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Limb Morphology of Domestic and Wild Canids: The Influence of Development on Morphologic Change

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ABSTRACT Biomechanical hypotheses are often invoked to explain the characteristic scaling of limb proportions. Patterns of static allometry and morphologic diversity, however, may also reflect the developmental mechanisms underlying morphologic change. In this study I document the importance of such developmental influences on the evolution of limb morphology in the extremely polymorphic domestic dog and in wild canid species. I use bivariate and discriminant function analyses to compare the limb morphology of adult dogs and wild canid species. I then compare ontogenetic allometry of four dog breeds with static allometry of domestic and wild canids.

Results reveal, first, that there is considerable similarity between dogs and wild canid species; many wolf-like canids cannot be distinguished from domestic dogs of equivalent size. However, all dogs are consistently separated from fox-sized, wild canids by subtle but evolutionarily significant differences in olecranon, metapodial, and scapula morphology. Second, in domestic dogs the pattern of static allometry is nearly identical to that of ontogenetic allometry. This finding can be attributed to simple heterochronic alterations of postnatal growth rates. Apparently the diversity of limb proportions among adult domestic dogs and the observed difference between dogs and wild canids are somewhat predetermined, as they directly reflect the diversity of limb proportions evident during development of the domestic dog.

The influence of biomechanical constraints on morphologic evolution is suggested by the regularity in which certain limb proportions change with size among a group of related organisms (McMahon, '75; Alexander, '77). Deviants from such allometric relationships are regarded as differing functionally from those individuals that follow the allometric trend. However, patterns of morphologic and allometric change among organisms may also reflect limitations caused by the way in which limbs grow. Vertebrate limb development is a tightly integrated process, and changes in limb development that lead to evolutionary change are likely to reflect this integration (Hinchliffe and Johnson, '80). Thus, the spectrum of adult limb conformations available to natural selection can be limited by the intrinsic architecture of development (Alberch, '80).

In this study I investigate the extent to which similarities in limb morphology between domestic dogs and wild canids is a consequence of a developmental pattern common to all domestic dogs. I first compare bivariate allometry in wild and domestic canids to determine their similarities in scaling. Next, I use discriminant function analysis to assess the multivariate correspondence of dogs and wild canids. In discriminant function analysis, morphologic variation between species is maximized in the derivation of canonical axes, and thus positional differences among taxa on these axes should reflect evolutionary distance (Sokal and Sneath, '73). Finally, allometric scaling of adult dogs is compared to that of juveniles of different ages from four breeds. An idealized growth model is then used to understand the similarities between these two levels of morphologic variation.

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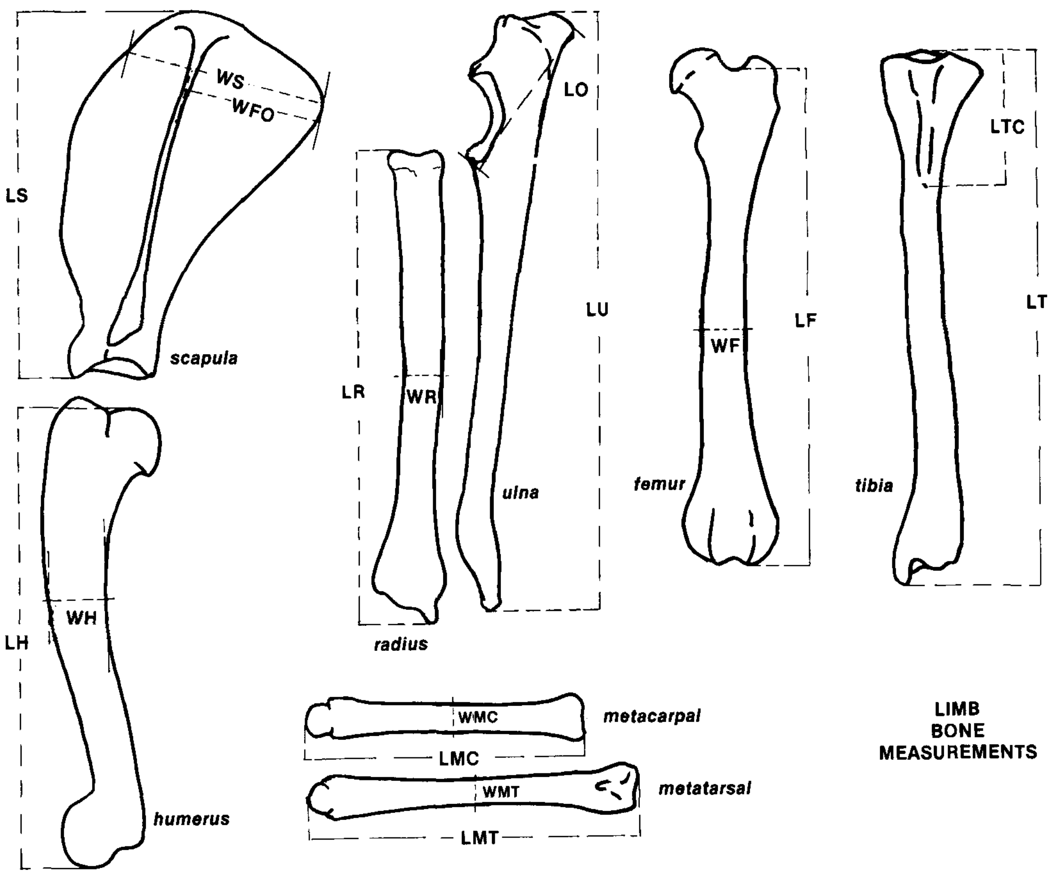


Fig. 1. Diagrams of limb bones illustrating measurements of length and width. Measurements not shown in the Figure are briefly described below; those measurements with asterisks were made on both skeletons and radiographs, and those measurements without were made on skeletons only. 1) Long bone length: LF, femur*; LMC, metacarpal*; LR, radius*; LU, ulna*; LH, humerus*; LMT, metatarsal*; LT, tibia*; LTC, tibial crest; LO, olecranon*; LFD, femoral diaphysis (maximum length of shaft between epiphyseal sutures); LHD, humeral diaphysis (maximum length of shaft between epiphyseal sutures). 2) Long bone width: WMC, metacarpal (minimum diameter); WH, humerus* (diameter at maximum extension of deltopectoral crest); WMT, metatarsal (minimum diameter); WF, femur* (minimum diameter); WFE, femoral end (maximum anterior/posterior width femoral condyles); WR, radius (minimum diameter); WRO, radius one (minimum anterior/posterior width of the radius). 3) Scapula length and width: LS, length scapula*; WS, width scapula*; WSFO, width infraspinous fossa.

MATERIALS AND METHODS

Measurements

Twenty-one measurements were taken of the adult appendicular skeleton of 118 domestic dogs representing 65 breeds and of 192 wild canids representing 27 canid species (Fig. 1; Table 1). All skeletons were from North American museums. A subset of the 21 measurements was taken from radiographs of four growing dogs, each from a different breed: Lhasa Apso, Cocker Spaniel, Labrador Retriever, and Great Dane. These breeds were chosen because they span a wide range of body size and conformation. Radiographs were taken over a 9-month period, from 3 weeks to 10 months of age. Dogs were radiographed initially every 2 weeks and then monthly in older puppies. All animals were radiographed in a standard position and orientation. Morphologic measurements (Fig. 1) are grouped according to the type of bone

TABLE 1. Common and scientific names, number of specimens measured, and mean or modal body weight (if known) for each canid species[1]

