

# HANGING BEARS FROM PHYLOGENETIC TREES: INVESTIGATING PATTERNS OF MACROEVOLUTION

JOHN L. GITTLEMAN,<sup>1</sup> Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

**Abstract:** Phylogenetic information of the family Ursidae is well resolved and readily available for investigating macroevolutionary questions. Using complete phylogenies of the ursids and related terrestrial carnivores, I investigate whether patterns of body size and life history evolution in bears differ from other carnivores with respect to cladogenesis, species richness, and overall phyletic trends. Large body size in bears is not related to their phylogenetic history, in contrast to most other carnivore taxa; this may relate to bears' relatively recent evolutionary history or their large body size, which is flexible for utilizing low-quality foods, thus buffering environmental change. Also, rates of body size evolution in bears are average or perhaps slightly slower than other carnivores. Certain life history traits (birth weight, age eyes open, inter-birth interval, longevity) are very different in bears relative to other carnivores, even after accounting for body size and phylogeny. In general, large body size, flexibility in phyletic change in size, and slow life histories of ursids may be an effective evolutionary strategy for dealing with recent environmental stresses.

*Ursus* 11:29–40

**Key words:** bears, body size, life history, macroevolution, Ursidae

Bears are evolutionarily related to terrestrial carnivores including canids, mustelids, hyaenas, and felids. Systematically, ursids are separated from these other taxa by: (1) unspecialized incisors and molars with broad, flat, tuberculated crowns; (2) the shearing function of carnassials in ancestral taxa largely replaced by a crushing function; (3) large and powerful legs, with plantigrade posture; (4) an omnivorous diet, with most species leaning toward frugivory and folivory; and, (5) most distinctive of all, a gigantic body. Clearly, these features are not only useful for systematics, they also elicit interesting ecological and evolutionary questions. Does large body size in bears contribute to higher extinction (or lower speciation) rates relative to other carnivores? Are bears hampered reproductively with respect to life histories because of the length of time it takes to grow large? These questions are comparative in nature, specifically requiring detailed information about relative differences with other carnivore species and knowledge of evolutionary history.

Fortunately, we now have considerable information from basic natural history field studies and, more recently, from phylogenetic systematics. Armed with phylogenetic trees, we can examine the timing and pattern of macroevolutionary changes among bears and closely related lineages. In this paper, I present findings from recent studies comparing trends in bears relative to other carnivores with respect to: (1) phylogenetic trees, (2) macroevolutionary trends of speciation and body size changes using these trees, and (3) variation in life history patterns. My aim is to show how bears differ from other carnivores as well as to illustrate by example how mod ana-

lytical techniques can be used to test macroevolutionary hypotheses using phylogenies.

Two caveats are needed. Many of the patterns detected here are preliminary; validity will rest with more and better data. Also, emphasis is placed on patterns of macroevolutionary differences between bears and other carnivores rather than explanations for these differences. Future work, especially at the population level, will sort out why bears are unique.

## URSID SYSTEMATICS

### A Brief History of Taxonomy

Reviews of ursid systematics are found elsewhere (Simpson 1945; Ewer 1973; Stains 1984; Flynn et al. 1988; Wayne et al. 1989; Wozencraft 1989a,b; Flynn 1996). Excluding the giant (*Ailuropoda melanoleuca*) and red (*Ailurus fulgens*) pandas, the family Ursidae comprises the following species:

*Helarctos malayanus*, Malayan sun bear

*Melursus ursinus*, sloth bear

*Tremarctos ornatus*, Andean (spectacled) bear

*Ursus americanus*, American black bear

*Ursus arctos*, brown bear

*Ursus maritimus*, polar bear

*Ursus thibetanus*, Asiatic black bear

Relative to other carnivore families, the taxonomy of bears is uncontroversial. Ursidae is one of the most recent taxonomic units for familial designation in the class Mammalia (Simpson 1945), the last family of arctoids to appear in the fossil record (Stains 1984), and one of

<sup>1</sup> Present address: Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, VA 22903-2477, USA, e-mail: JLGittleman@Virginia.edu

the most homogeneous Carnivoran families, as reflected by minimal subfamilial (i.e., Tremarctinae) levels (see Wozencraft 1989b, 1993). Population variance in many ursids is significant and continues to be assessed, particularly in the brown bear and polar bear (see Wayne and Koepfli 1996). Indeed, Kurtén and Anderson (1980:184) exclaimed in reference to brown and grizzly bear systematics: "Some 232 Recent and 39 fossil "species" and "subspecies" (list in Erdbrink, 1953) have been proposed for this taxon- a waste of systematic effort which, as far as we know, is unparalleled." Fortunately, with the exception of some generic names (see above species listing; also, Zhang and Ryder 1993), species identification is stable; therefore, the present analysis is not hampered by species uncertainty. Of course, there is debate about taxonomic placement of the pandas, especially the giant panda, which shares many features (herbivorous, plantigrade and gigantic) with ursids (O'Brien et al. 1985, 1991; Schaller et al. 1985; Mayr 1986.) Both familial and ordinal analyses (e.g., Wyss and Flynn 1993, Zhang and Ryder 1993, Vrana et al. 1994, Bininda-Emonds et al. 1999) strongly indicate that the giant panda is closely related to the bears. The red panda is more of an enigma, as it arguably can be placed in its own family, in the Procyonidae or in the Ursidae (Roberts and Gittleman 1984, Bininda-Emonds et al. 1999). The comparative analyses presented here will consider the red panda as a procyonid because of the many functional characters suggesting this placement and to not obscure observed trends between the ursids and other carnivores.

