0.04	0.17	0.19
LCL	0.06	0.18	0.11	0.03	0.10	0.13
UCrL	0.02	0.05	0.01	0.03	0.06	0.01
UCrW	0.06	0.11	0.10	0.07	0.07	0.11
UCarea	0.18	0.27	0.17	0.07	0.24	0.09
MAT/MAR [^]	0.10	0.11	0.07	—	—	—

Allometric variables are: body weight (BW), skull length (SL), and basicranial axis length (BCAL).

⁺ All correlation coefficients are not significant

[^] Phylogenetic residuals were not calculated for MAT/MAR because no phylogenetic correlation was detected with this variable

to adipose tissue. Basicranial axis length (Radinsky, 1984) represents skull size independent of snout length. Allometric patterns were consistent among all three variables: there is no significant correlation between any of the three body size measures and any measure of dimorphism (Table IV). Differences in relative correlation values also were not detected among teeth variables, either with or without phylogenetically transforming the data.

Because allometric patterns could possibly be obscured by relatively large dimorphism in the smaller mustelids and small dimorphism in larger canids, analyses were also performed within the four families with the largest sample sizes (Mustelidae; Viverridae; Felidae; Canidae). Across all families but Mustelidae, no significant correlations are found between body weight, skull length or basicranial axis length and any measure of dimorphism. Within mustelids, canine dimorphism is *negatively* correlated with skull length and body weight ($P < 0.05$, Fig. 1). In sum, no allometric patterns are observed across the order, only one family showed any allometric effect and in this case there was a negative relationship. Remaining analyses of behavioural and ecological patterns therefore omit possible allometric effects and strictly analyse functional patterns of dimorphism in relation to absolute values.

Craniodental covariation in dimorphism

Each of the indices of canine dimorphism was examined in relation to dimorphism in upper/lower carnassials, muscle moment arm variables (MAT, MAM, MAR, MAT/MAR), and the two indices of upper canine bending strength. Despite the lack of significant correlation with body size (as above), all measures of canine dimorphism are significantly related to dimorphism in nine of ten examined variables of other craniodental and functional measures (Table V); the only non-significant relationship was with MAT/MAR. Therefore, analyses of behavioural/ecological patterns also investigated univariate results of each of these other craniodental variables and bivariate results with variation in canine dimorphism.

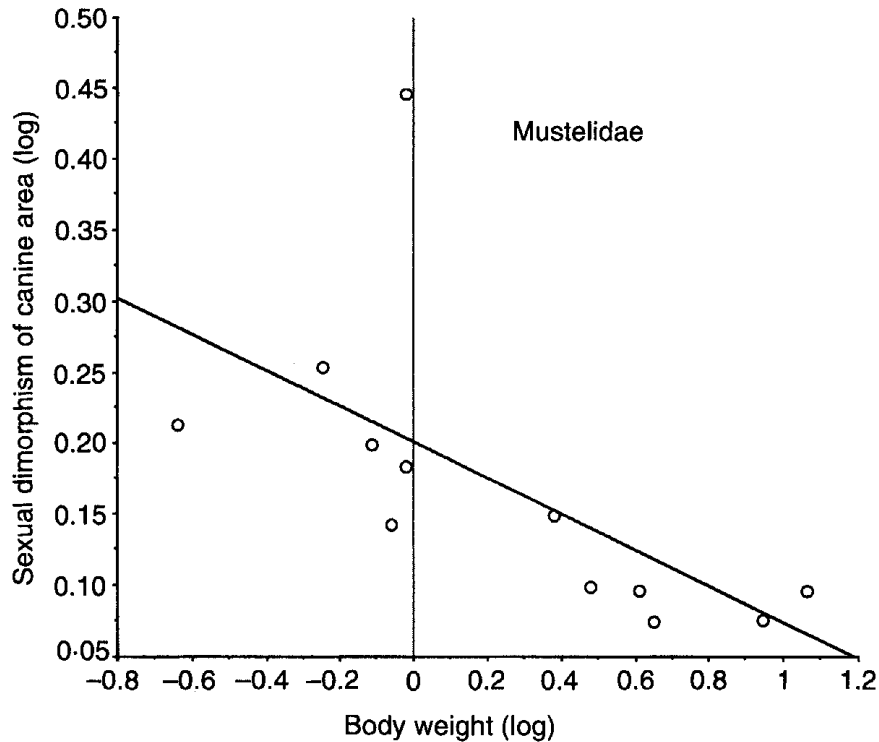


FIG. 1. Sexual dimorphism of canine area (log) regressed on body weight (log) across the family Mustelidae ($y = -127x + 0.201$, $r^2 = 0.386$). Note: The relatively high sexual dimorphism is observed in *Mustela erminea*.