	Weight (kg)	N	Weight references[2]
Wolf-like species			
Canis familiaris (domestic dog)	0.5–90	118	7
Canis lupus (grey wolf)	45	10	1,2
Canis niger (red wolf)	30	5	1
Canis latrans (coyote)	15	21	1,3
Canis aureus (golden jackal)	7	5	4
Canis adustus (side-striped jackal)	7	4	5
Canis mesomelas (black-backed jackal)	7	2	4
Cuon alpinus (dhole)	17	5	1
Lycaon pictus (Cape hunting dog)	25	5	1
Vulpine foxes			
Vulpes vulpes (red fox)	8.5	12	1
Vulpes velox (swift fox)	2	3	1
Vulpes macrotis (kit fox)	2	7	1
Vulpes rueppelli (sand fox)	2.7	4	1
Vulpes chama (cape fox)	4	2	1
Alopex lagopus (artic fox)	5.2	4	1
South American foxes			
Dusicyon culpaeus	3.5	1	8
Dusicyon griseus (chico grey fox)	6.5	6	1,4
Dusicyon gymnocercus (pampas fox)	4.4	9	8
Dusicyon sechurae (sechura fox)	—	1	—
Dusicyon vetulus (small-toothed dog)	4	2	1
Cerdocyon thous (crab-eating fox)	6.5	21	1
Fennec fox			
Fennecus zerda (fennec)	1.2	10	1
Grey fox			
Urocyon cinereoargenteus (grey fox)	4.5	10	6
Aberrant canids			
Nyctereutes procyonoides (raccoon dog)	7	7	1
Speothos venaticus (bushdog)	6	13	1
Chrysocyon brachyurus (maned-wolf)	22	7	1
Otocyon megalotis (bat-earred fox)	4.2	8	1
Atelocynus microtis (zorro)	9.5	8	1

[1] Species are arranged according to taxonomic affinity (Langguth, '69; Clutton-Brock et al., '76; Van Gelder, '78).
[2] References: 1) Nowak and Paradiso ('83), 2) Mech ('66), 3) Burt and Grossenheider ('76), 4) Schaller ('72), 5) Kingdon ('77), 6) Feuntes and Jaksic ('79), 7) American Kennel Club Guide ('82), 8) Crespo ('75).

growth responsible for change in a particular dimension: endochondral ossification (long bone growth in length), appositional growth (growth in long bone width), and scapula growth (growth in length and width) (Enlow, '63; Sissons, '71; Hinchliffe and Johnson, '80).

Bivariate analysis

The objective of the allometric analysis was to determine whether the scaling of limb measurements is the same among domestic dogs and species of wild canids. Allometry in this study is defined as the regular way in which limb measurements change in size with a change in femur length (FL). Such allometric change in the length of measurements relative to a single index frequently has the appearance of a law-like relationship and delineates phylogenetic or functional groupings (Huxley, '32; Rensch, '59; Kurten, '54; Cock, '66; Gould, '66, '75, '77; McMahon, '75; Harvey and Mace, '80). It follows that the consistency of an allometric relationship can be an expression of both the level of morphologic and developmental integration and the strength of selection (Olson and Miller, '58; Lauder, '81; Cheverud, '82). Apparent differences exist in the direction of natural and artificial selection. Presumably, the limb morphology of wild carnivores reflects adaptations for locomotion, prey capture, habitat use, and escape behavior (Howells, '44; Hopwood, '45; Smith and Savage, '56; Ewer, '73; Hildebrand, '74; Gambaryan, '74; Taylor, '70, '74; Gonyea, '76; Van Valkenburgh, '84). Although the morphologic features relating to some of these behaviors may have been selected for during the evolution of large working or hunting breeds, they would appear unimportant to the development of most toy, miniature, or mid-sized breeds, as these dogs are not required to hunt regularly, to catch and dismember prey, or to compete with carnivore species. Dogs in the last three categories make up the bulk of breeds measured in this study. Moreover, despite the obscure origin of most breeds, they clearly have originated in numerous places, under varied conditions and at various times (Zeuner, '63; Scott, '68; Epstein, '71). As a result, except for the requirement to walk, the locomotor requirements of different breeds would seem as varied as the breeds themselves. In view of this profound difference in the nature of selection operating in the evolution of domestic and wild canids, if allometric scaling of limb elements is similar in the two groups, then this suggests that developmental constraints may have limited the morphologic diversity of domestic and wild canids.

The y intercept (a) and slope (b) of the bivariate equation $y = a + bx$ (where x = logarithm of the independent variable, and y = logarithm of the dependent variable) were determined using least squares regression. Separate regressions were calculated for wild canid species (interspecific), for domestic dogs (dog-intraspecific), and for juvenile dogs of different ages (dog-ontogenetic). For all bivariate regressions, femur length was used as the independent variable, because both empirical and biomechanical studies have demonstrated that differences in locomotion may be revealed as differences in allometric scaling using femur length as the standard of comparison (Smith and Savage, '56; Hildebrand, '74; McMahon, '75; Alexander, '77; Aiello, '81; Bakker, '83 Van Valkenburgh, '84; Jungers '85). Femur length has also been used as a surrogate for body weight (Gould, '75), but it is unclear whether femur length is necessarily the best indicator of body weight in this data set. My primary objective, however, is to determine whether intermembral allometry as an index of developmental canalization and locomotor function is the same in domestic and wild canids. This question concerns relative rather than absolute scaling, and, as I have determined by using other long bone measurements as the index of comparison, the conclusions of this study are not dependent on the choice of femur length as the independent variable (Wayne, unpublished observations).

Discriminant analysis

Discriminant analysis is used to assess whether the pattern of morphologic differences among wild canid species is similar to that among domestic dogs. One might expect that the morphologic and developmental differences separating most canid genera are more profound than those separating dog breeds. If so, then dogs are likely to share morphologic characteristics that distinguish them as a group from distantly related wild canids. Discriminant analysis is an excellent multivariate technique for testing these ideas because morphologic differences *among* rather than *within* predefined groups (species) are maximized. In discriminant analysis, morphologic differences between breeds and species can be effectively summarized on a few discriminant axes. Moreover, some indication of which variables are important to species discrimination is suggested by their weights on these axes (Tatsuoka, '70; Nei et al., '75), but see Campbell and Achley ('81) for exceptions. The overall similarity of breeds and species may then be assessed by determining the classification of breeds within wild canid species (Tatsuoka, '70; Sokal and Sneath, '73; Nei et al., '75).

All analyses were done using SPSS subprogram DISCRIMINANT (Nei et al., '75). Raw data on only wild species were used in the derivation of the discriminant functions. Each wild species defined a separate discriminant group. To check for the effects of differences in sample sizes of wild species the discriminant analysis was also performed with groupings by genus. Both analyses yielded a very similar separation of groups.

In this study, data on domestic dogs were not used in the derivation of the discriminant functions but are entered into the analysis as if their species membership were unknown. The multidimensional position of each breed is then calculated and compared with that of wild species. This procedure is unusual, as domestic dogs are not actually members of any of the discriminant groups. This approach was followed to determine whether dog breeds could be discriminated from wild canids by the same morphologic criteria that separate wild species from each other. Entering domestic dogs into the analysis as a separate group would emphasize

TABLE 2. Static allometry of domestic and wild canids[1]

Dependent variable[2]	Species interspecific				Dog intraspecific			
	SE	r	b	a	SE	r	b	a
Long bone length								
LR*	.029	.98	1.08*	−0.12	.023	.99	1.04*	−0.07
LU	.030	.98	1.05*	−0.02	.017	.99	1.02	0.02
LH	.016	.99	0.95*	0.03	.014	.99	0.95*	0.02
LT*	.026	.98	0.95*	0.09	.020	.99	1.01	0.09
LTC*	.037	.97	0.98	−0.61	.060	.96	1.03	−0.63
LFD	.007	.99	1.01	−0.06	.022	.99	1.03	−0.10
LHD*	.024	.98	0.94*	−0.05	.028	.99	1.01	−0.15
LO**	.052	.94	0.99	−0.62	.045	.97	0.83*	−0.36
LMC**	.030	.98	1.04*	−0.45	.032	.94	0.90*	−0.29
LMT*	.037	.96	0.89*	−0.21	.207	.99	0.93*	−0.29
Long bone width								
WMC*	.103	.82	1.00	−1.50	.120	.82	0.85*	−1.18
WH*	.056	.93	0.96*	−1.10	.088	.90	0.85*	−0.89
WMT*	.060	.91	0.91*	−1.32	.075	.90	0.76*	−1.05
WF*	.043	.95	0.88*	−1.00	.074	.90	0.76*	−0.78
WFE*	.036	.96	0.92*	−0.59	.066	.94	0.89*	−0.50
Relative width								
WMC:WMT	.081	.88	1.08	−0.02	.108	.87	1.08	−0.01
WH:WF	.040	.96	1.07*	−0.02	.050	.97	1.09*	−0.01
WMC:WH	.098	.83	1.00	−0.30	.108	.85	0.92	−0.29
WMT:WF	.055	.92	1.00	−0.28	.057	.95	0.95	−0.26
Scapula length and width								
LS**	.038	.97	1.06	−0.21	.037	.98	0.87*	0.08
WS	.044	.95	0.89*	−0.23	.067	.93	0.84*	−0.17
WSFO**	.047	.94	0.94*	−0.48	.070	.92	0.82*	−0.33