### Phylogenies: Molecular and Morphological

Due to the relatively small number of taxa, accessibility of sample material, the extended time that bears have evolved, and a fairly complete fossil record, ursids have received a great deal of phylogenetic study (Martin 1989, Wayne et al. 1989). At least 28 phylogenetic trees are available for ursids (Table 1), which is a relatively high number compared to other carnivore families, considering the number of species. Further, many different types of characters, including morphological, molecular, and behavioral and ecological elements, have been used in phylogenetic studies (Wayne et al. 1989, Wozencraft 1989a, Bininda-Emonds et al. 1999). As for all organisms (Page and Holmes 1998), molecular phylogenies recently have become plentiful for ursids; for example, new phylogenies for the entire family are available from cytochrome b gene (Zhang and Ryder 1993), combined cytochrome b/tRNA<sup>Pro</sup> and tRNA<sup>Thr</sup> genes (Talbot and Shields 1996), and partial sequence information from 6 regions of mtDNA (Waits et al. 1999). In general, con-

**Table 1. Indices relating to the distribution of taxonomic coverage for and the resolution of a composite tree of the Carnivora (from Bininda-Emonds et al. 1999). The parenthetical value of percent resolution for the herpestids refers to when safe taxonomic reduction (Wilkinson 1995) was used to improve the resolution of this family**

Taxon	Number of source trees	Number of elements	Percent resolution	Elements/taxon	Elements/source tree/taxon
Higher groups	62	202	100	16.8	0.27
Mustelidae	30	155	72.7	3.4	0.11
Otariidae	15	46	69.2	3.3	0.22
Phocidae	21	118	94.4	6.2	0.30
Ursidae	28	50	85.7	6.2	0.22
Canidae	36	180	69.7	5.3	0.15
Felidae	40	282	97.1	7.8	0.20
Hyaenidae	6	8	66.7	2.0	0.33
Herpestidae	9	53	27.8 (58.3)	1.4	0.16
Viverridae	9	90	97	2.6	0.29

gruence among phylogenies places the giant panda and Andean (spectacled) bear as initial lineages in ursid evolution, the sloth bear as an ancient monotypic lineage, and the black and polar bears as recent taxa. Also, throughout the family, there is complete resolution among nodes, a major improvement from one of the first molecular phylogenies (see Wayne et al. 1989). Of course, with the many phylogenies available for the ursids and no clear methods for how to weight some characters (or phylogenies) against others, it is important to assess agreement among all the available phylogenetic hypotheses.

### A Complete Phylogeny

Bininda-Emonds et al. (1999) assembled a complete phylogeny for all 271 species of Carnivora, derived from 166 phylogenies using matrix representation with parsimony analysis (Baum 1992, Ragan 1992). Essentially, matrix representation permits combination of phylogenetic trees derived from various data sources, even though the data may not be congruent; different phylogenies and elements are given equal weighting.

Most source trees are available for "higher" carnivore taxa; ursids have the fourth greatest number at the family level behind felids, canids, and mustelids (Table 1). The groups that have been studied most intensively also tend to have the most elements used for study, although the ursids lag behind in this respect. A possible explanation for this trend is that postcranial material is less accessible for such large-bodied animals as bears, due to the difficulties in transporting and housing them in museum collections. Ursids do, however, compare favor-

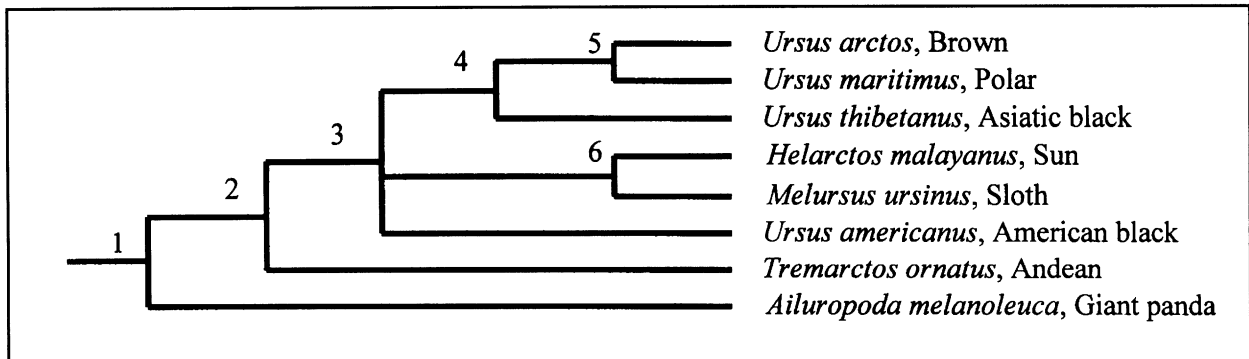


Fig. 1. A composite tree of the Ursidae (from Bininda-Emonds et al. 1999). Numbers refer to primary nodes supported when merging trees.

ably with respect to the number of elements studied per taxon and the number of elements per source tree per taxon.

