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ARE PINNIPEDS FUNCTIONALLY DIFFERENT FROM FISSIPED CARNIVORES? THE IMPORTANCE OF PHYLOGENETIC COMPARATIVE ANALYSES

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Abstract.—It is widely assumed that adaptations to an aquatic lifestyle are so profound as to produce only obvious differences between pinnipeds and the remaining, largely terrestrial carnivore species (''fissipeds''). Thus, comparative studies of the order Carnivora routinely examine these groups independently. This approach is invalid for two reasons. First, fissipeds are a paraphyletic assemblage, which raises the general issue of when it is appropriate to ignore monophyly as a criterion for inclusion in comparative studies. Second, the claim that most functional characters (beyond a few undoubted characteristic features) are different in pinnipeds and fissipeds has never been quantitatively examined, nor with phylogenetic comparative methods. We test for possible differences between these two groups in relation to 20 morphological, life-history, physiological, and ecological variables. Comparisons employed the method of independent contrasts based on a complete and dated species-level phylogeny of the extant Carnivora. Pinnipeds differ from fissipeds only through evolutionary grade shifts in a limited number of life-history traits: litter weight (vs. gestation length), birth weight, and age of eyes opening (both vs. size). Otherwise, pinnipeds display the same rate of evolution as phylogenetically equivalent fissiped taxa for all variables. Overall functional differences between pinnipeds and fissipeds appear to have been overstated and may be no greater than those among major fissiped groups. Recognition of this fact should lead to a more complete understanding of carnivore biology as a whole through more unified comparative tests. Comparative studies that do not include monophyletic groups for phylogenetically based comparative tests should be reconsidered.

Key words.—Aquatic adaptations, Carnivora, comparative biology, independent comparisons, life histories, monophyly, pinnipeds.

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Comparative studies in evolutionary biology have been revolutionized by phylogenies (Harvey and Pagel 1991; Harvey et al. 1996). Phylogenetic trees permit rigorous tests of adaptive hypotheses, correlated evolution among quantitative traits, lability and rates of evolutionary change, and reconstruction of ancestral conditions. Phylogenies are also a guide to basic methodological decisions that go into any comparative study. Aside from issues about quality and quantity of comparative data, a researcher must decide at the outset which taxa to include in a study. This involves an upper and lower bound to taxonomic, or ideally phylogenetic, selection. Typically, the lower level is the species. Not only are most comparative data collected at this level, but species are the fundamental taxonomic unit in biology and, as such, are the focus of many ecological and evolutionary hypotheses. With species values in hand, comparative analyses are then conducted among sister taxa that represent independent evolutionary units (Felsenstein 1985). Selecting an upper taxonomic unit is more ambiguous, driven largely by what question is asked. If one is interested in evolutionary convergence, then the upper bound might encompass broad ordinal comparisons (e.g., insectivores vs. rodents). If the question involves coevolution of parasites and hosts, then the upper level might be restricted to a lower taxonomic unit such as a family or genus. The essential element for inclusion at this level is monophyly (Brooks and McLennan 1991; Harvey and Pagel 1991); that is, a group consisting of all and only those species descending from a common ancestor. In this paper, we consider the adverse effects from one long-standing example where this phylogenetic criterion has been routinely ignored due to supposed functional considerations: exclusion of the aquatic pinnipeds from comparative studies of carnivores. Other examples from the comparative literature, such as excluding volant bats from mammal studies (Millar 1981; Hofman 1993) or sea birds from avian comparisons (Blackburn et al. 1996), suggest that this is not an isolated case.

Evolutionary studies of aquatic organisms have been controversial and confusing (see Taylor 1914; McLaren 1960; Edwards 1985; Bateman 1996). For example, across amniotes (''higher vertebrates'') many groups including sea snakes, cetaceans, sirenians, otters, pinnipeds, and penguins have independently become secondarily aquatic, often confusing evolutionary relationships and patterns for these taxa (Wyss 1988; Coates 1991; Coates and Clack 1991). Among mammals, a difficult problem involves the origin and evolution of the Pinnipedia—seals (Phocidae), sea lions (Otariidae) and walruses (Odobenidae)—within the order Carnivora. Although the close relationship of pinnipeds to arctoid carnivores has been largely unquestioned since the middle of the 19th century (e.g., Turner 1848; Flower 1869), their precise sister group relations within arctoids remain controversial. Until recently, the same was true of their now widely accepted monophyletic status as well (for a review, see Bininda-Emonds and Russell 1996). A division is thus often made within carnivores between pinnipeds (literally, ''fin-foot'') and the remaining, mostly terrestrial forms, the fissipeds (literally, ''claw-foot''). This is reflected in many taxonomies, which present pinnipeds as a separate suborder within carnivores (e.g., Turner 1848; Flower 1869; Mivart 1885; Simp-

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son 1945; King 1983) or even an order unto themselves (e.g., Scheffer 1958; Ewer 1973; Hall 1981; Corbet and Hill 1991; Nowak 1991). In part, this confusion has resulted in the near-complete separation of pinnipeds and fissipeds in comparative studies of carnivores, an approach certainly unfounded phylogenetically and perhaps functionally.

The more driving justification behind a nonphylogenetic distinction is simply that pinnipeds are very different due to their aquatic specializations. Simpson (1944), for example, cited carnivores as one of the most fascinating illustrations of how numerous ''adaptive zones'' can be expressed in a single taxon, well-illustrated by the ''sharply discontinuous'' pattern between aquatic carnivores and the remaining taxa. Clearly, pinnipeds do not resemble another fissiped lineage morphologically, behaviorally, or reproductively. Comparative studies of carnivores thus typically exclude pinnipeds for a variety of reasons. These include historical uncertainty over a possible dual origin for the group (for a review, see Wyss 1989), the impression that aquatic specializations will mask functional patterns across terrestrial carnivores (Eisenberg 1981), and subjective decisions that pinnipeds must be different from ''true carnivores'' despite their phylogenetic history. A summary of the argument is provided by Gittleman (1989a, p. ix) in the preface to a book on carnivores: ''I have thus excluded the pinnipeds from discussion; the behavioral, ecological, and evolutionary features of adaptations for aquatic living set this group apart from the other terrestrial carnivores. A further, more practical reason is that other volumes nicely synthesize recent advances on research on the pinnipeds.'' The final sentence illustrates that the pinniped-fissiped distinction is also upheld by pinniped biologists.