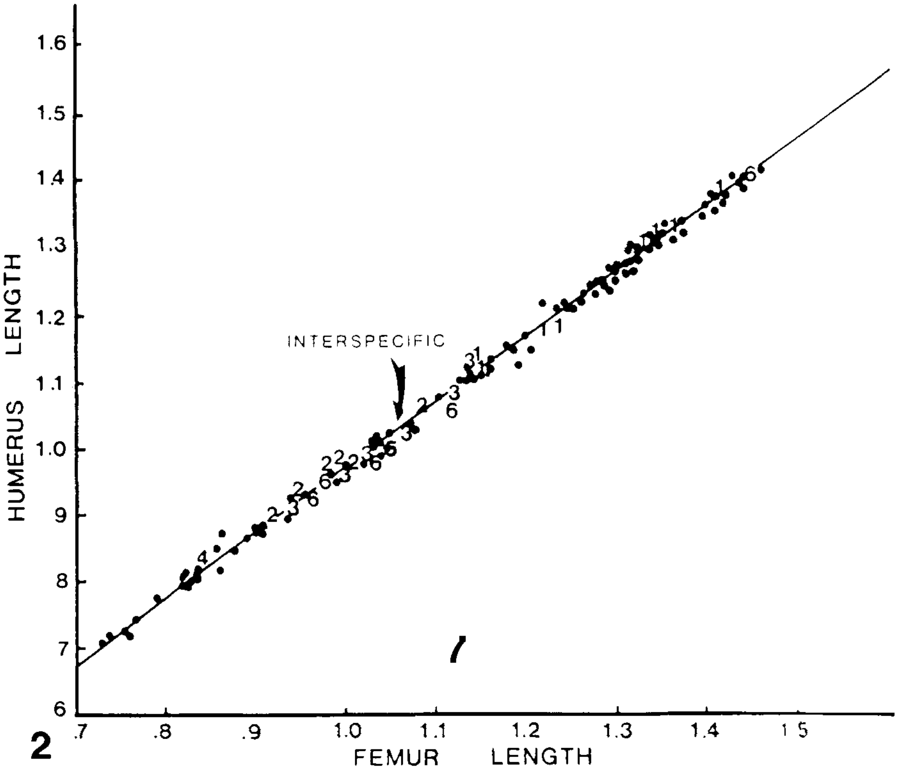
[1] Interspecific and intraspecific slopes (b), y intercepts (a), correlation coefficients (r), and standard error of the residuals (SE) for the regression of the log of the dependent variable on the log of total femur length (FL).

[2] Variables with asterisks indicate that interspecific and intraspecific regressions are significantly different at the .05 (*) or .01 (**) level (two-tailed t test; Zar '84). Slopes with asterisks are significantly different from one at the .05 level.

morphologic measurements that effectively separate wild canid species from all domestic dogs rather than emphasize measurements that vary among wild canids. This bias would be extremely pronounced because the discrimination emphasis is to some extent sample-size dependent, and my sample size of domestic dogs (118) is an order of magnitude larger than for any wild canid species. Moreover, I view the domestic dog as an extremely recent offshoot of its progenitor, the grey wolf, *Canis lupus* (less than 15,000 years; Olsen and Olsen, '77; Olsen, '85), and of dubious specific status. In fact, there are no known genetic differences between wolves and dogs in allozyme frequencies or chromosome morphology (Fisher et al., '76; Simonsen, '76, Wurster-Hill and Centerwall, '82), and both species will interbreed freely and have fertile offspring (Iljin, '41; Gray, '72; Simonsen, '76; Wurster-Hill and Centerwall, '82). The division of the domestic dog into a separate species is a somewhat arbitrary distinction based on the extreme morphologic variability exhibited by domestic dogs. Thus, it would be interesting to determine whether, despite their extreme morphologic variability, domestic dogs are separated from other canids in the same way as is the grey wolf.

Developmental growth rates of domestic dogs

Two properties of the specific growth rate (SGR) make it a desirable measure of growth. First, since it expresses the proportional increment in growth within an increase in age, animals of different sizes can be compared on an equivalent basis. Second, since the ratio of specific growth rates for two measurements at any point in time equals their allometric slope, specific growth rates are useful in explaining patterns of bivariate allometry (Laird, '65; Atchley and Rutledge, '81). Specific growth rates of individual limb elements were estimated for developing domestic dogs (Brody, '45; Laird, '65) according to the relation: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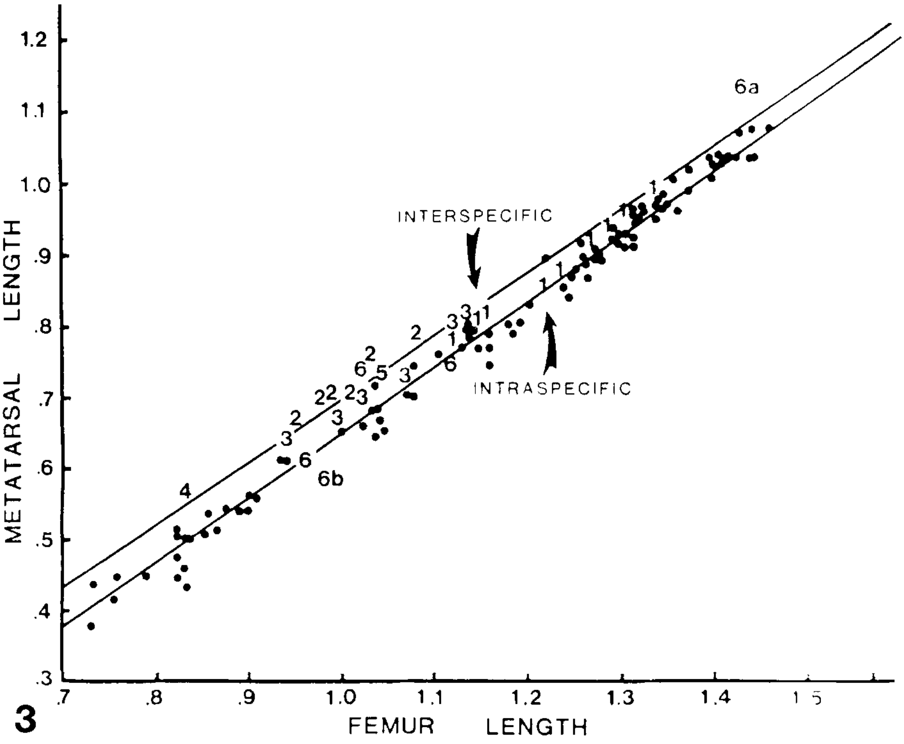
METATARSAL LENGTH
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FEMUR LENGTH
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1.1
1.2
1.3
1.4
1 5

3

$$SGR = \frac{(\ln X2 - \ln X1)}{T2 - T1}$$

where X1 and X2 are limb measurements at time 1 (T1) and time 2 (T2), respectively. For bivariate plots, each specific growth rate was associated with the day at the midpoint of the time range spanned by limb measurements X1 and X2. The resulting curves were fitted with a flexible rule. For a mathematical description of specific growth rate curves, see Wayne, ('86a).

RESULTS

Bivariate analysis

Long bone lengths

The slope and intercept of corresponding interspecific and dog-intraspecific regressions are very similar (Table 2). In some cases, the two regression lines are not statistically different (LU, LH, LFD, Table 2). Scaling similarities are apparent in bivariate plots of limb bone lengths, as in Figure 2, where humerus length is plotted against femur length. In this plot, dogs and wild canids have similar limb bone proportions over the measured range of femur lengths.