Behavioural ecology

Craniodental characters and biomechanical indices were analysed in relation to categorical variables (see **Materials and methods**) of activity pattern, diet, zonation and breeding system (see Table VI). Using either absolute species values or phylogenetic residuals, there are no significant relationships with activity pattern or zonation. Also, there is no significant correlation (r) between population group size and any of the following canine dimorphism measures (species values and

TABLE V

Covariation of canine dimorphism with dimorphism in other craniodental and functional variables. Data analysis follows phylogenetic transformation (except with MAT/MAR (M/MAR)). Sample size is 45 and all correlations (r) are significant at 0.01 or 0.001 levels except with the ratio MAT/MAR. Variables are defined in Table I and text

Canines	Craniodental and functional variables								Sx	Sy
	UCrL	UCrW	LCrL	LCrW	MAT	MAM	MAR	M/MAR		
UCH	0.76	0.63	0.76	0.74	0.73	0.62	0.81	0.12	0.53	0.55
UCW	0.79	0.52	0.74	0.72	0.74	0.68	0.82	0.12	0.81	0.56
UCL	0.78	0.53	0.75	0.76	0.78	0.66	0.81	0.22	0.87	0.57
LCH	0.60	0.56	0.62	0.59	0.56	0.44	0.63	0.16	0.57	0.51
LCW	0.60	0.50	0.61	0.56	0.57	0.56	0.65	0.14	0.61	0.70
LCL	0.58	0.42	0.56	0.45	0.50	0.41	0.55	0.19	0.51	0.90
UCarea	0.80	0.54	0.76	0.75	0.78	0.68	0.83	0.11	0.86	0.57

TABLE VI

Differences in sexual dimorphism of canine size, other craniodental characters, and biomechanical indices in relation to behavioural and ecological variables. Statistical analyses include Analysis of Variance (F) using absolute species values (left) and phylogenetic autoregressive residuals (right). Degrees of freedom for each independent variable are: activity (4,40), diet (3,41), zonation (2,42) and breeding system (2,30). Levels of significance are given in parentheses otherwise F-values are not significant

Character	Species values				Phylogenetic residuals			
	Activity	Diet	Zonation	Breeding	Activity	Diet	Zonation	Breeding
UCH	1.30	0.90	0.36	6.19 (0.006)	0.85	0.25	0.78	3.93 (0.031)
UCW	2.04	1.78	0.71	4.64 (0.018)	1.00	0.62	0.97	4.74 (0.016)
UCL	0.94	1.84	1.07	5.08 (0.013)	0.21	0.73	0.46	3.62 (0.040)
LCH	1.43	1.41	0.40	4.36 (0.022)	1.22	1.32	0.95	4.20 (0.025)
LCW	1.19	0.94	0.43	3.26 (0.05)	1.32	0.83	0.91	3.50 (0.05)
LCL	0.99	0.90	0.62	2.55	1.11	0.87	0.75	3.44 (0.05)
UCarea	1.31	1.87	0.88	5.06 (0.013)	0.70	0.76	0.89	4.99 (0.025)
SL	1.36	4.41 (0.009)	1.04	2.17	0.51	1.76	0.77	2.40
BCAL	1.80	3.56	1.75	7.80 (0.002)	1.03	1.79	0.77	5.57 (0.009)
UCHL	2.09	5.24 (0.004)	1.40	2.88	0.31	2.62 (0.05)	1.39	1.57
UCrW	1.04	3.01 (0.041)	0.19	3.66 (0.04)	1.43	3.22 (0.042)	0.66	2.87
LCL	2.46	6.05 (0.002)	0.31	2.98	1.45	4.99 (0.005)	0.73	2.84
LCrW	0.88	4.38 (0.009)	0.35	2.34	0.79	3.55 (0.025)	0.94	2.01
MAT	1.16	4.69 (0.007)	0.73	4.69 (0.02)	1.24	3.94 (0.025)	0.36	3.34 (0.05)
MAM	2.49	4.28 (0.010)	0.48	3.40 (0.05)	2.21	2.86 (0.05)	0.67	4.21 (0.025)
MAR	1.23	3.99 (0.014)	0.48	4.95 (0.014)	1.45	3.77 (0.025)	0.88	3.55 (0.05)
MAT/MAR	0.77	1.31	0.60	0.71	—	—	—	—
Sx	0.72	1.86	2.52	3.07	0.19	1.06	2.05	0.23
Sy	1.92	2.39	1.63	3.24	0.43	0.71	0.21	2.73