This nonsystematic distinction may be unproductive and obscure possible similarities among all carnivores and differences within pinnipeds. Estes (1989) noted the lack of any clear and unambiguous differences between aquatic and terrestrial carnivores, adding that most carnivores are good swimmers. Elsewhere (Bininda-Emonds 1998; O. R. P. Bininda-Emonds, J. L. Gittleman, and C. K. Kelly, unpubl. ms.), we provide empirical support for Estes's contention and show that functional differences between aquatic and terrestrial carnivores are limited to a few characters: head and body length, brain weight, litter size, interbirth interval, and longevity. As within fissipeds (see Gittleman 1984, 1986b, 1993), functional differences also occur within pinnipeds; for example, clear differences in reproductive strategies, hematological parameters, and diving ability exist between otariids and phocids (for a review, see King 1983). However, the existence of these differences are often unappreciated by nonpinniped biologists. Any functional justification behind the pinniped-fissiped distinction is also questionable considering that the most aquatic of all carnivores, the sea otter (Estes 1980; Kenyon 1981), is included among fissipeds.

Aside from the methodological issue of arbitrarily removing taxa from a monophyletic group, the separation of fissipeds and pinnipeds has serious empirical consequences. With 34 species (including the recently extinct Caribbean monk seal), pinnipeds constitute a substantial proportion of extant carnivores (12.5%). Their exclusion from comparative analyses of ''carnivores'' (actually only fissipeds; e.g., Gittleman 1986b, 1991, 1993, 1994) could lead to misleading results (for a discussion of taxon sampling in comparative analyses, see Gittleman 1989b).

Empirical support for this division within carnivores has not been tested. Here, we use phylogenetic comparative methods to investigate: (1) possible functional differences between pinnipeds and the remaining fissiped carnivores; (2) what functional traits underlie observed differences between the two groups and the evolutionary consequences of these differences; and (3) the effects of accounting for phylogeny versus using cross-species analysis. We focus on a wide variety of allometric, physiological, and life-history traits proposed as general aquatic adaptations (following Bartholomew 1970; Repenning 1976; Estes 1989) because these should reveal potential taxonomic differences.

MATERIALS AND METHODS

Data

We collated data on 20 morphological, life-history, physiological, and ecological variables that directly test putative aquatic adaptations hypothesized by Bartholomew (1970), Repenning (1976), and Estes (1989) (see Appendix 1; also Bininda-Emonds 1998; O. R. P. Bininda-Emonds, J. L. Gittleman, and C. K. Kelly, unpubl. ms.). Specifically, we examine traits that emphasize possible differences in size, physiology, and life history in contrast to those strictly relating to locomotion and sensory modalities (e.g., vision, olfaction, and audition). We do not test the latter traits because we accept that some obvious, and characteristic, functional differences exist between fissipeds and pinnipeds (e.g., flippers vs. feet). Instead, we are more concerned with testing whether aquatic adaptations influence pinniped biology more generally. Admittedly, the traits we examine may not be where some of the more important differences lie (e.g., overall brain size compared to olfactory bulb size, which is greatly reduced in pinnipeds; Fish 1898; Hubbard 1968); however, important functional differences in many of these same traits have been previously hypothesized (see also Bininda-Emonds 1998). Also, limitations in available quantitative data across all taxa prohibit some comparisons.

Morphological variables included male and female median values as well as species means for each of body weight, head and body length, and brain weight. Life histories comprised median species values for litter size, gestation length (excluding delayed implantation), birth weight, litter weight, weaning age, age of independence, male and female ages at sexual maturity, interbirth interval, age of eyes opening, and longevity. Physiological and ecological variables included species medians of basal metabolic rate (BMR; absolute and mass-specific), body temperature, percentage of red blood cells (hematocrit), hemoglobin concentration, red blood cell (RBC) count, heart rate, and population density (nonbreeding area).

Most of the fissiped data are from Gittleman (1984, 1985, 1986a,b, 1991, 1993, unpubl. data). Supplemental information for fissipeds and all pinniped data except for most brain weights were from the published literature, with primary papers preferred over review articles or encyclopedic sources (e.g., Mammalian Species Accounts; Parker 1990; Nowak 1991). Additional brain weight values for pinnipeds were estimated from volumetric measures of cranial capacities of