The greatest dissimilarity in regression lines exists between interspecific and dog-intraspecific regressions of metapodial length (LMC, $P< .01$; LMT $P < .05$) and olecranon length (LO, $P < .01$). A bivariate plot of these variables demonstrates that dogs, especially small ones, are proportioned differently than wild species of equivalent femur length (Figs. 3–5). Figure 3 shows that small and mid-sized dogs (less than 12.5 cm in femur length or 1.1 on log scale) differ from large dogs in having relatively shorter metatarsals than wild species. Large dogs, on the other hand, are proportioned more like the closest living relatives of all dogs, the wolf-like canids (1 in Fig. 3). Similarly for olecranon length, interspecific and intraspecific lines converge at large femur length; hence, all small breeds can be morphologically distinguished from fox-sized wild species by their relatively larger olecranon (Fig. 4). In contrast, the plot of metacarpal length against femur length shows regression lines intersecting at an intermediate femur length (Fig. 5). In this case, smaller breeds tend to have relatively longer metacarpals; mid-sized and larger breeds tend toward shorter metacarpals than wild species of equivalent femur size, although there is considerable overlap in metacarpal proportions between a number of dogs and wild canids.

The lengths of most long bones scale with only weak inter- or intraspecific allometry (slopes equal to .95–1.08); moreover, for several long bones, lengths scale isometrically (slopes not significantly different from 1) (Table 2). Thus, intermembral proportions of large and small canids are only slightly different. For instance, the proportion of humerus to femur length is .92 in the largest canid, the grey wolf (*Canis lupus*), and is .98 in the smallest canid, the fennec (*Fennecus zerda*).

Long bone width

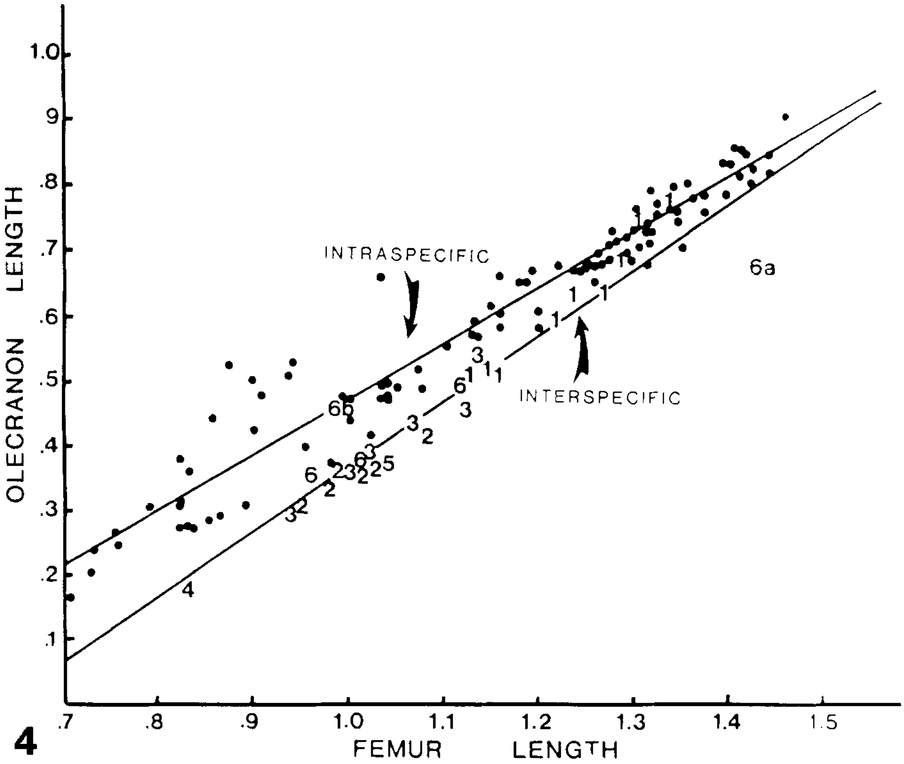
In contrast to long bone length, inter- and intraspecific regressions of long bone width against femur length are all statistically different ($P < .05$; Table 2). Intraspecific slopes are always lower and intercepts higher than the corresponding interspecific coefficients. As a result, all dog breeds, especially small dogs, have wider bones relative to wild species of the same femur length. Width regressions also differ from long bone length regressions, as there is more scatter about regression lines of long bone width (increased SE values; Table 2). The scaling of long bone width shows a tendency toward negative allometry. In all width regressions except one (interspecific, WMC), slopes are significantly less than one. Thus, small dogs and small wild canids have on average wider bones than their larger counterparts.

Relative width

The allometric pattern of relative long bone width does not differ significantly between domestic dogs and wild canids (Table 2).

Fig. 2. Log/log plot of humerus length (LH) vs. femur length (FL) for the mean value of each wild species and for individual domestic dogs. Dots indicate breeds. 1) *Canis, Cuon, Lycaon* (wolf-like canids); 2) *Vulpes, Alopex* (vulpine foxes); 3) *Cerdocyon, Dusicyon* (South American foxes); 4) *Fennecus* (fennec); 5) *Urocyon* (grey fox); 6) aberrant genera. Interspecific regression line only is shown. Measurements are in centimeters. See Table 2 for statistics.

Fig. 3. Log/log plot of metatarsal length (LMT) vs. total femur length for the mean value of each wild species and for individual domestic dogs. 6a) *Chrysocyon brachyurus;* 6b) *Speothos venaticus*; other symbols as in Figure 2. Inter- and intraspecific regression lines are shown. Measurements are in centimeters. See Table 2 for statistics.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INTRASPECIFIC
INTERSPECIFIC
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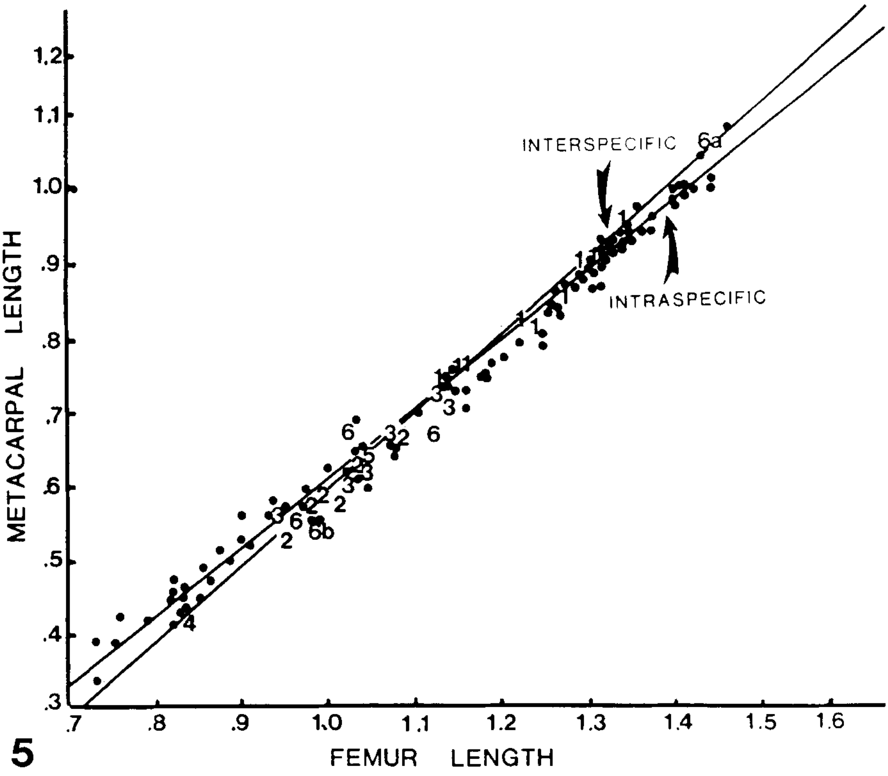
4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1.3
1.4
1.5
1.6
INTERSPECIFIC
INTRASPECIFIC
6a
6b

5

Thus, although breeds have relatively wider bones than wild species of equivalent femur length, width has been increased by the same proportion for all limb bones in domestic dogs. Allometric scaling of relative width is nearly isometric. In six out of eight of the regressions, slopes are not significantly different from one (Table 1). Apparently, the relative width of long bones does not differ appreciably between large and small canids.