What does a composite bear phylogeny look like, how resolved is it, and how robust? Generally, the tree is fairly well resolved (Fig. 1), showing 86.7% resolution, and is reasonably robust based on Bremer support values for the nodes (Bininda-Emonds et al. 1999). Details of the tree indicate:

1. The giant panda and the Andean (spectacled) bear are the oldest lineages, supporting recent molecular results (Zhang and Ryder 1993, Talbot and Shields 1996).
2. The position of the American black bear remains unclear and merits further work, especially with the monophyly of *Ursus* uncertain, as pointed out by others (Goldman et al. 1989, Zhang and Ryder 1994). This is an especially vexing result given that non-monophyly is rare across the entire order (e.g., *Phoca*, *Vulpes*, *Lutra*, *Mustela*, *Leopardus*, *Onciphelis*).
3. There are sister taxon links between the brown bear–polar bear and sun bear–sloth bear, also suggested in other studies (Cronin et al. 1991, Talbot and Shields 1996).

Clearly, the major weakness in the composite phylogeny is the ancestral clade leading to the ursines; also, elevation of the polar bear to its own genus does not appear appropriate.

## MACROEVOLUTIONARY TRENDS

Complete species-level phylogenies permit macroevolutionary study hitherto not possible (Purvis 1996). Phylogenies are necessary for any test involving evolutionary history, but this information is often unavailable or misleading from taxonomies. A complete phylogeny makes tests of macroevolutionary pattern more robust, less likely to produce mistakes simply due to biased taxonomic sam-

pling, and accessible to questions about speciation and rates of evolution. The following results are based on the complete carnivore phylogeny of Bininda-Emonds et al. (1999; see Fig. 2) unless otherwise noted.

## Speciation Rates

Regarding the entire phylogeny of the carnivores, do some lineages contain significantly more species than others? The null expectation comes from a model where all extant taxa have the same possibility to diversify (Nee et al. 1995). The comparative test identifies ancestral lineages that have given rise to a disproportionate number of extant species in comparison to their contemporaries (Purvis et al. 1995). The results show that 8 lineages contain significantly more species than expected (Fig. 2). (It should be cautioned that the radiations are not independent; a radiation is more likely to give rise to more taxa.) The bears are not one of these, despite the fact that all of the significant radiations lie in the caniforms. It is interesting to speculate whether some of the general characteristics uniting this group (e.g., primitive bullar construction, basicranial arterial circulation, postcranial skeleton) has encouraged species richness relative to the feliforms.

## Body Size

The most common explanation for the unequal distribution of species among lineages rests with body size (Gittleman and Purvis 1998): small body size is associated with high diversity because of niche partitioning, metabolic rate, reproductive rate, or brain size. Carnivores are a good group to test this hypothesis in because the range of body sizes is greater than any other mammalian order, spanning over 4 orders of magnitude (Gittleman 1985). Moreover, as shown, we know that there are significant differences in species-richness among lineages of the same age.

Using the complete species-level phylogenies of the carnivores and the ursids, we can test whether larger-