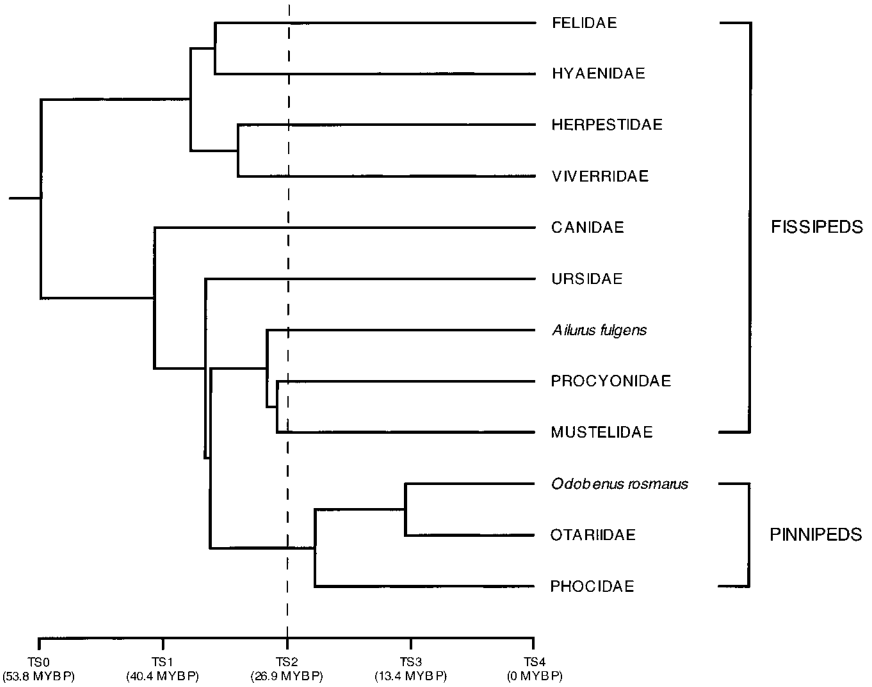

FIG. 1. Higher level phylogeny of the carnivores showing approximate times of divergence (from Bininda-Emonds et al. 1999) and location of the five time slices (TS) used in this study. MYBP, million years before present. Dashed line denotes phylogenetic taxa used for comparison herein (see Table 1).

specimens housed at the Natural History Museum, London. Two specimens (generally one male, one female) were measured for each species (Bininda-Emonds 1998, 2000) and measurement protocol followed Gittleman (1986a): the volume of cleaned, undamaged skulls was determined using 2.0-mm plastic beads and this value was used to directly estimate brain weight assuming 1 ml = 1 g. Descriptions of all variables are presented in Appendix 1 and the pinniped dataset is presented in Appendix 2; the complete dataset is available from the authors (see also Bininda-Emonds 1998).

Comparative Analyses

Species values in comparative tests are often not independent due to evolutionary descent with modification: species sharing a common ancestor are likely to be more similar than distantly related species, rendering cross-species regression invalid (Harvey and Pagel 1991; Pagel 1993; Purvis et al. 1994). We corrected for phylogenetic nonindependence using the method of independent contrasts (Felsenstein 1985) as implemented in the CAIC computer package (Purvis and Rambaut 1995). Based on a phylogeny of n taxa, branch length information, and some specified predictor variable, CAIC calculates ''contrasts'' (i.e., differences) among the descendants of each node, allowing $n - 1$ independent contrasts to be computed for the traits of interest.

Analyses used the complete species-level carnivore phylogeny and associated ''best estimate'' divergence times of Bininda-Emonds et al. (1999). We did not include the herpestids *Dologale dybowskii* and *Rhynchogale melleri* in the analyses because of the noted uncertainty in their phylogenetic position. All quantitative variables were log transformed (base e) to better conform to CAIC's underlying random walk model of evolution (Felsenstein 1985; Purvis and Rambaut 1995), to equalize variances between the different groups (see below), and to necessarily convert the many allometric power relationships into linear ones (Harvey 1982). For age of eyes opening, it was necessary to add one to the raw values before log transformation.

We diagnosed whether the assumption for employing independent contrasts (i.e., statistical dependence in the data due to phylogeny) was upheld and, if so, at what phylogenetic level(s). We used the Moran's I statistic as implemented in the Phylogenetic Autocorrelation computer package (Gittleman and Kot 1990; Purvis et al. 1994); this procedure is appropriate for relatively large sample sizes, as examined here (Martins 1996). To apply Moran's I, the carnivore tree was divided into five intervals of 13.45 million years (see Fig. 1), the time period roughly coinciding with the intervals separating the major taxonomic subdivisions (e.g., suborders, families) recognized within carnivores. We refer to these intervals as ''time slices'' (TS) and number them from 0 (highest; equivalent to the entire order) to 4 (lowest; equivalent to species).

Most of the variables, particularly the life-history traits, are related to size. Therefore, we performed a series of CRUNCH analyses in CAIC with size as the independent, continuous predictor variable to produce size-corrected variables when necessary (see Purvis and Rambaut 1995). We used species values of size in all cases except for life-history traits where female values were employed (or male values for age at male sexual maturity; see Gittleman 1986b).

Measurement of size in large-bodied carnivores is problematic (Cattet et al. 1997). Typically, body weight is used

TABLE 1. Monophyletic lineages occurring at the level of time slice 2 (TS2; 26.9 million years before present) and examined in this study (see also Fig. 1). Names follow Wozencraft (1993) with Pinnipedia comprised of Phocidae, Otariidae, and *Odobenus rosmarus.*

Mustelidae
Procyonidae
Ailurus fulgens
Pinnipedia
Ursidae (excluding *Ailurus*)
Canidae
Hyaenidae
Felidae
Herpestidae
Genetta spp. + *Osbornictis piscivora* + *Poiana richarsdsonii* + *Prionodon* spp.
Civettictis civetta + *Viverra* spp. + *Viverricula indica*
Nandiniinae + Paradoxurinae
Hemigalinae
Cryptoproctinae + Euplerinae

to estimate size in comparative studies; however, weight is highly variable in large species, changing with seasonal fluctuations in food, reproductive condition, and physical condition, among other factors (Gittleman 1986b). Brain weight is often a better estimator of size than body weight simply because it is less variable intraspecifically, thus reducing the amount of noise (Economos 1980). Here, we are interested in accounting for size in other variables and searching for general allometric patterns. Therefore, we tested all variables against both body and brain weight and used the size measure that revealed the stronger relationship based on *P*-values, followed by the one with the higher coefficient of determination (r^2). This procedure was used instead of multiple regression because strong collinearity of body and brain weight renders the latter invalid.

Direct comparisons between pinnipeds and (all) fissipeds are invalid because the latter are a paraphyletic clustering of taxa, some of which are more closely related to pinnipeds than to other fissipeds (see Fig. 1). We therefore derived a set of fissiped taxa comparable to pinnipeds using the only time slice at which pinnipeds formed a single taxon, TS2 (Table 1). Recognized taxa were simply those monophyletic lineages occurring at the level of TS2. Results from the Moran's *I* test (see below) indicated that TS2 was indeed the valid level for comparison.