phylogenetic residuals, respectively; $n = 41$): UCH (0.23; 0.10), UCW (0.25; 0.14), UCL (0.15; 0.02), LCH (0.10; 0.14), LCW (0.02; 0.09), LCL (0.02; 0.14), UCarea (0.16; 0.08).

Significant and consistent patterns are observed with breeding system and diet (Table VI). Generally, differences in canine dimorphism relate to breeding system and differences in carnassial dimorphism relate to diet. All but one (LCL) of the measures of canine size, along with the three measures relevant to bite mechanics, are significantly different among breeding categories: mean indices of canine dimorphism indicate that species having uni-male, multi-female groups are the most dimorphic, followed by multi-male, multi-female groups and then monogamous pairs (Table VII). Pairwise comparisons reveal that only uni-male, multi-female groups and monogamous pairs differ significantly in dimorphism; differences between multi-male, multi-female groups and monogamous pairs were not significant (Table VIII). All measures of carnassial dimorphism are significantly different among dietary categories: mean dimorphism indices of carnivorous (meat-eating) species are greater than those of omnivorous, frugivorous and insectivorous species (Table IX). Pairwise comparisons of dietary patterns (Table X) indicate that significant differences are between carnivores and two other categories (omnivores; insectivores).

Significant differences were observed in three indices of jaw muscle mechanics (MAT, MAR, MAM) in relation to both diet and breeding system, suggesting that there is the greatest strength dimorphism in carnivorous, single-male species (see Tables VII and IX). However, no significant patterns are observed with the ratio of MAT/MAR, which is a better predictor of leverage of the temporalis (Van Valkenburgh & Ruff, 1987) than the single indices. These data indicate that, although males tend to have absolutely larger jaw muscles and skulls than females, the mechanical advantage of

TABLE VII
Canine dimorphism and breeding system

Type of breeding system	N	Mean sexual dimorphism									
		UCH	UCW	UCL	LCH	LCW	UCarea	BCAL	MAT	MAM	MAR
Uni-male group	16	1.20	1.19	1.20	1.24	1.18	1.46	1.11	1.17	1.18	1.14
Multi-male group	10	1.07	1.09	1.11	1.14	1.14	1.22	1.05	1.06	1.07	1.04
Monogamous pair	7	1.04	1.05	1.03	1.03	1.03	1.09	1.02	1.02	1.05	1.02

the muscles is the same in both sexes. Dietary effects are somewhat suggestive, with carnivores having greater ratios than the other dietary categories. Unfortunately, sample sizes among the various behavioural and ecological categories prohibit a multivariate analysis.

Discussion and conclusions

Comparing carnivores and primates

Data comparable to ours are available for canine size dimorphism in primates and show that the span of male/female values for upper canine basal width, length, and area is similar in both primates and carnivores. For example, dimorphism in canine basal area ranges from 0.9–2.35 in a sample of 45 primates (Martin *et al.*, 1994) and 0.8–2.79 in our carnivore sample. However, primates display greater extremes of dimorphism in canine crown height, with some males having upper canines that are two to four times the length of those of females (Plavcan & van Schaik, 1992). By contrast, among carnivores the same ratio never exceeds two. It appears that relative to carnivores, selection on the canines of some male primates has emphasized crown height over basal area. As a result, the very long canines of males of some primate species are likely to be much weaker in bending strength than the canines of females, which are shorter but similar to males in basal diameter. The fact that we do not see the same pattern among carnivores suggests that selection on male carnivores to increase canine size is more constrained by the need to retain strength, presumably for killing and feeding. The canine