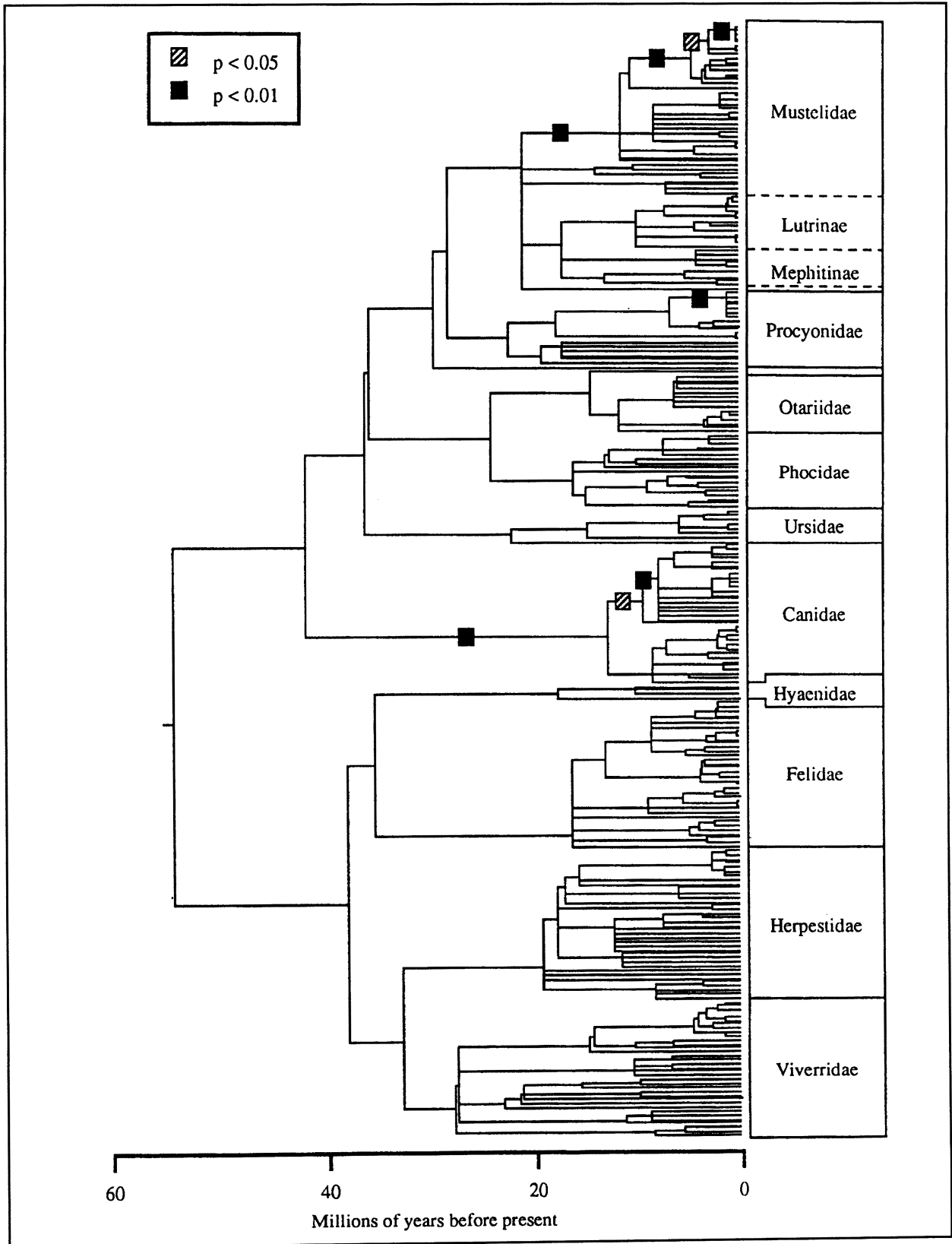
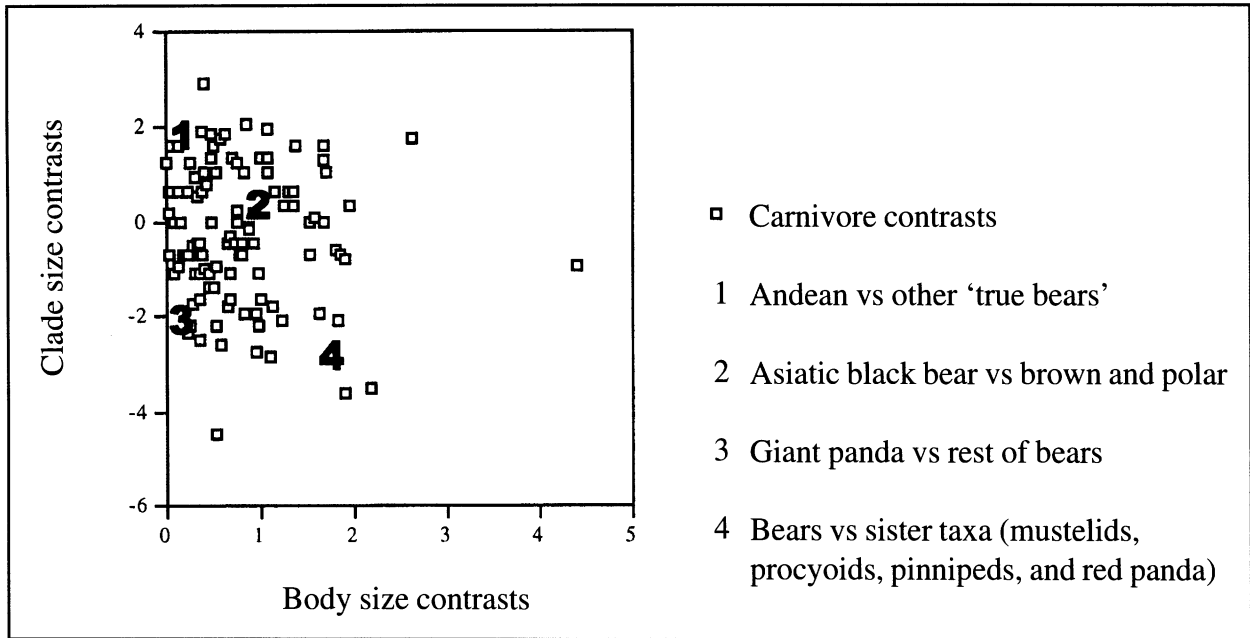


Fig. 2. A composite tree for all 271 species of Carnivora (from Bininda-Emonds et al. 1999), including estimated times of divergence as well as which lineages have given rise to significantly more extant descendants than expected.



**Fig. 3.** Clade size and body size contrasts in carnivores (Gittleman and Purvis 1998). The comparison on the extreme right is between *Allurus* and the mustelid/procyonid clade.

bodied clades (i.e., bears) contain more species than smaller-bodied clades. Once body masses are calculated for species within clades, differences between sister clades are used to search for changes in size (Gittleman and Purvis 1998). Five sets of (clade) contrasts are useful here: (1) contrasts across all carnivores; (2) ursids versus sister taxa (mustelids, procyonids, pinnipeds, red panda); (3) contrasts between *Tremarctos* and the other 'true' bears; (4) contrasts between *Ursus thibetanus* and *U. arctos*–*U. maritimus*; and (5) contrasts between *Ailuropoda* and all the other bears. Overall, the caniform carnivores (canids, procyonids, pinnipeds, ursids and mustelids) do show a tendency for smaller bodied lineages to have more species (Gittleman and Purvis 1998). However, on closer inspection the contrasts involving the bears do not reveal a consistent pattern (Fig. 3): clade contrasts of 3 and 4, for example, both have low clade size contrasts but very different size contrasts. Although body size is often implicated as a correlate of species-richness in mammals, much of the variation in diversity cannot be attributed to size differences.