Observed differences between pinnipeds and fissipeds could arise in three ways: (1) differential rates of evolution; (2) divergent patterns of evolution; or (3) different ''starting points'' between groups (i.e., grade effects). The latter two are tested by comparing slopes and intercepts, respectively, of regression equations between groups. With independent contrasts, however, regressions must pass through the origin; grade effects are detected instead by the relevant contrast being a significant outlier from all other contrasts (Purvis and Rambaut 1995). Rates of evolution are estimated directly by CAIC's standardized contrasts.

Although most variables were significantly related to the predictor variable over the entire order, these same relationships were often nonsignificant within each of the TS2 taxa (results not shown; see also Discussion), meaning that patterns of evolution for these groups could not be compared. Therefore, for the remaining tests, corrections for the independent variable (typically size), when necessary, used residuals from the regression for the entire order.

Tests for differences in evolutionary rate employed a Kruskal-Wallis analysis comparing the standardized contrasts or size-corrected residuals among TS2 taxa. We corrected for multiple comparisons using a sequential Bonferroni technique (Rice 1989). Differences between groups were localized using a nonparametric Student-Newman-Keuls test with pinnipeds as the control taxon (Zar 1984). We identified putative grade shifts in pinnipeds by whether the standardized contrast (or size-corrected residual) for the node connecting pinnipeds to their fissiped sister taxon (mustelids, procyonids, and the red panda *Ailurus*; see Fig. 1) was greater than 1.96 standard deviations away from the mean of all remaining contrasts using *Z*-scores (i.e., within either 2.5% tail of the distribution).

RESULTS

Presence and Location of Phylogenetic Autocorrelation

Dividing the phylogeny into five time slices at intervals of 13.45 million years (Fig. 1) produced taxa with 1, 3, 14, 57, and 271 members (for TS0 to TS4), corresponding to one order, two suborders, 12 families, 123 genera, and 271 species of a standard taxonomy (Wozencraft 1993). Thus, the rate of increase in lineage number between time slices was more uniform than that between ranks in the taxonomy. There was roughly a fourfold increase between each slice compared to a range of twofold to tenfold between taxonomic ranks. This steady rate of increase does not appear to be an artifact of the pure birth model used in Bininda-Emonds et al. (1999) to establish divergence times for nodes where literature estimates were lacking. Only dates derived in this manner from nodes older than 13.45 million years could potentially affect taxon numbers in TS1 to TS3. However, this was true for only 35 dates (16.6% of the 211 nodes in the phylogeny), of which only 15 (7.1%) were themselves older than 13.45 million years. This should not affect taxon numbers in the intermediate time slices to any great extent.

All variables displayed both criteria listed by Gittleman and Kot (1990) that indicate significant phylogenetic correlation under the Moran's *I* test: (1) the *Z*-score (associated standard deviates of *I*) for at least one time slice was greater than 1.96 ($P \leq 0.05$); and (2) *Z*-scores were positive and large at the lower slices (i.e., TS2 or TS3) before decaying to negative values at the higher slices (results not shown; see Bininda-Emonds 1998). The transition point from positive to negative values, which indicates where most of the variation is occurring, was at the TS2 level for most variables. Only weaning age (TS1) and age of independence, interbirth interval, age of eyes opening, hematocrit, and hemoglobin concentration (all TS3) did not follow this pattern. This reinforced our decision to search for differences among groups at the TS2 level (see Table 1). Generally, TS2 taxa equate with the recognized carnivore families, exceptions being the red panda (*Ailurus fulgens*), the pinnipeds as a single group, and the subdivision of viverrids into five lineages, roughly along subfamilial lines.

TABLE 2. Summary of the relationship between each functional variable and size (body or brain weight), assessed by least-squares regression of independent contrasts through the origin (IC) or simple cross-species regression (CS). Analyses were performed across the entire order. Numbers are coefficients of determination with level of significance indicated by asterisks (*$P \leq 0.05$ but not significant due to correcting for multiple comparisons; **$P \leq 0.05$ and significant; ***$P \leq 0.01$; ****$P \leq 0.0001$). See Appendix 1 for complete names of dependent variables.

Dependent variable	Independent variable			
	Body weight		Brain weight	
	IC	CS	IC	CS
SWt	n/a	n/a	0.718****	0.951****
SHB	0.533****	0.957****	0.726****	0.946****
SBr	0.714****	0.951****	n/a	n/a
LS	0.001	0.363****	0.075***	0.449****
GL	0.060***	0.638****	0.176****	0.666****
BWt	0.440****	0.852****	0.747****	0.881****
LWt	0.480****	0.866****	0.736****	0.884****
WA	0.044*	0.065***	0.070***	0.088***
AI	0.075*	0.008	0.043	0.007
MMat	0.163****	0.650****	0.322****	0.655****
FMat	0.069***	0.606****	0.324****	0.661****
IB	0.052*	0.254****	0.139***	0.263****
EO	0.020	0.488****	0.045*	0.509****
LY	0.121****	0.510****	0.216****	0.524****
mBMR	0.147***	0.486****	0.171***	0.464****
tBMR	0.926****	0.928****	0.819****	0.871****
T_B	0.000	0.177****	0.047	0.133***
Hct	0.020	0.064*	0.007	0.071**
Hb	0.016	0.265****	0.024	0.284****
RBC	0.120***	0.505****	0.117***	0.527****
HR	0.237***	0.444****	0.128*	0.459****
PD	0.197***	0.218****	0.290****	0.191****

Correlations with Size and Other Independent Variables

Using independent contrasts across the entire order, most variables displayed a significant relationship with size (body or brain weight) except for age of independence, age of eyes opening, body temperature, hematocrit, and hemoglobin concentration (summarized in Table 2; for complete results, see Bininda-Emonds 1998). Brain weight usually correlated slightly higher than body weight with a given variable; only total BMR and RBC count were slightly more closely related to body weight. Variables that regressed significantly on only one size measure were litter size, age of weaning, interbirth interval (all with brain size), and heart rate (with body weight). This difference usually arose from the correction for multiple comparisons. Except for litter size, uncorrected P-values were less than 0.05 for these variables when they were regressed on the other size estimator.