Scapula length and width

Interspecific and intraspecific regressions of scapula length against femur length are significantly different ($P < .05$; Table 2; Fig. 6). In this case, all small and mid-sized breeds have a relatively longer scapula than wild species of equivalent femur size. Overlap in proportion is evident only between large dogs and their close relatives, the wolf-like canids (1 in Fig. 6). In contrast, the scapula width regression is not significantly different in dogs and wild canids (WS; Table 2). The regression of width of the infraspinous fossa (WSFO) is different in the two groups, however, suggesting the widths of supra- and infraspinatus regions of the scapula are not proportioned equivalently in dogs and their wild counterparts.

Discriminant analysis

As might be expected, separation of breeds and species on the first canonical axis (Fig. 7) reflects an ordering of taxa by long bone length or body weight. For instance, the largest wild canid species, the grey wolf (*C. lupus*, 1a), and the smallest canid species, the fennec (*Fennecus zerda*, 4), have respectively the largest and smallest values of any wild canid on axis one. Between these two are arranged the other species approximately in order of body weight (Table 1). Similarly, breeds are distributed from smallest (Chihuahua, A) to largest (Irish wolfhound, B). Breeds and species overlap completely on axis one; so also do their measurements on variables important to discrimination on this axis, including radius length and femur diaphysis length (LR and LFD, large positive weights), which are in contrast to humerus and femur length (LH and LF, large negative weights) (Table 3).

On the second discriminant axis (Fig. 7) many of the wolf-like canids (1), *Speothos* (6a), *Nyctereutes* (6b), and *Atelocynus* (6c) are distinguished from the South American foxes (3) and the Holartic foxes (2 and 5). Furthermore, all dog breeds (dots) are separated from the fox-sized wild species (2 to 5). Breeds overlap significantly only with the closely related wolf-like species (1) and the diminutive bushdog (6a). There is a clear contrast on this axis between the negative weight of metatarsal length (LMT) and the positive weight of olecranon length (LO) (Table 3), suggesting that the species with large positive values on this axis have relatively small metatarsals or large olecranons. Thus, these loadings corroborate the results of the bivariate analysis, which showed that most domestic dogs and wolf-sized wild species could be distinguished from fox-sized canid species by their values on these measurements (Figs. 3, 4).

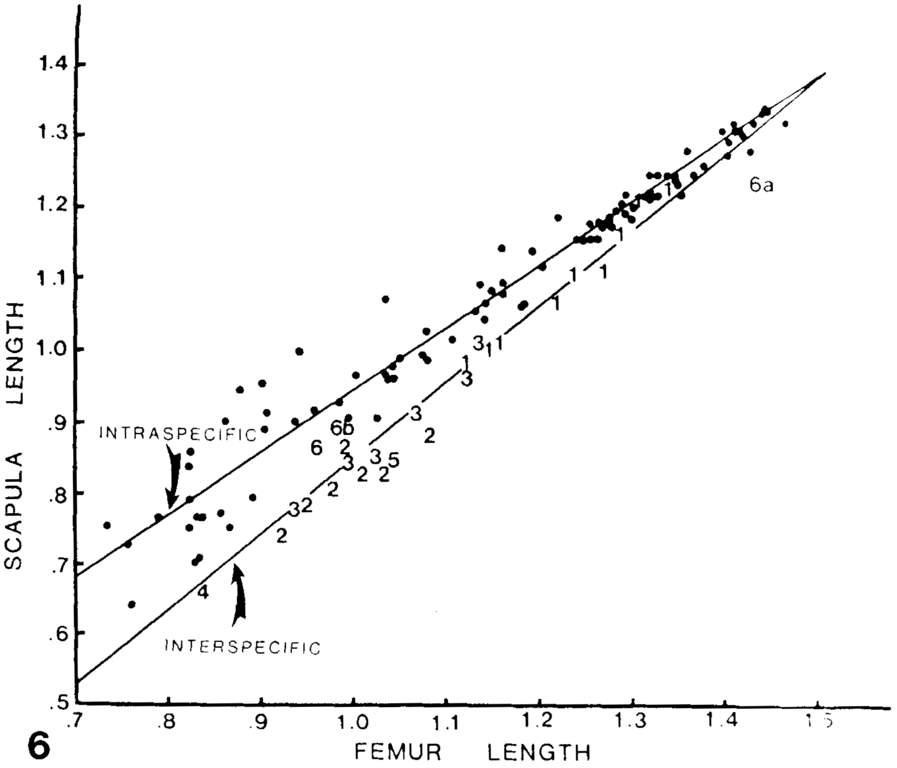
The similarity of dog breeds and wolf-like species is also apparent in the classification analysis. Most breeds (65%) are classified with the wolf-like canids *Lycaon* (18%) and *Canis* (47%). Other breeds are classified with the bushdog (*Speothos*, 22%) and the raccoon dog (*Nyctereutes*, 11%), both of which overlap with dogs on the first two discriminant axes but, unlike the wolf-like canids, are thought to be only distantly related to the domestic dog (Langguth, '69; Clutton-Brock et al., '76; Van Gelder, '78).

Ontogenetic analysis

Statistical comparisons of the slope and intercept of corresponding dog-intraspecific and dog-ontogenetic regressions reveal a striking similarity (Tables 2, 4). Allometric scaling of long bone length and width measurements are either statistically indistinguishable between the two groups or are very similar. Moreover, in contrast to the previous comparison of static interspecific and intraspecific allometry, the scaling of metapodial or olecranon length is not statistically different

Fig. 4. Log/log plot of olecranon length (LO) vs. total femur length for the mean value of each wild species and for individual domestic dogs. Symbols as in Figures 2 and 3. Inter- and intraspecific regression lines are shown. Measurements are in centimeters. See Table 2 for statistics.

Fig. 5. Log/log plot of metacarpal length (LMC) vs. total femur length for the mean value of each wild species and for individual domestic dogs. Symbols as in Figures 2 and 3. Inter- and intraspecific regression lines are shown. Measurements are in centimeters. See Table 2 for statistics.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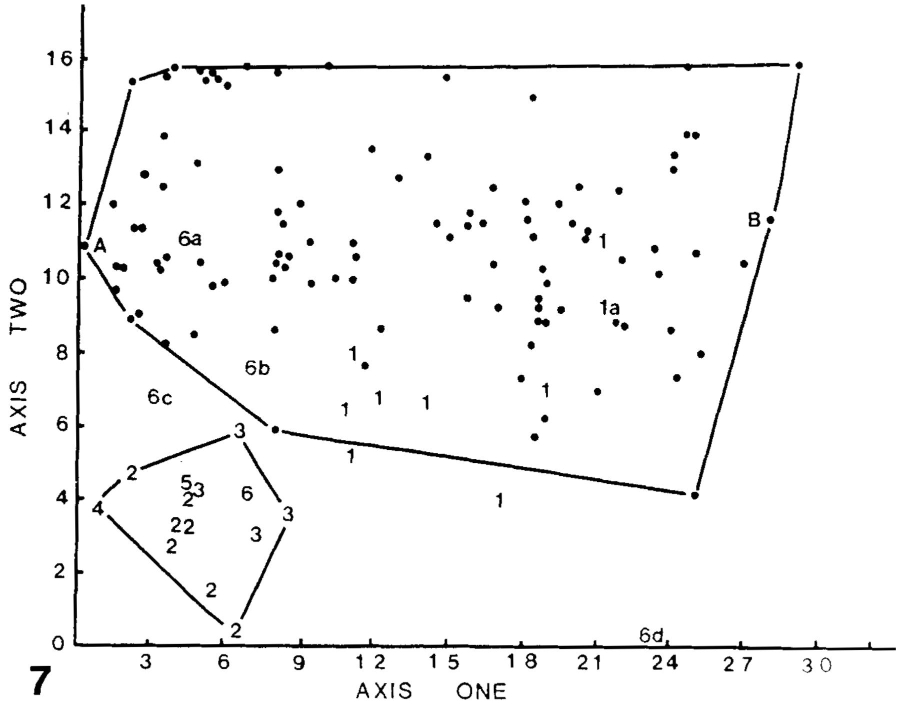
AXIS TWO
AXIS ONE
A
B
6a
6b
6c
6d
1a
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14
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9
12
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18
21
24
27
30

7

TABLE 3. Largest variable weights on the first and second canonical axes of the discriminant analysis

Canonical axis one		Canonical axis two	
Variable	Weight	Variable	Weight
LR	1.58	LMT	−1.43
LFD	1.48	LF	1.24
LF	−1.08	LO	1.12
LH	−1.00	LT	−0.78
LT	−0.59	LMC	0.77
WS	−0.52	LFD	−0.67
LO	0.44	WF	−0.35
WR	0.39	WFE	0.34
% variance[1]	55		23

[1] Percent variance is the total sample variance accounted for by each axis.

in adult or juvenile dogs. As might be expected from these results, bivariate plots of long bone length and width against femur length show a complete overlap of proportions between adults from different breeds and puppies of different ages. For example, in Figure 8, the allometry of humerous length is shown for juveniles of four dog breeds (open circles) and for adults of many breeds (dots). As with other long bone measurements, adults of some breeds are identical in size and proportion to juveniles from larger breeds. Exceptions to this pattern are apparent in the measurements of scapula length and width, in which intraspecific and ontogenetic regressions are significantly different.