TABLE VIII
Statistical analysis of canine dimorphism and breeding system

Character	t-tests		
	Uni-male vs. multi-male (<i>d.f.</i> , 24)	Uni-male vs. monogamous (<i>d.f.</i> , 21)	Multi-male vs. monogamous (<i>d.f.</i> , 15)
UCH	$t = 2.54, P < 0.02$	$t = 2.72, P < 0.01$	$t = 0.42, \text{NS}$
UCW	$t = 2.11, P < 0.05$	$t = 2.51, P < 0.02$	$t = 0.59, \text{NS}$
UCL	$t = 1.74, \text{NS}$	$t = 2.84, P < 0.01$	$t = 1.19, \text{NS}$
LCH	$t = 1.39, \text{NS}$	$t = 2.61, P < 0.02$	$t = 1.26, \text{NS}$
LCW	$t = 0.62, \text{NS}$	$t = 2.28, P < 0.05$	$t = 1.59, \text{NS}$
UCarea	$t = 2.13, P < 0.05$	$t = 2.49, P < 0.05$	$t = 0.79, \text{NS}$
BCAL	$t = 2.73, P < 0.02$	$t = 3.48, P < 0.01$	$t = 0.96, \text{NS}$
MAT	$t = 2.19, P < 0.05$	$t = 2.55, P < 0.02$	$t = 0.55, \text{NS}$
MAM	$t = 2.05, \text{NS}$	$t = 2.08, P < 0.05$	$t = 0.24, \text{NS}$
MAR	$t = 2.24, P < 0.05$	$t = 2.41, P < 0.05$	$t = 0.38, \text{NS}$

TABLE IX
Carnassial dimorphism and diet

Type of diet	N	Mean sexual dimorphism						
		UCrL	UCrW	LCrL	LCrW	MAT	MAM	MAR
Carnivore	18	1.08	1.09	1.11	1.14	1.16	1.17	1.13
Omnivore	20	1.02	1.01	1.01	1.01	1.05	1.04	1.04
Frugivore	2	1.00	1.01	1.01	0.97	1.04	0.97	1.02
Insectivore	5	0.97	1.00	0.98	1.01	1.03	1.03	1.01

teeth of carnivores are frequently broken in life, attesting to the large loads they bear (Van Valkenburgh, 1988).

As noted in the **Introduction**, previous work on primates has documented correlations between the degree of canine dimorphism and body size (Leutenegger & Cheverud, 1982, 1985; Plavcan & van Schaik, 1992), zonation (Leutenegger, 1982; Plavcan & van Schaik, 1992), and activity pattern (Harvey *et al.*, 1978). Our study found no such correlations among carnivores. Some of the most dimorphic species were the small weasels (*Mustela* spp.) and the least included the hyaenas and most canids (Table II). Thus, in carnivores, it does not seem that selection for large size has been accompanied by greater dimorphism as in primates, and consequently, it is not a general mammalian pattern.

In primates, terrestrial species tend to be more dimorphic than arboreal species, and it has been argued that this is due to a greater need for defence against predators in more open, terrestrial habitats. Although terrestrial carnivores might be expected to suffer a similar relative increase in predator pressure (Gittleman, 1989b), they do not show a parallel increase in canine dimorphism. This might reflect the fact that, unlike most carnivores, primates are social and males are somewhat more active than females in defending a group against predators. Among carnivores, neither sex is more active in predator defence and, consequently, differences in relative predator pressure should not be associated with differences in dimorphism.

The third factor that differs in its effect on primates and carnivores is activity pattern. Diurnal primates are more dimorphic in canine dimensions than nocturnal primates, perhaps because visual displays are more effective in daylight and nocturnal species can more easily avoid predators through

TABLE X
Statistical analysis of carnassial dimorphism and diet

Character	t-tests		
	Carnivore vs. omnivore (<i>d.f.</i> , 36)	Carnivore vs. frugivore* (<i>d.f.</i> , 18)	Carnivore vs. insectivore (<i>d.f.</i> , 21)
UCrL	$t = 2.89, P < 0.01$	$t = 1.51, \text{NS}$	$t = 3.18, P < 0.01$
UCrW	$t = 2.84, P < 0.01$	$t = 1.19, \text{NS}$	$t = 1.81, \text{NS}$
LCrL	$t = 3.44, P < 0.01$	$t = 1.55, \text{NS}$	$t = 2.97, P < 0.01$
LCrW	$t = 2.96, P < 0.01$	$t = 1.73, \text{NS}$	$t = 2.08, P < 0.05$
MAT	$t = 3.18, P < 0.01$	$t = 1.58, \text{NS}$	$t = 2.44, P < 0.05$
MAM	$t = 3.01, P < 0.01$	$t = 1.95, \text{NS}$	$t = 1.99, \text{NS}$
MAR	$t = 2.71, P < 0.01$	$t = 1.45, \text{NS}$	$t = 2.40, P < 0.05$

* Sample size limited to two frugivores

concealment (Leutnegger & Cheverud, 1982). Both of these explanations should apply to carnivores and yet there was no association between activity pattern and degree of dimorphism in our sample. This suggests that alternative explanations for the primate pattern should be sought.