Significant relationships with other independent variables were also observed (Table 3). Male values of body weight, head and body length, brain weight, and age at sexual maturity showed strong relationships with their female analogs. Only two of the nine ''miscellaneous'' hypotheses did not display significant regressions. Weaning age was independent of the age of eye opening and population density was independent of mass-specific BMR despite showing a significant relationship with total BMR.

Reanalyzing all relationships without accounting for phylogeny by using cross-species regression (i.e., species points assumed to be independent) almost always improved the strength of the regression as measured by the coefficient of determination (Tables 2, 3). The only exceptions were the allometric regression for age of independence and most of the ''dimorphism'' and ''miscellaneous'' relationships.

Pinniped versus Fissiped Comparisons

Rates of evolution.—Only three sets of relationships using independent contrasts showed differences among the TS2 taxa with $P \leq 0.05$—body weight, weaning age, and interbirth interval (all vs. size)—but all three differences were nonsignificant when multiple comparisons were corrected for (Table 4). A nonparametric Student-Newman-Keuls test with pinnipeds as the control also revealed that pinnipeds were not significantly different from any other TS2 taxa for each

TABLE 3. Summary of the relationship between selected functional variables (corrected for both body and brain size), assessed by least-squares regression of independent contrasts through the origin (IC) or simple cross-species regression (CS). Analyses were performed across the entire order. Numbers are coefficients of determination with level of significance indicated by asterisks (*$P \leq 0.05$ but not significant due to correcting for multiple comparisons; **$P \leq 0.05$ and significant; ***$P \leq 0.01$; ****$P \leq 0.0001$). See Appendix 1 for complete names of variables.

Dependent variable	Independent variable	Corrected for body weight		Corrected for brain weight	
		IC	CS	IC	CS
Dimorphism					
MWt	FWt	n/a	n/a	0.886****	0.473****
MHB	FHB	0.809****	0.380****	0.805****	0.443****
MBr	FBr	0.902****	0.844****	n/a	n/a
MMat	FMat	0.244****	0.458****	0.212****	0.419****
Miscellaneous					
SBr	GL	0.074***	0.004	n/a	n/a
SBr	EO	0.044*	0.001	n/a	n/a
LWt	GL	0.066***	0.215****	0.177****	0.232****
AI	WA	0.316****	0.696****	0.321****	0.687****
MMat	LY	0.079***	0.041*	0.091***	0.019
FMat	LY	0.168****	0.151****	0.190****	0.146****
WA	EO	0.018	0.021	0.000	0.047*
PD	mBMR	0.061	0.012	0.129*	0.005
PD	tBMR	0.272***	0.012	0.323***	0.039

TABLE 4. Nonparametric tests (corrected for ties) examining for differences in rates of evolution between time slice 2 (TS2) groups (Kruskal-Wallis) or between pinnipeds and fissipeds (Mann-Whitney *U*). Variables were corrected for possible phylogenetic effects using the method of independent contrasts. Independent variables, if not size, are listed in parentheses. Differences were not significant when a sequential Bonferroni correction for multiple comparisons was used. See Appendix 1 for complete names of variables.

Comparison	$P \leq 0.05$	$0.05 < P \leq 0.10$	$0.10 < P \leq 0.50$	$0.50 < P > 0.50$
Between TS2 taxa	IB SWt WA	EO Hb MHB (FHB) MMat (LY) PD (mBMR) RBC SBr (EO)	BWt FMat GL Hct LS LWt LY mBMR MMat (FMat) SBr SHB tBMR T_B WA (EO)	AI AI (WA) FMat (LY) HR LWt (GL) MBr (FBr) MMat MWt (FWt) PD PD (tBMR) SBr (GL)
Pinnipeds versus fissipeds	EO IB MMat (LY) WA WA (EO)	AI BWt FMat (LY) LWt MBr (FBr) MMat (FMat) SBr	FMat GL Hb Hct HR MMat PD (mBMR) RBC SBr (EO) SBr (GL) SWt tBMR T_B	Al (WA) LS LWt (GL) LY mBMR MHB (FHB) MWt (FWt) PD PD (tBMR) SHB

variable (results not shown); any differences were thus due to an outlying fissiped taxon.

We mimicked previous investigations by comparing pinnipeds to fissipeds as a whole and also repeating all analyses using cross-species regression. Comparisons between pinnipeds and all fissipeds using independent contrasts (Table 4) revealed the same pattern of few significant differences (five), none of which remained when multiple comparisons were corrected for. However, there was considerable variation between the two analyses. Twelve sets of relationships fell into the same ''bin'' of probability ranges (e.g., $0.05 < P \leq 0.10$), but 13 were placed in a bin with a lower *P*-value and 10 in a bin with a higher value by the pinniped-fissiped comparisons with respect to the TS2 taxa comparisons.

The use of cross-species regression rather than contrasts increased the likelihood of detecting significant differences (Table 5). When comparing among TS2 taxa, virtually every relationship presented an uncorrected $P \leq 0.05$; most remained significant when multiple comparisons were taken into account. Again, a Student-Newman-Keuls test revealed that pinnipeds were not the outlying taxon giving rise to the differences (results not shown). Despite this, comparing pinnipeds to fissipeds as a whole caused the majority of relationships to display an uncorrected $P \leq 0.05$ under a Mann-Whitney *U* (with half remaining significant when corrected for multiple comparisons), thereby indicating differences between pinnipeds and fissipeds.

Grade shifts.—The contrast representing the node linking pinnipeds to mustelids, procyonids, and *Ailurus* was a significant outlier for three of the 35 sets of relationships from Table 4: litter weight (vs. gestation), birth weight, and age of eyes opening (both vs. size). Inferred grade effects were as rare for other higher level contrasts. Of all possible contrasts bearing on the origin of the 14 TS2 taxa or of the pinniped families, only two produced values that were outliers for at least one variable: ursid origin—birth and litter weights (both vs. size), and phocid origin—weaning age (vs. size and age of eyes opening) and age of independence (vs. size). These represent outlier frequencies of 8.6% (pinnipeds), 9.1% (phocids), and 5.7% (ursids).