### Phylogenetic Pattern

The above phylogenetic tests fail to show that cladogenesis in bears is unusual relative to other carnivore taxa or that large body size is, as predicted, correlated with species richness. An obvious explanation is that body size in bears does not reflect phylogenetic history,

either within the ursids or relative to other carnivores. Again, using a phylogeny, we can investigate this lack of pattern. For such a test, though, it is necessary to use phylogenetic information that is totally independent of the character evolution we are tracing (i.e., body size), otherwise the test may not be independent (Gittleman et al. 1996). Taxonomic ranks (Wozencraft 1989b) are therefore employed along with a statistic (Moran's *I*; Gittleman and Kot 1989) to assess whether phylogenetic change of body size in bears is unusual relative to other carnivores (data on carnivore body weight are from Gittleman and Purvis 1998 and available from the author). The simple answer is yes. A 'correlogram' shows that all carnivore families other than the ursids, herpestids, and hyaenids show significant correlation between taxonomic rank and body size (Fig. 4). In other words, close phylogenetic relationship in the 3 families does not necessarily predict variation in size.

If a taxonomy reflects phylogenetic relationships and closely related taxa are phenotypically more alike, then body size should correlate with phylogeny (or in this case, taxonomic ranks). Ursids are clearly very different in this respect: along with hyenids and herpestids, ursids show no phylogenetic pattern in body size. An obvious explanation for this is small sample size. This may explain some of the lack of correlation, but not all, as the procyonids are a small family and show significance while the herpestids are a relatively large group and do not show significant correlation.

## Rates of Evolution

One mechanism for the decoupling of body size evolution from phylogenetic distance lies in differential rates of evolution. If body size in ursids either changes slowly or increases and decreases at unequal rates, as Kurtén (1968) once proposed, then statistical tests of phylogeny and body size will reveal different patterns than that produced by a typical gradual model of evolutionary change. One method for exploring this idea is to calculate rates of evolutionary change in body size through phylogenetic time. We (Gittleman et al. 1996) calculated rates of evolution in Darwin's — quantitative change in a character from its initial dimension to its final dimension divided by the amount of time elapsed (Gingerich 1993) — for body size and other traits among various mammal taxa and found that, in general, morphological traits evolved at slower rates than ecological or life history traits. Might there be differences in rates of evolution of body size change *within* carnivores? The general pattern is a negative relationship between rates of evolution

and time (Fig. 5), as expected, given that measures of rate change decline over longer periods (Gingerich 1993). Against this overall trend we can see that the ursids appear to change slightly slower than the other carnivore taxa. This suggests that perhaps the bears are indeed adopting an evolutionary strategy of "life in the slow lane" (Macdonald 1992), a classic *K*-selection strategy for dealing with stable but stressful environments. Although it has clearly been shown that the *r*-*K* selection theory is not useful at population level (Stearns 1992), phylogenetic analyses are now showing that the theory may apply to significant divergences in size, life histories and abundance across higher taxonomic levels (McKinney and Gittleman 1995, McKinney 1997).

In summary, the gigantic size of bears is an obvious distinguishing characteristic compared to other terrestrial carnivores. The above phylogenetic tests show that, despite unequal speciation rates across carnivore taxa, the large body size of bears is unrelated to species richness. Further, a simple test of correlation between phy-