Our results did confirm one association between behaviour and dimorphism that has been well documented in primates, that between breeding system and canine dimorphism (Harvey *et al.*, 1978; Kay *et al.*, 1988; Plavcan & van Schaik, 1992). In both carnivores and primates, the most dimorphic species are those in which competition among males for access to females is relatively intense. In our sample, species with uni-male, multi-female breeding systems tend to be more dimorphic than monogamous species.

Canine dimorphism and breeding system

Functional explanations for a correlation between breeding system and canine size require two elements. First, canine size should be associated with particular behavioural differences reflected in types of breeding systems. For example, if competition in polygynous systems is greater than in monogamous systems and canine size is hypothesized to confer advantages in competitive encounters, then canines should be an integral component of settling agonistic encounters. Second, the typically larger size of canines in male carnivores suggests that the relationship between canine size and functional behaviours must be qualitatively different in males than females. No field or laboratory study of any carnivore species has explicitly collected these kinds of requisite data. However, as we describe in the following, general natural history information suggests that the relationship between canine size and competition may be more commonly observed in polygynous species in which canine display is featured in settling and/or escalating disputes.

A direct test of how mating system is related to levels of aggression is simply to make comparisons across carnivore taxa, as carried out for other mammalian orders (see Eisenberg, 1981). This comparison is not currently possible owing to a lack of data and the fact that the limited information available does not represent consistent behavioural measures among studies. Two lines of indirect evidence, however, suggest differences in levels of aggression within various breeding systems. First, the incidence of infanticide is generally recorded more frequently in polygynous than monogamous carnivores, largely reflecting male reproductive strategies in which male-male competition is severe (Packer & Pusey, 1984). Second, intrasexual (mainly male-male) competition appears less in monogamous than polygynous carnivore species (Kleiman, 1977); it should, however, be pointed out that no single study, either captive or field, has used the same methods directly to measure levels of aggression in two carnivore species with different breeding systems (see Kleiman, 1981).

Though not necessarily within the context of mate competition, the most detailed analyses of fighting and aggressive behaviours are in classic ethological descriptive studies. In domestic cats, Leyhausen (1979) used experimental manipulations of individuals to assess the contextual and developmental features of attack and defensive encounters. Leyhausen describes how cats change morphologically (pupil size, ear position, lip curl, head position) and behaviourally (vocalizations, lunging) as the motivation for fighting increases. Teeth are not used or even shown at the onset of an encounter. However, as the likelihood of fighting increases, hissing vocalizations (with partial canine display) change into growls, at which point attack is imminent. Just prior to an attack, the cat lunges forward in association with a spit and the jaws are wide open, with full canine display. Importantly, even though disputes may reach this point of agonistic physical contact, attack fighting frequently does not occur and the dispute is often settled by display. Because they are conspicuous, canines would certainly be an effective cue for settling a contest between individual carnivores in which the costs

from wounds are potentially high (see Maynard Smith, 1982; Packer & Pusey, 1982). Such a communicatory function of canines in aggressive-defensive threat situations is given more support by Schaller's (1972) detailed descriptions of the 'bared-teeth face' in African lions, *Panthera leo*. In more low-grade agonistic encounters, a low growl is emitted with an associated lifting of the upper lip, exposing a canine on the side of the face; with more intense encounters, the corners of the mouth are pulled back further, lips everted, and the teeth are fully exposed. Similar aggressive behaviour patterns of graded postures, vocalizations and canine flashing are also observed in polecats, *Mustela putoris* (Poole, 1967). The greatest canine sexual dimorphism occurs in the weasels, but, unfortunately, there are no data available on the relationship between mating behaviour and canine function in various *Mustela* species (King, 1989).