DISCUSSION

Comparative Methodology

Our results comparing pinnipeds and fissipeds raise two general issues regarding comparative methods. First, as found in other studies, cross-species correlates are usually much stronger than analogous ones obtained using independent contrasts (see Harvey and Pagel 1991). This is both because of greater sample sizes using species points (particularly if the phylogeny is poorly resolved; see Purvis et al. 1994) and because closely related species will tend to resemble one another. By accounting for nonindependence among species, independent contrasts reveal the strength of a relationship more accurately (although both techniques yield reliable estimates of slope; Pagel 1993).

Second, and more interestingly, comparative results between higher level taxa appear to depend on comparative methodology and taxonomic selection. Cross-species regression may accentuate differences between higher taxa because

TABLE 5. Nonparametric tests (corrected for ties) examining for differences in rates of evolution between time slice 2 (TS2) groups (Kruskal-Wallis) or between pinnipeds and fissipeds (Mann-Whitney *U*). Variables were not corrected for possible phylogenetic effects (i.e., cross-species analysis was used). Independent variables, if not size, are listed in parentheses. Unless denoted by an asterisk, differences were not significant when a sequential Bonferroni correction for multiple comparisons was used. See Appendix 1 for complete names of variables.

Comparison	$P \leq 0.05$	$0.05 < P \leq 0.10$	$0.10 < P \leq 0.50$	$0.50 < P > 0.50$
Between TS2 taxa	all variables (and all significant) except as noted HR LY mBMR PD (mBMR) PD (tBMR) SBr (EO) tBMR WA WA (EO)	MHB (FHB)	T_B	
Pinnipeds versus fissipeds	AI* BWt* EO* GL* Hct* LS* LWt* MMat (FMat)* RBC* AI (WA) Hb HR IB mBMR MMat MMat (LY) PD tBMR	SW WA	FMat FMat (LY) LWt (GL) MBr (FBr) MHB (FHB) MWt (FWt) SHB SBr (GL) T_B WA (EO)	LY PD (mBMR) PD (tBMR) SBr SBr (EO)

species nonindependence results in underestimated confidence intervals. Our findings revealed pinnipeds to be more different from fissipeds when using species values compared to contrasts. Also, when we contrasted pinnipeds to fissipeds as a whole (as is usually done), the results clearly bore no relation to those when we compared among TS2, or phylogenetically equivalent, taxa (cf. Tables 4 and 5). Weak differences between pinnipeds and fissipeds were indicated (i.e., variables with $P \leq 0.10$) where analogous comparisons among TS2 taxa revealed that pinnipeds were not different from the remaining taxa. This inconsistency arises because pinnipeds, although not displaying the most extreme values for a variable, rarely possess median values either. For example, pinnipeds have relatively short ages of weaning. Pooling fissipeds together accentuates this (as most have relatively longer weaning ages) and makes pinnipeds appear different.

Thus, a simple but important step in comparative studies of higher taxonomic levels is to investigate whether it is valid to omit certain taxa a priori. We suggest that comparative studies should be as inclusive as possible when comparing taxa within a well-defined monophyletic group.

Differences between Pinnipeds and Fissipeds

Pinnipeds evolved from terrestrial carnivores. Therefore, it seems logical that the principal factor that has influenced pinniped evolution is habitat, specifically the constraint of balancing marine feeding and terrestrial parturition (see Bartholomew 1970). Comparatively, there are three potential evolutionary pathways along which pinnipeds may have diverged functionally from fissipeds. However, we found few differences among the variables we examined and those that are present are better explained in terms of increasing neonate survival.

First, pinnipeds may differ from fissipeds in their pattern or direction of evolution. Unfortunately, comparisons between individual TS2 taxa could not be made because most variables did not regress significantly with the independent variable (typically size) for these taxa, despite doing so over the entire order. This result contrasts with previous findings (e.g., see Gittleman 1986b) and derives from our use of independent contrasts, which shows the relationships to be weaker than previously thought. Coefficients of determination were low, usually below 0.5 and often less than 0.2 (see Tables 2, 3). Smaller sample sizes at the TS2 level made it difficult to detect significant trends. Only the allometric relationships for body weight, head and body length, and brain weight and the dimorphic relationships for body weight and brain weight displayed significant regressions for a majority of the TS2 taxa (results not shown). Not surprisingly, these relationships possessed some of the highest coefficients of determination (all greater than 0.7) and largest overall sample sizes.

Second, pinnipeds could be distinguished from fissipeds by having a different rate of evolution; however, no such differences were shown among any of the 35 sets of relationships using independent contrasts. Although three allometric patterns (for body weight, age of weaning, and interbirth interval) were different among TS2 taxa at the (uncorrected) 0.05 level, additional statistical analysis indicated that pinnipeds were not one of the discrepant taxa. In other words, the differences were exclusively between fissiped taxa.

Third, pinnipeds may differ because of grade effects. Contrary to Gittleman's (1986b) findings across fissipeds, marked grade effects were not observed across all carnivore taxa. However, three grade shifts involving the early phases of parturition clearly distinguish pinnipeds: heavy birth and litter weights, and early age of eyes opening. Together, these life histories indicate relatively more precocious pups in pinnipeds, a trend found across aquatic carnivore species in general (Bininda-Emonds 1998; O. R. P. Bininda-Emonds, J. L. Gittleman, and C. K. Kelly, unpubl. ms.).