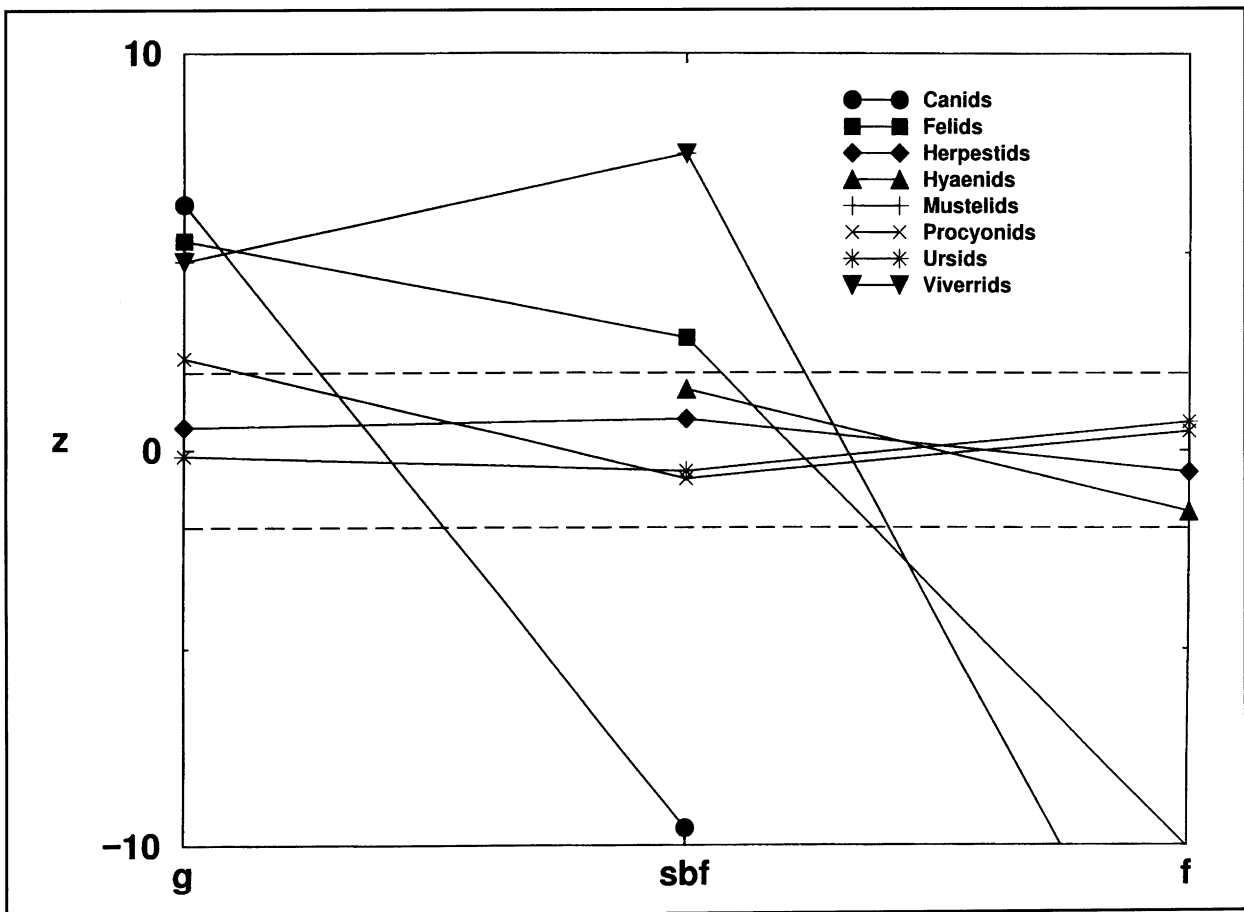


Fig. 4. Correlogram showing observed patterns of z scores (from Moran's *I*) for body weight across carnivore families. Phylogenetic patterns reflect correlation of body weight (from left to right) among species with genera, genera within subfamilies, and subfamilies within families.