In the monogamous striped hyaena (*Hyaena hyaena*), although throat biting and open-mouth threats are shown in agonistic encounters, canines are relatively cryptic (Rieger, 1978). Likewise, in the monogamous arctic fox (*Alopex lagopus*) agonistic displays involve elevation of head, ears and tail, coupled with high leaps, a stare, sometimes a growl and open mouth (Wakeley & Mallory, 1988). However, in this series of agonistic displays, the elements of stare and mouth gape are often absent and the canines are not shown. In the golden jackal (*Canis aureus*), although canines are used in intense fighting, threat displays and agonistic postures involve head stares in which the "lips are opened wide enough that the incisors but not the canine teeth are visible" (Wandrey, 1975: 370). Thus, in canids which use a mouth gape or grimace in various social contexts, canines do not appear to be as conspicuous as in other carnivore species, even though they may be displayed and used in intensive fights (see Fox, 1971). This certainly is consistent with the comparative finding of diminished canine dimorphism in the monogamous canids and the striped hyaena.

The comparative results further support the idea that canines function more for display than actual fighting. Even though the various measures of canine dimorphism are significantly correlated with dimorphism in upper canine bending strength (Table V), indices of canine strength (i.e. S_x , S_y) do not differ between types of breeding system (Table VI). Therefore, in species with uni-male, multi-female breeding systems, the canines of males differ from those of females more in size than strength, suggesting that display is more important than function in male-male encounters.

To a certain extent the above relationships among canines, types of communication and social structure can be viewed in a broader context, especially in understanding the differences between canids and felids. Canids tend to be omnivorous, have large litter sizes, and promote the development of social tolerance via monogamous pair bonds (Kleiman & Eisenberg, 1973; Geffen *et al.*, 1996). Much of their social and feeding ecology involves both visual and olfactory communication. By contrast, felids tend to be exclusively carnivorous, have small litters, and are solitary outside the breeding system while polygynous during mating periods (Kleiman & Eisenberg, 1973; Caro, 1989, 1994). Although scent-marking is used in territorial contexts, felids rely more exclusively on visual senses (perhaps the greatest binocular vision of all carnivores: Kitchener, 1991), as reflected in their relatively large eyes, ability to discriminate fine-grained spectral changes, and focus on facial areas during social encounters. Further, although relative brain size is around 25% smaller in felids than canids (Gittleman, 1986), detailed brain anatomy in fossil and extant taxa shows greater occipital lobe expansion in felids than in canids, suggesting expansion of visual cortical areas (Radinsky, 1973, 1975). An additional difference in the degree to which olfaction is used between canids and felids is that canids have, compared with other carnivores and for their size, very large olfactory bulbs, whereas felids have small bulbs (Gittleman, 1991). Thus, in terms of elements of communication and associated anatomical characters, canine teeth would be expected to be used more in polygynous felids than in monogamous canids.

Canine dimorphism vs. carnassial dimorphism

Of the measured characters, canine tooth dimensions were the most dimorphic. The canines of males were typically 11–15% larger in linear dimensions and as much as 45% stronger than those of females. All other measures of skull, jaw muscle and carnassial size were much less dimorphic, with males exceeding females usually by no more than 10%. Similar patterns have been observed intraspecifically in the mountain lion, *Puma concolor* (Kurten, 1973; Gay & Best, 1995), four small felid species (Dayan *et al.*, 1990), and three canid species (Dayan *et al.*, 1992). This suggests that males of many dimorphic species are not simple proportional enlargements of females.

The fact that canine dimorphism is greater than that observed for carnassials lends further support to the effects of breeding system. If sexual dimorphism is driven through competition for prey, then one might expect that the largest cheek teeth, the carnassials, would enlarge similarly. The larger sex is assumed to be killing larger prey as well as eating absolutely more to sustain its greater mass, and consequently its entire trophic apparatus is expected to enlarge. However, the carnassials show almost no dimorphism except among the carnivorous species.