Comparative studies indicate that age-specific mortality is a determinant of life-history variation across placental mammals (Harvey et al. 1989; Gittleman 1993). Neonate mortality in many pinniped species is about 20% (Harcourt 1992; Le Boeuf et al. 1994) and is directly related to the population density of the rookery (Doidge et al. 1984; Fowler 1987, 1990; Bowen 1991; Harcourt 1992; Baldi et al. 1996). Pinnipeds are highly selective in giving birth at isolated and undisturbed sites. Potential areas meeting this condition while offering easy access to the water are limited and thus rookeries tend to be very crowded in many species. Density estimates range from 20,000 pups/km^2 (= 0.02 pups/m^2) in the harp seal (Myers and Bowen 1989) to seven breeding females per 180 m^2 in the northern elephant seal (Ribic 1988) to 1.2–1.9 pups/m^2 in Antarctic fur seals (Lunn 1992). Major causes of pup mortality include being trampled by the adult males or being fatally wounded by other aggressive females. Both factors are amplified at higher densities through accidental separation of the pup from its protective mother (Anderson et al. 1979; McCann 1982; Doidge et al. 1984; Bowen 1991; Harcourt 1992; Baldi et al. 1996). We suggest that the three observed grade shifts are adaptations to decrease pup mortality. Larger pups that can see and move around shortly after birth are better able to avoid or withstand these factors, which are often, but not always, fatal (McCann 1982; Doidge et al. 1984).

As in other aquatic carnivores, precociality is also advantageous because of substantial risks aquatic living places on newborns (e.g., drowning, problems with flotation) and increased demands of traversing both terrestrial and aquatic habitats (Bininda-Emonds 1998; O. R. P. Bininda-Emonds, J. L. Gittleman, and C. K. Kelly, unpubl. ms.). Drowning does not appear to be a major cause of neonate mortality (Doidge et al. 1984), suggesting precociality may indeed be beneficial. In phocids at least, pup precociality also covaries with an extremely short weaning period and age to independence (note the grade shifts in these characters relative to otarioids). This may allow phocids to utilize extremely unstable habitats for parturition (Stirling 1983; Boness and Bowen 1996).

CONCLUSIONS

It appears that too much has been made historically of distinctive features separating pinnipeds from fissipeds, but not enough of the characteristics revealing adaptive trends across the Carnivora as a whole. Pinnipeds undoubtedly display many adaptations to aquatic environments (e.g., bullar morphology, streamlining, flippers, and hematology). But, do these features justify a distinct status for pinnipeds more than those analogous ones that uniquely characterize other distinct ecomorphological groups (see Radinsky 1985; Werdelin 1996) such as arboreal viverrids, hypercarnivorous hyaenas, or predatory felids? Our phylogenetic comparative analyses suggest not. The blanket grouping of pinnipeds as ''aquatic forms'' also tends to conceal important differences among the major groups to nonpinniped biologists. For example, otariids and phocids possess different reproductive strategies. Otariids are invariably polygynous and the young are dependent on the mother for long periods, often upward of a year or more. In contrast, phocids are polygynous, monogamous, or even promiscuous and display some of the most rapid lactation and parental dependency periods of any eutherian mammals (Stirling 1983; Bowen et al. 1985; Boness and Bowen 1996). Differences in hematological parameters are also present between pinniped families (see Lenfant et al. 1970).

In summary, previous support for the pinniped-fissiped split appears largely intuitive or based on questionable methodology. Those that have doubted the close phylogenetic *and* functional relationship between pinnipeds and fissipeds (e.g., Eisenberg 1981; Gittleman 1989a) must now at least empirically question this distinction. Presupposing the split by comparing pinnipeds to (the paraphyletic) fissipeds only increases the likelihood of finding differences between the two. We demonstrate the importance of taking phylogeny into account and comparing either sister taxa or taxa of equivalent rank: comparisons between pinnipeds and fissipeds as a whole revealed differences that were not supported when pinnipeds were compared to individual fissiped groups of an equivalent rank. Use of a phylogenetic comparative method virtually eliminates many of the differences found in previous studies, even some differences due to large size (allometric) effects. Fortunately, the growing trend to produce classifications that reflect considerations of monophyly means that pinnipeds are now being properly placed in a taxonomic context (e.g., Wozencraft 1993; McKenna and Bell 1997). Our results indicate that there is no basis for analyzing the pinnipeds separately from the remaining carnivores with respect to their general morphology, life-history traits, or physiology. This recognition should lead to greater understanding of carnivore evolution as a whole.

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APPENDIX 1

Comparative Traits and Definitions

1. Body weight (SWt, MWt, and FWt): average adult body weight (kg). We attempted to exclude estimates for individuals that were pregnant, preparing to begin or end hibernation, or were in exceptionally good or poor condition. Averages were calculated for species values (SWt) and medians for male (MWt) and female weight (FWt).

2. Head and body length (SHB, MHB, and FHB): distance from the tip of the snout to the base of the tail (cm). Head and body length is not typically recorded for pinnipeds. Instead, we used standard length, which is the distance from the snout to the tail tip, measured with the animal on its back (American Society of Mammalogists, Committee on Marine Mammals 1967). Despite including the tail, standard length is a roughly equivalent measure because pinniped tails are negligible in length compared to the head and body. In all cases, the species value (SHB) was calculated as the average of male (MHB) and female (FHB) values.

3. Brain weight (SBr, MBr, FBr): weight of the brain (in g). When only the brain volume or cranial capacity was known, we assumed that 1 ml of brain tissue weighed 1 g. The species value (SBr) was calculated as the median of estimates that did not specify a gender and the average of male (MBr) and female brain weight (FBr).

4. Litter size: average number of offspring at birth.

5. (Active) gestation length (GL): average time from conception to birth (in days), minus any period of delayed implantation.

6. Birth weight (BWt): average weight of a single neonate at birth (in g).

7. Litter weight (LWt): litter size multiplied by birth weight (in g).

8. Weaning age (WA): time from birth of the young to independence from maternal milk (in days). In cases where weaning occurs over a protracted period, we followed Gittleman (1984, 1986b) in using the largest value to reflect complete nutritional independence from the mother.

9. Age of independence (AI): age when the juvenile disperses from the natal territory or is independent of parental care in group-living species (in days).

10. Age at sexual maturity (MMat and FMat): age at first conception (in days). Unlike Gittleman (1984, 1986b), we determined separate estimates for males (MMat) and females (FMat).