As with dog-intraspecific scaling, many long bone measurements are only weakly allometric, changing relatively little in proportion with a change in bone length. For instance, the proportion of humerus length to femur length in a greyhound is .99 at 57 days of age and .93 at 265 days of age. In contrast, the corresponding values for olecranon length (slope = .83) are .38 and .24, which represent a considerable change in proportion. Measurements of long bone width show the strongest allometry and scale negatively, with slopes of .82 and .76 for humerus and femur width, respectively. As before, scatter around the regression line is also larger for these variables, as indicated by the relatively large standard errors (Table 4).

Fig. 6. Log/log plot of scapula length (LS) vs. total femur length for the mean value of each wild species and for individual domestic dogs. Symbols as in Figures 2 and 3. Inter- and intraspecific regression lines are shown. Measurements are in centimeters. See Table 2 for statistics.

Fig. 7. Coordinate positions of individual domestic dogs and wild species' centroids on the first two canonical axes. Units are in standardized discriminant scores corrected to positive values. Separate least convex polygons are drawn around all fox-sized species' centroids (numbers 2 to 5) and around all breeds (dots). All species labeled as in Figure 2, except as follows: 1a) *Canis lupus*, the grey wolf; 6a) *Speothos venaticus*, the bushdog; 6b) *Nyctereutes procyonoides*, the raccoon dog; 6c) *Atelocynus microtis;* A) Chihuahua; B) Irish wolfhound.

DISCUSSION

Bivariate analysis

The allometric scaling of long bone length relative to femur length is generally similar between domestic dogs and wild canid species. There are subtle differences, primarily between small dogs and fox-like wild species, but the general coincidence of regression lines is surprising considering the phyletic distance separating many wild species and the domestic dog; domestic dogs have been phyletically distinct from the vulpine foxes and the grey fox for approximately 10 million years (Kurten and Anderson, '80; Savage and Russell, '83). Moreover, if limb proportions are indicative of some aspects of locomotor ability, e.g., locomotion, food acquisition, defense, and escape behaviors (see references in Materials and Methods), then these aspects of locomotor ability could appear to be similar in domestic dogs and wild canids. This is an unexpected result, given the differences in life habits and in the conditions of evolution of dogs and wild canids; few domestic breeds, especially the smaller breeds, are required to pursue frequently or to catch and dismember live prey. In contrast, cranial allometry is profoundly different in dogs and wild canids (Wayne, '86b). Also, in contrast to the scaling of limb measurements in the domestic dog, regressions of cranial measurements relative to total skull length are strongly allometric (slopes range from .10 to 1.37).

Differences between dogs, especially small dogs, and some wild canids are evident, however, in relative metapodial length, scapula length, and olecranon length. These differences may, in fact, reflect a locomotor difference between dogs and wild species (Bakker, '83; Van Valkenburgh, '84); yet the pervasive similarity of many allometric slopes and the extensive overlap on bivariate plots of dogs and wild species (Table 2; Figs. 2–6) suggest

TABLE 4. Ontogenetic allometry of the domestic dog[1]

Dependent variable[2]	SE	r	b	a
Long bone length				
LR	.012	.99	1.00	−0.07
LU*	.024	.99	0.98	0.04
LH	.018	.99	0.95*	0.01
LT*	.023	.99	1.06*	−0.11
LO	.037	.97	0.83*	0.30
LMC	.030	.99	0.93*	−0.31
LMT	.023	.99	0.93*	−0.27
Long bone width				
WH	.871	.97	0.82*	−0.77
WF	.420	.97	0.76*	−0.73
Relative width				
WH:WF	.381	.98	1.07*	0.02
Scapula length and width				
LS*	.029	.99	0.92*	−0.09
WS*	.053	.96	0.93*	−0.23

[1] Slopes (b), y intercepts (a), correlation coefficients (r) and standard error of the residuals (SE) for the regression of the log of the dependent variable on the log of total femur length. Data are from measurements on radiographs of four developing puppies of different breeds.

[2] Variables with asterisks are different at the .05 (*) level from the corresponding intraspecific regression (two-tailed t test; Zar, '84). Slopes with asterisks are significantly different from one at the .05 level.

that strong functional selection is not needed to generate much of the diversity in limb proportions of the Canidae. Especially in the wolf-like canids, where parallelism between breeds and species is most evident (Figs. 2–6), size selection is sufficient to generate the morphologic diversity of these genera. In fact, size selection is likely to be a predominant force in canid evolution, because size differences among large carnivores help to mitigate interspecific competition (Rosenzweig, '68; McNab, '71; Kleiman and Eisenberg, '73; Feuntes and Jaksic, '79).

The bivariate analysis demonstrates that relatively metapodial length and olecranon length differ (1) between small dogs and wild species and (2) among the six taxonomic groups of wild canids (Figs. 2–5). The latter result is supported by other workers, several of whom discuss the functional implications of these skeletal differences (Lumer, '40; Hildebrand, '52; Langguth, '69; Bückner, '71). Bückner's allometric analysis of forelimb morphology of wild canids includes several dog breeds. His results thus are relevant to this study, but unfortunately his analysis is not directly comparable. In Bückner's study, separate regressions are fitted to several different taxonomic groupings of canids, and residual values of dog breeds are calculated to each of these separate regressions. One of his conclusions is that, as in this study, differences in relative long bone length are most apparent between the smaller fox-sized species and domestic dogs.

The scaling of long bone width for both inter- and intraspecific allometry is significantly less than that expected on the basis of elastic similarity. In ungulates, long bone width scales to the 3/2 power of long bone length (slope equals 1.5) so that mechanical similarity is maintained (McMahon, '75; Alexander, '77). Allometric slopes of long bone width are much less than 1.5 in domestic and wild canids; in addition, as interspecific and intraspecific slopes differ, a separate mechanical scaling characterizes dog breeds and wild species. Whether this difference translates into a locomotor difference between breeds and wild species is unknown.

Diet varies greatly among domestic dogs, and changes in nutritional regime have a dramatic influence on the external diameter of long bones such that an improved nutritional regime produces adults with relatively wider bones (Palsson and Verges, '52; Lodge and Lamming, '67; Johnson, '79). Thus, the increased variability about the regression line of long bone width measurements of canids is likely due to an increase in the environmental, in addition to the genetic component of variance (Falconer, '60). Moreover, the wider long bones of most breeds relative to wild species of the same size may in part be due to the improved nutrition of dog breeds in captivity.

Discriminant analysis

A primary objective of this study was to determine if morphologic change under domestication is fundamentally different from that in nature. The allometric analysis clearly shows that there are some differences in the scaling of long bones in domestic dogs and wild canids, but it is difficult to assess quantitatively their evolutionary significance. Discriminant analysis permits such an evaluation because canonical axes are defined according to that component of morphologic variability that best separates natural taxa. The positions of domestic dogs on these axes are calculated according to equations based on data from wild species only.