Diet had a significant effect on the degree of both carnassial and jaw muscle (MAT, MAM) dimorphism. Carnivorous species, such as mustelids and felids, appear to be more dimorphic in these characters than all other dietary groups. At present we have no explanation for this result. The planned allometric analysis of relative tooth size by sex within species may provide some insights. It might be argued that the greater dimorphism of carnassial size in carnivorous species reflects selection for character displacement between the sexes in response to competition for food. However, recent studies of possible character displacement among sympatric mustelids and felids found no significant patterns of size separation in carnassial dimensions, even when the sexes are treated as separate morphospecies (Dayan *et al.*, 1989, 1990). Instead, the anteroposterior diameter of the upper canine was the only measure that showed little overlap between sexes or species. More perplexing still, Dayan *et al.* (1992) did find evidence for displacement in carnassial length in five Israeli canid species, several of which are omnivorous. The authors argued that the differences in carnassial size among the canids reflect interspecific differences in prey size or diet. It is difficult to reconcile the disparate results of the felid and mustelid studies, on the one hand, and the canids on the other. Without more data on tooth use and diet in sympatric carnivores, it is difficult to understand why sympatric, highly carnivorous species would show less interspecific separation in carnassial dimensions than sympatric, omnivorous species.

Canine dimorphism and character displacement

In a series of important papers Dayan, Simberloff and colleagues showed that: (1) three sympatric, small felid species (*Felis silvestris*, *F. chaus*, *F. caracal*) in Israel reveal non-overlapping patterns of canine dimorphism but not of other craniodental features (Dayan *et al.*, 1990); (2) three sympatric *Mustela* species (*erminea*, *frenata*, *nivalis*) in North America and five sympatric mustelid-viverrid species in Israel (*Vormela peregusna*, *Martes foina*, *Meles meles*, *Mellivora capensis*, *Herpestes ichneumon*) are remarkably equal in a graded series of non-overlapping canine dimorphism ratios (Dayan *et al.*, 1989); (3) although dimorphism is less than in felids and mustelids, five sympatric canid species (*Canis lupus*, *C. aureus*, *Vulpes vulpes*, *V. rueppelli*, *V. cana*) in Israel show remarkably even size ratios in all craniodental features, including canine diameter, carnassial length and skull length (Dayan *et al.*, 1992); and (4) five sympatric mustelid species (*Meles meles*, *Martes martes*, *Mustela putorius*, *M. erminea*, *M. nivalis*) in Britain show community-wide

character displacement in canine dimorphism but not in skull length (Dayan & Simberloff, 1994). Despite the authors indicating that no (quantitative genetics) model explicitly treats sexual dimorphism and competitive character displacement, these empirical patterns are explained exclusively in terms of character displacement: size dimorphism in canines is selected to minimize competition for prey among species. Admittedly, the authors state, competition is inferred from general descriptions of dietary content even though prey size, type, availability and their relationship to canine size are unknown. It is argued that character displacement is a preferred explanation for patterns in canine dimorphism because other hypotheses involving sexual selection or displays would not predict such even, non-overlapping ratios. We agree that it is unlikely that sexual selection can entirely account for these patterns of size ratio equality; however, we suggest that sexual selection must also be influential for a variety of reasons.

There are some confounding patterns with the character displacement hypothesis. It seems unlikely that character displacement exclusively, or even primarily, influences canine dimorphism because: (1) Greater differences in strength dimorphism, as reflected in how canines are used on prey, should be reflected in carnivores feeding on different kinds of foods. (2) The direction of dimorphism is almost always in males being larger than females, which is not predicted by the character displacement hypothesis. (3) Species that have very different diets (i.e. omnivorous canids vs. carnivorous felids) are somewhat dimorphic, with relative variation in dimorphism relating more to breeding system (i.e. monogamous canids vs. polygynous felids). Taken together, our findings and those of Dayan and colleagues suggest that the effects of sexual selection and diet on canine dimorphism may be one of evolutionary origin. Sexual selection may have initially driven differences in size. Once these size differences arise, then patterns of dimorphism are more likely to be generated, or reinforced, by dietary patterns. Three tests would help examine this hypothesis. First, with an explicit phylogeny of all taxa, it would be possible to examine whether variation in dimorphism varied ancestrally with mating patterns or dietary shifts. Second, a comparative multivariate analysis with dietary factors representing levels of character displacement and breeding system factors representing different levels of competition would tease apart relative effects. Third, a behavioural analysis of how much canine dimorphism impacts differences in feeding ecology and levels of agonistic interactions would clarify the functional significance of size differences.

Finally, to understand the selective importance of carnassial and canine size in the Carnivora better, it would be useful to analyse the effect of various behavioural variables on female canine size. As pointed out recently by Plavcan *et al.* (1995), studies of sexual dimorphism have focused almost exclusively on a model of sexual selection favouring increased male size and have ignored potential effects of selection on female size. Clearly, selection favouring reduced female size will also result in enhanced dimorphism.

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