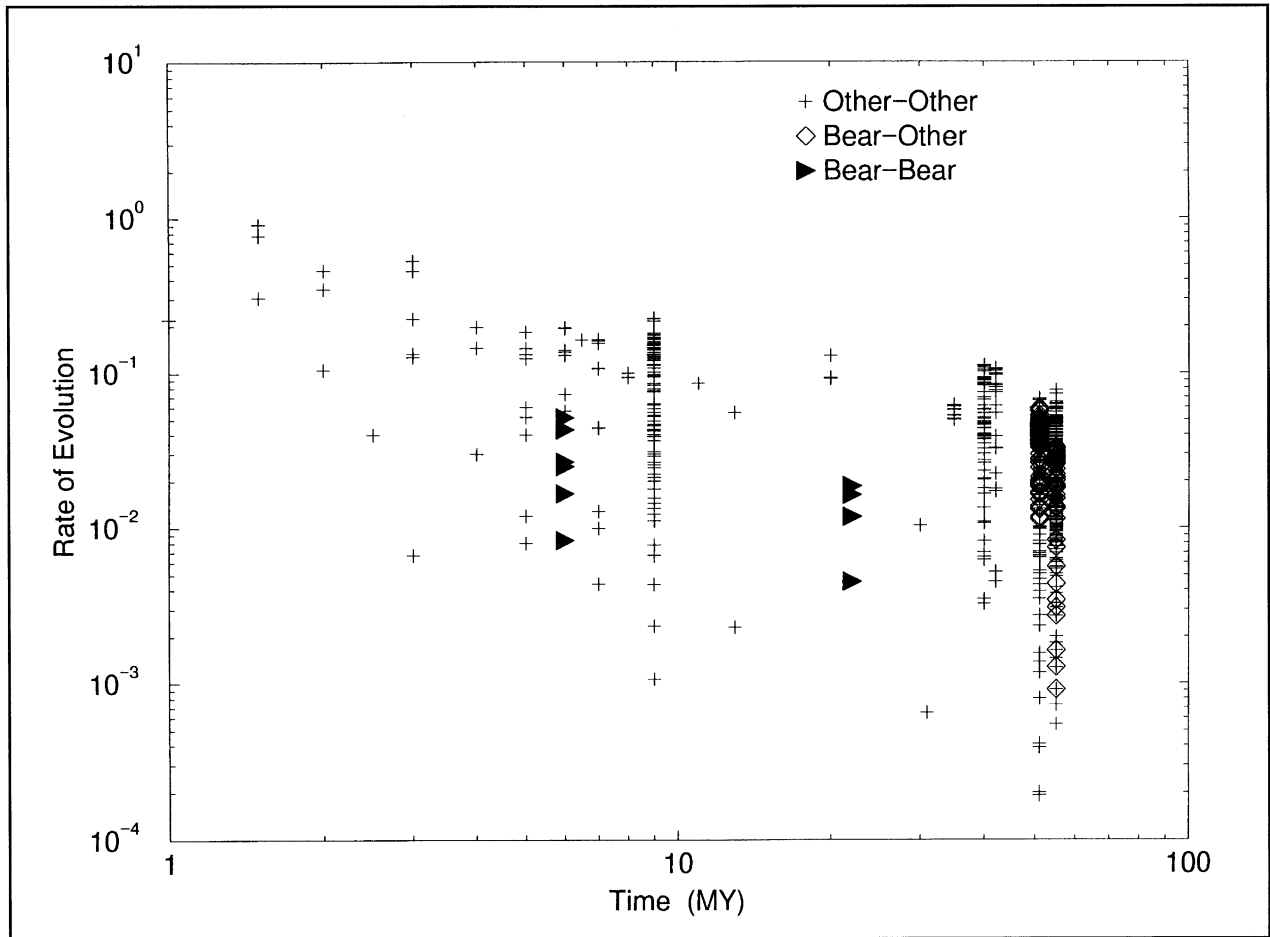


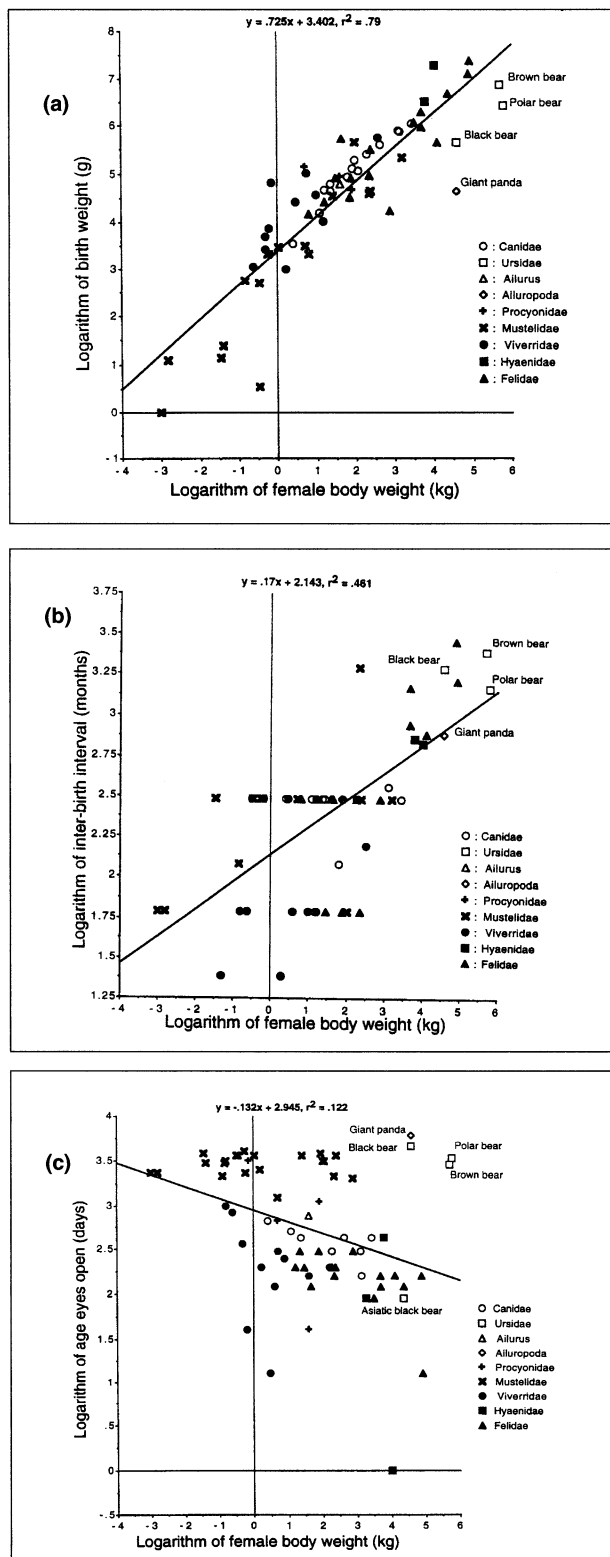
Fig. 5. Log of evolutionary rate (darwins) versus log time interval (million years ago) observed across designated carnivores for body weight.

logenetic distance and body size is not significant in the bears, which is unusual for carnivores and mammals in general. There are many potential reasons for these negative results, including the possibility that the phylogenetic information used here is wrong. One biological explanation is that rates of evolutionary change in body size are different in the bears; here, some support is given to this view. Also, the dramatic size increase in bear body size may have surpassed expected change given their relatively recent evolutionary history. Another more ecological explanation (Stirling and Derocher 1990) is that the large size in bears confers an adaptive strategy, lending flexibility to environmental change, which separates bears from expected phylogenetic pattern. Clearly, the massive within-species variability in body size, for example the 2–3-fold increase in total body mass of polar bears during the spring foraging season (Cattet et al. 1997), is indication that body size evolution is unusual in bears.

## COMPARISONS WITH OTHER CARNIVORES

### Tinkering with Size, Life Histories, and Phylogeny

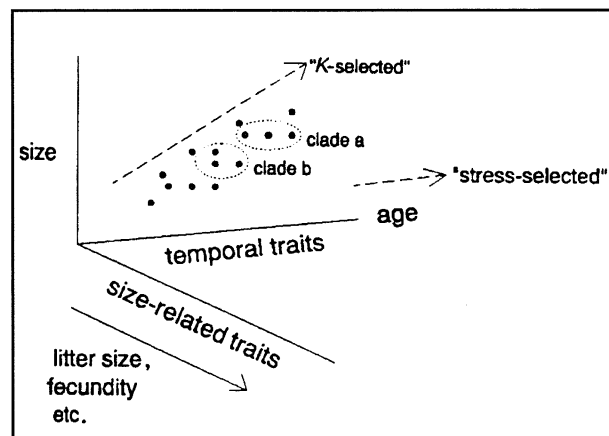
Life history patterns in carnivores are extremely diverse (Gittleman 1986, 1993). For example, simple comparison of the largest and smallest species is profound: By the time a female polar bear reaches sexual maturity at around 5–6 years of age, a least weasel (*Mustela nivalis*) would already have 56 descendants! Such a fundamental difference has significant effects on population dynamics, ecological adaptations, and evolutionary change. Comparisons of mammalian life history patterns involve many traits such as gestation length, birth weight, inter-birth interval, and longevity. By comparing single traits across the carnivores, it is possible to isolate which variables are significantly different in the bears, thus revealing relative macroevolutionary shifts in the ursids and



**Fig. 6.** Plots of residual values — following allometric and phylogenetic autoregressive conversions — for carnivore life history traits and female body weight. Included are (a) birth weight, (b) inter-birth interval, and (c) age eyes open.