A clear conclusion from the pattern of separation on the first two canonical axes is that, despite an impressive diversity in limb

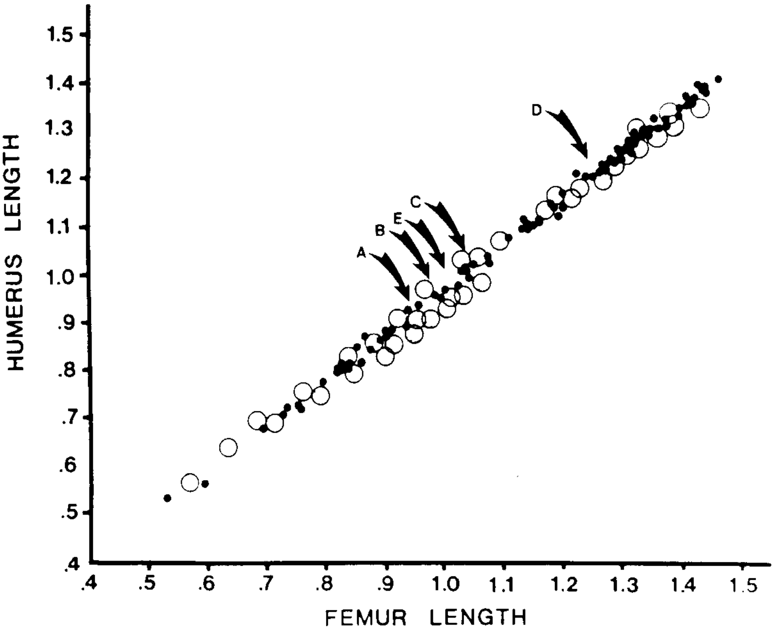
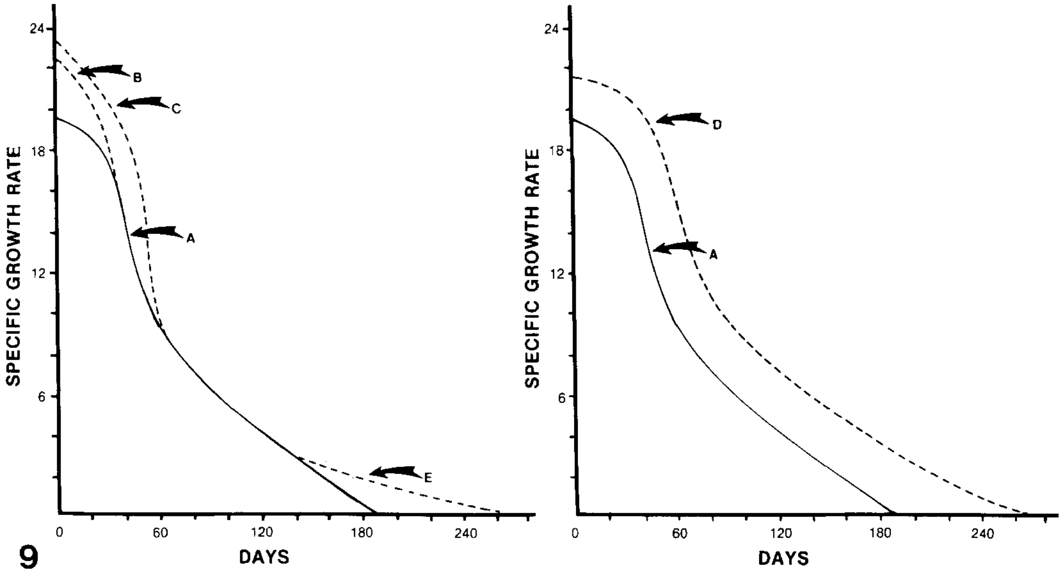


Fig. 8. Log/log plot of humerus length vs. femur length for juvenile dogs from four breeds (circles) and adult domestic dogs (dots). A) The normal 250-day old juvenile of the Lhasa Apso. B–E) The morphology that results if the specific growth rate of a Lhasa Apso neonate is increased according to Figure 9.

size and proportion, domestic dogs can be completely distinguished from all wild canids except their close phylogenetic relatives, the wolf-like canids. As suggested by the pattern of loading on the canonical axes and by the results of the bivariate analysis, morphologic separation of wild canids from each other and of breeds and wild species are due in part to differences in metatarsal and olecranon morphology. This suggests that, even among domestic dogs, morphologic evolution follows phylogenetic boundaries. An exception to this generalization is the bushdog, which is morphologically similar to some dog breeds. As argued elsewhere, this unexpected morphologic correspondence may be due to similarities in gestation time and growth rate between domestic dogs and the bushdog (Wayne, '86a). Moreover, there is some evidence that, like many small dog breeds, the bushdog is a recent dwarf of a larger wolf-like canid (Berta, '85).

Ontogenetic analysis

The similarity of dog-intraspecific and dog-ontogenetic allometry indicates that limb proportions of adults of small dog breeds correspond to those of juveniles of mid-sized and large breeds. That is, small dog breeds are paedomorphic (sensu Gould, '77). Similarly, proportions of adults from the largest breeds represent an extension of ontogenetic allometry and hence are hypermorphic. The former result is consistent with studies of cranial morphology of dogs that suggest that the skulls of many small breeds are characteristically puppy-like in proportion (Sommer, '31; Lumer, '40; Weidenreich, '41; Klatt, '48; Dechambre, '49; Zeuner, '63; Epstein, '71; Wayne, '86b). Moreover, the close similarity of static and ontogenetic allometry suggests that much of the diversity in limb proportions among adults is somewhat predetermined and presumably is reflected in the development of a single dog. The evolution of dog breeds is, of course, due to the artificial selection of specific morphologic variants, but the results presented here suggest that the spectrum of viable variants is limited. Despite the great differences among dog breeds in the traits selected for by breeders (e.g., for hunting, herding, racing, pulling, fighting, and for unusual appearance), all dogs share the same allometric scaling of limb proportions.



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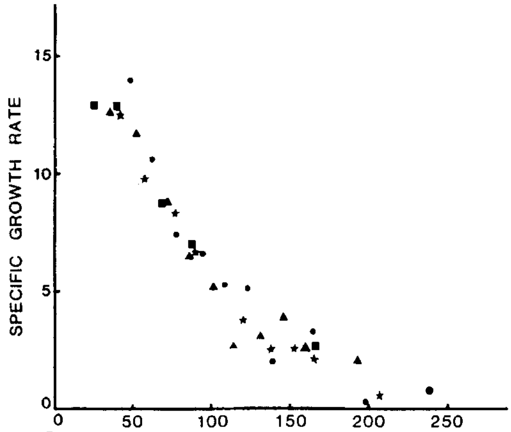

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Fig. 9. Hypothetical and real composite growth rate curves for femur and humerus growth. A) Normal composite growth rate curve taken from Figure 11. B) A growth rate increase over the perinatal period (0–25 days). C) A growth rate increase over the entire period of rapid growth (0–60 days). D) An equivalent increase in specific growth rate throughout development. E) A growth rate increase late in ontogeny. Specific growth rate is in units of 1/day × 1,000.

Fig. 10. Specific growth rate of radius length vs. age for Great Dane (solid circles), Labrador Retriever (stars), Cocker Spaniel (triangles), and Lhaso Apso (solid squares). Specific growth rate is in units of 1/day × 1,000.

Parallels between ontogenetic and static allometry are often explained as the result of heterochronic alterations of development, i.e., a mechanistically simple change in developmental rate or timing (Gould, '77). Several examples of such developmental alterations are presented in Figure 9. In general, intraspecific allometry will always reflect ontogenetic allometry if the specific growth rate curves for each measuremnt are changed by the same proportion. For instance, in Figure 9 the growth of humerus and femur length are represented by the same curve (A). Larger adults may be produced by increasing the initial growth rate (D), by increasing growth rate during the perinatal period (B), by increasing growth over the entire period of rapid growth (C), or by extending the total growth period (E). The opposite growth alterations would produce breeds of smaller adult size. Because these growth alterations have acted equivalently on both femur and humerus growth, intraspecific allometry coincides with ontogenetic allometry (Fig. 8A–E). For these bones, the coincidence of static and ontogenetic regression lines is a necessary consequence of the simple requirement that specific growth rates of each limb bone dimension are always changed by the same proportion in the evolution of new breeds.

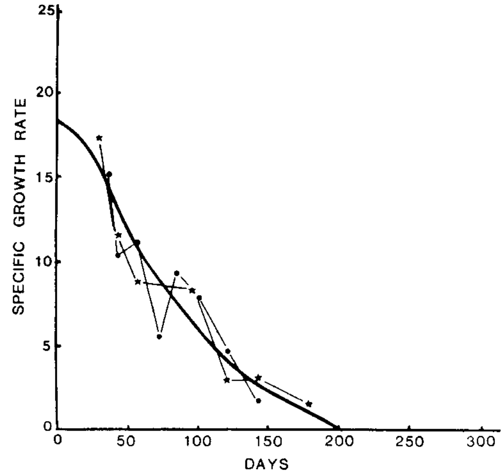

Fig. 11. Specific growth rates of femur length (solid circles) and humerus length (stars) vs. age for the Lhasa Apso. Composite growth rate curve is fitted empirically with flexible rule and shown as a solid line. Specific growth rate is in units of 1/day × 1,000.

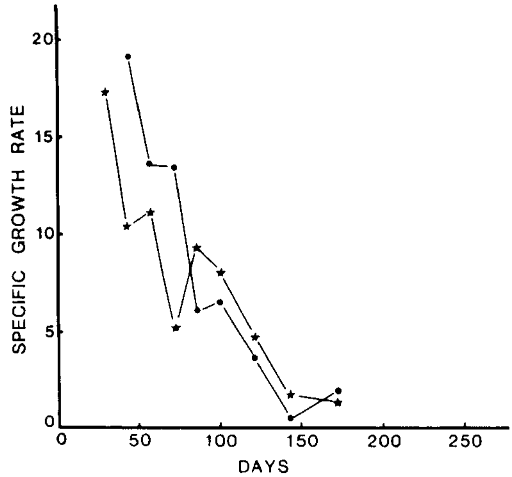

Fig. 12. Specific growth rates of metatarsal length (solid circles) and femur length (stars) vs. age for the Lhasa Apso. Specific growth rate is in units of 1/day × 1,000.

Comparative growth data from the four breeds measured in this study do not support growth alterations C and D (Fig. 9) as a likely explanation for differences in adult size or conformation. Specific growth rates for each breed, as exemplified by the growth of radius length (Fig. 10), are nearly coincident over the period of growth measured in this study (24 to 250 days). Apparently, despite a considerable difference in adult size, the long bones of the four breeds increase at the same proportional rate for most of postnatal development. Thus, either postnatal growth rates differ among the breeds during a period of growth not included in this study (Fig. 9B,E), or breeds are born at different relative sizes. Because dog breeds are relatively more similar in size and conformation at birth than as adults (Baumann and Huber, '46; Altman and Ditter, '62, p. 359; Fox '63; Wayne, '86b), it is likely that growth rates are increased in large dogs relative to small dogs for a short period after birth (Fig. 9B). Moreover, since large dogs continue to grow after growth in small dogs has stopped (10 months, Lhasa Apso; 2 years, Great Dane), growth alteration E (Fig. 9) may be important to breed evolution. See Wayne ('86a) for further discussion and mathematical modeling of growth curves.

Specific growth rate models are also useful for explaining differences in the allometric scaling of limb measurements. Over any fixed growth interval, an ontogenetic slope is by definition equal to the logarithmic change in the dependent variable (long bone measurement) divided by the logarithmic change in the independent variable (femur length), i.e., a ratio of specific growth rates. Therefore, isometry between any two dimensions will result if their specific growth rates are equal throughout ontogeny. For instance, in Figure 11 the specific growth rates of humerus length (LH) and femur length (LF) are plotted for the ontogeny of the Lhasa Apso. These points are approximately coincident throughout ontogeny; hence, bivariate ontogenetic allometry is nearly isometric (slope equals .95; Table 4).

In Figure 12, the specific growth rate curves are given for the growth of metatarsal and femur length in the Lhasa Apso. The metapodial specific growth rate is at first greater than the femur growth rate but crosses the femur growth rate curve at approximately 85 days. Thereafter, the specific growth rate of the metatarsus is lower than that of the femur. This relationship is similar in all breeds measured in this study; metapodials grow faster than the femur for the first 75 to 100 days of growth and then slower than the femur for the remainder of development. The bivariate slope of metatarsal and femur growth is then at first steep (slope > 1) and then shallow (slope < 1). As a result, puppies have relatively larger feet than adults. In general, the ontogenetic scaling of limb bones (Table 4) is unlikely to be isometric if specific growth rate curves cross or are offset.

Growth mechanics and breed evolution

The nearly isometric scaling of intraspecific and ontogenetic allometry and the suggested proportionality of changes in specific growth rate are an expected consequence of long bone growth mechanics. Growth in long bone length is due to the proliferation of cartilage cells in the epiphyseal growth plates, which are located at the proximal and distal ends of long bones (Hinchliffe and Johnson, '80). The epiphyseal growth plate is composed of a thin band of cartilage surrounded by bone. A longitudinal section of the growth plate shows cartilage cells dividing in the proliferation zone, gradually maturing, and finally being completely replaced by bone at the diaphysis. In the growth plate, the rate of cell division, the width of the proliferative zone, and the size of the maturing, hypertrophic cells determine the longitudinal growth rate of a long bone (Kember, '77, '79). Therefore, any nonspecific growth promoter (e.g., human growth hormone; Palmiter et al., '83), that increases equivalently (in all long bones) the division rate of proliferative cells or the width of the proliferative zone will cause the same proportionate increase in the specific growth rate of each bone. Hence, as observed in this study, the pattern of ontogenetic allometry will be identical to that of intraspecific allometry.

There are several hormones that directly affect the growth rate of long bones (Williams and Hughes, '77). For instance, when the pituitary gland, a major producer of growth hormones, is removed from rats, the division rate of proliferative cells falls considerably (Kember, '71). Growth hormone deficiencies that show a Mendelian pattern of inheritance give rise to spontaneous dwarfs within certain breeds (Andersen et al., '74; Andersen and Willeberg, '75). Most size and stature differences between dog breeds, however, appear to be polygenic (Stockard, '41; Hutt, '79, p. 81), and therefore breeds may differ in the concentration of several growth hormones throughout development, each with an independent genetic basis.

Allometric growth of measurements that span a single growth epiphysis (LMT, LMC, LO) show large deviations from isometry (Tables 2, 4). As previously shown, isometry results if the specific growth rate curves of long bone length and femur length are coincident. Such coincidence is less likely if the number of growth centers differs for each of the two bones. In bones with two growth centers, the specific growth rate curve represents a composite of growth rates and growth schedules at each growth center. Within such bones, growth rate is rarely equal (Sissons and Kember, '77; Hinchliffe and Johnson, '80, p. 88), and cessation of growth is not synchronous at both growth centers (Chapman, '65). Consequently, the shape or position of the composite curve for bones with two growth centers is likely to differ from that of bones with a single growth center (see Figs. 11, 12), Thus, relative growth between bones of single and double growth centers may not be isometric.

CONCLUSIONS

Simple changes in specific growth rates of developing long bones account for the pervasive similarity observed between ontogenetic and intraspecific allometry in the domestic dog. However, the actual developmental alterations that give rise to new breeds are undoubtedly more complex. Whatever the specific developmental mechanism, the empirical similarity between ontogenetic and intraspecific allometry suggests that the diversity in limb proportions expressed in dog breeds is largely determined by the magnitude of ontogenetic scaling. The extent and direction of breed evolution and the observed difference between domestic and wild dogs seemingly are reflected in the development of a single domestic dog. An analogous result has been presented elsewhere for cranial evolution (Wayne, '86b). Dog breeds are extremely diverse in cranial morphology, but the allometry of morphologic change among breeds is similar to that among juvenile domestic dogs rather than among present-day wild species. Hence breeds can be discriminated from most wild species in a multivariate analysis of cranial measurements.

Ontogenetic and breed allometry may also be closely associated in other domestic animals, especially in species where the conditions of evolution are analogous to that of the domestic dog, e.g., other pet species. If breed evolution in other domestic animals results from proportionate, whole-body changes in growth rate, then, as in domestic dogs, the potential range of breed morphologies will be determined by the range of proportions evident in ontogeny. Only morphologic characters whose ontogenetic scaling departs significantly from isometry (such as metapodial and olecranon length in the domestic dog) are predicted to show between-breed differences in adult proportions. As has been found in several vertebrate species, such developmental constraints may strongly influence the extent and direction of morphologic evolution (Wake, '66; Larson, '80; Alberch, '80, 83; Shea, '81).

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