**Table 2.** Comparative relations of life history patterns among carnivore families after statistically removing effects of size and taxonomy. \* $P < 0.05$ ; \*\* $P < 0.001$ . All other tests are not significant.

Life history trait	Family comparisons (sample size)
Gestation length	2.02 (6,90)
Birth weight	3.12 (6,61)**
Weaning age	1.11 (6,64)
Longevity	2.50 (6,48)*
Age at sexual maturity	0.80 (6,58)
Inter-birth interval	2.64 (6,50)*
Age eyes open	7.01 (6,63)**
Growth rate	0.81 (3,36)



**Fig. 7.** A model of clade diffusion with respect to size and size-related traits (e.g., life histories). Species in more closely related clades such as the bears tend to be more similar and reflect how increased size and life histories may decouple when “stress-selected”. After McKinney and Gittleman (1995).

potential life history features that are critical for management and conservation decisions.

To perform systematic comparisons of life histories across carnivores, it is necessary to account for 2 variables. First, body size clearly is involved: a least weasel cannot give birth to young the size of a polar bear, nor can a polar bear reproduce as often as a weasel. Thus, comparisons of life histories must initially include plotting the allometry of life history traits against body size (typically female body weight, as we are interested in reproductive traits), then using residuals for comparative tests (see Gittleman 1986, 1993). Second, as with most traits (Harvey and Pagel 1991), life histories are correlated with phylogeny, thus comparative tests may be weakened by not using independent data points. Indeed, in a study of 13 life history traits across carnivores, each trait was significantly related to phylogeny

(Gittleman 1993). There are many ways to solve this statistical problem (Purvis et al. 1994, Martins and Hansen 1996). Here, I use an autoregressive method because it is appropriate when using taxonomic rank information and sample sizes commensurate with the carnivores. In sum, the following analyses are based on 2 sets of residuals (allometric and autoregressive), thus providing conservative tests for which variables the bears differ (or do not) from other carnivores. The carnivore life history data, definitions of variables, and details of methodology are in Gittleman (1986, 1993).

I examined 8 life history traits for differences between bears and the remaining carnivore families (due to availability of data, most analyses only include brown, black, and polar bears, and giant panda). Four traits showed significant differences: birth weight, longevity, inter-birth interval, and age eyes first open (Table 2). In each of these the ursids lie at the extreme of bivariate distributions: bears have comparatively small neonates (Fig. 6a), long inter-birth intervals (Fig. 6b), and late developmental ages for opening eyes (Fig. 6c). These findings generally agree with previous work (e.g., Eisenberg 1981; Gittleman 1986, 1993), although greater emphasis now is placed on just how different the bears are with respect to some life histories, as a stringent test here accounts for size and phylogeny.

At least 6 general factors are considered to influence such life history differences (for reviews see Boyce 1988, Harvey et al. 1989, Gittleman 1994): body size, brain size, metabolic rate, phylogeny, ecology, and mortality. All of these may, to some extent, drive life histories among ursids. Along with the flexibility of body size evolution in bears, as shown above, some life histories appear to be relatively decoupled from allometric expectation. If we consider both large body size and slow life histories a response to environmental change or stress (Fig. 7), then a model for how these factors are simultaneously responding may be applicable (McKinney and Gittleman 1995, McKinney 1997). Some life history traits (birth weight, age eyes open, inter-birth interval) are clearly much slower in bears than in other carnivores. Environmental stresses such as fluctuating food supply or declining habitat availability may be sufficiently handled by reduced reproductive rates during these periods.

## IMPLICATIONS FOR LONG-TERM CONSERVATION AND EVOLUTION

Extinction, the end of a phyletic line without replacement, has occurred throughout the history of life and is the ultimate destiny of every species. Many mammals have gone through rapid and dramatic extinction events.

This is particularly evident in large predatory species, such as saber-toothed cats (*Smilodon*), which have had repeated extinction events (Van Valkenburgh 1991, 1999). In opting for a large body size, the ursids seemingly have employed a safer strategy: herbivory, flexibility in diet and size, and protracted life histories. Relative to other carnivores, this strategy may be working, at least over macroevolutionary time scales. The frequency of extinction of ursids during the Pleistocene appears relatively low compared to other carnivore taxa (Kurtén and Anderson 1980) and, at present, the only bear species to receive endangered classification is the giant panda. This is not a message for complacency. Rather, macroevolutionary trends suggest that the ursids have adopted a size and life history strategy for the long-haul. Bears, like all other animals, obviously have their limits; many large, charismatic mammals like mastodons (*Mammuthus*), Irish elk (*Megaloceros*), and saber-tooths are dramatic examples. We now need critical information to find out what precise environmental factors influence changes in size and life histories, the exact traits which make bears distinct from other carnivores as well as vulnerable to extinction.

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