11. Interbirth interval (IB): time between successive births (in months).

12. Age of eyes opening (EO): age when the eyes of the neonate first open (in days).

13. Longevity (LY): age of the oldest recorded individual (in months). Preference was given to records from captive individuals, reflecting the greater reliability and accuracy of such estimates. However, we also used what we felt to be reliable estimates determined from natural populations (e.g., mark-recapture studies).

14. Basal metabolic rate (mBMR and tBMR): metabolic rate for adult individuals fulfilling Kleiber's (1975) conditions of being postabsorptive, at rest, and in a thermoneutral environment. Total metabolic rates (tBMR; in ml O_2 min^{-1}) were derived from mass-

TABLE A1. Values of selected morphological characters for all extant species of pinniped (including *Monachus tropicalis*). See Appendix 1 for identity and descriptions of variables. Sources are given at the bottom of the table.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Odobenidae									
Odobenus rosmarus	1232.95	811.50	1022.23	315.75	260.00	287.88	1303.00	1340.50	1160.88
Otariidae									
Arctocephalus australis	159.00	48.50	103.75	189.25	141.25	165.25	350.00	265.00	307.50
Arctocephalus forsteri	164.38	55.00	109.69	199.38	141.88	170.63	340.00	300.00	320.00
Arctocephalus galapagoensis	64.50	27.40	45.95	151.25	120.00	135.63	302.50	280.00	291.25
Arctocephalus gazella	155.00	38.20	96.60	185.90	128.75	157.33	360.00	322.00	341.00
Arctocephalus philippii	140.00	50.00	95.00	200.00	140.00	170.00	415.00		415.00
Arctocephalus pusillus	279.50	78.00	178.75	220.00	161.00	190.50	401.25	337.50	369.38
Arctocephalus townsendi	145.00	49.55	97.28	200.30	141.60	170.95			
Arctocephalus tropicalis	152.50	50.00	101.25	180.00	145.00	162.50	322.50	330.00	326.25
Callorhinus ursinus	227.00	44.75	135.88	213.00	135.00	174.00	355.00	302.50	328.75
Eumetopias jubatus	1000.00	287.55	643.78	300.00	240.15	270.08	747.50	575.00	661.25
Neophoca cinerea	300.00	78.55	189.28	212.50	148.20	180.35	440.00	337.50	388.75
Otaria byronia	300.00	144.00	222.00	234.88	188.86	211.87	546.25	470.00	508.13
Phocarctos hookeri	364.00	183.00	273.50	225.00	180.00	202.50	417.50	370.00	393.75
Zalophus californianus	300.00	91.00	195.50	225.00	180.00	202.50	405.00	361.50	379.13
Phocidae									
Cystophora cristata	343.18	222.50	282.84	260.00	206.00	233.00	480.00	430.00	455.00
Erignathus barbatus	265.00	276.36	270.68	230.00	230.00	230.00		460.00	417.50
Halichoerus grypus	233.00	155.00	194.00	216.35	180.00	198.18	342.50	272.50	307.50
Hydrurga leptonyx	324.00	367.00	345.50	287.00	322.48	304.74	765.00	660.00	712.50
Leptonychotes weddellii	360.00	376.00	368.00	250.00	259.50	254.75	501.50	563.15	526.16
Lobodon carcinophagus	220.50	224.00	222.25	226.00	228.50	227.25	578.17	538.75	558.46
Mirounga angustirostris	2275.00	700.00	1487.50	450.00	295.00	372.50	700.00	640.00	670.00
Mirounga leonina	3510.00	503.00	2006.50	467.00	270.00	368.50	1431.25	898.75	1165.00
Monachus monachus	260.00	301.00	280.50	254.75	264.60	259.68	480.00	480.00	480.00
Monachus schauinslandi	173.00	265.00	219.00	214.20	233.70	223.95	370.00		370.00
Monachus tropicalis		160.00	160.00	233.00	225.63	229.31	460.00		460.00
Ommatophoca rossii	173.80	185.00	179.40	199.00	214.60	206.80	425.00	530.00	477.50
Phoca caspica	70.50	55.00	62.75	150.00	136.40	143.20	165.00	160.00	149.65
Phoca fasciata	94.80	80.36	87.58	153.00	154.70	153.85	257.50	240.00	248.75
Phoca groenlandica	135.00	129.50	132.25	176.00	169.30	172.65	297.50	252.50	276.50
Phoca hispida	71.67	66.50	69.08	129.30	128.90	129.10	229.25	220.00	189.31
Phoca largha	97.00	86.00	91.50	168.95	159.00	163.98	257.50	250.00	253.75
Phoca sibirica	89.50	89.50	89.50	130.00	125.35	127.68	185.00	190.00	187.50
Phoca vitulina	97.13	77.50	87.32	171.51	151.80	161.66	362.25	265.00	275.00

Odobenus rosmarus: Crile and Quiring (1940); Laws (1959); Bryden (1972); Brenton (1979b); Eisenberg (1981); Fay (1981, 1982, 1985); King (1983b); Dierauf (1990); Walsh et al. (1990); Nowak (1991); McLaren (1993); Silva and Downing (1995); Ferguson et al. (1996)

Otariidae: Laws (1959); Scheffer (1960); Keyes (1968); Bryden (1972); Sacher and Staffeldt (1974); Sobolevskij (1977); Aguayo (1979); Bonner (1979a,e, 1981b, 1982); Crawley and Warneke (1979); King and Marlow (1979); Lander (1979); Marlow and King (1979); Mate (1979); Mate and Gentry (1979); Shaughnessy (1979); Vaz-Ferreira (1979a,b, 1981, 1982a,b); Warneke (1979); Trillmich and Arnold (1980); Walker and Ling (1980, 1981a,b); Eisenberg (1981); Odell (1981); Schusterman (1981); Shaughnessy (1982a,b); Thurman et al. (1982); King (1983b); Trillmich (1984); Gentry and Kooyman (1986); Gentry et al. (1986); Croxall and Gentry (1987); Loughlin et al. (1987); Costa and Trillmich (1988); Costa et al. (1988, 1989); Boyd and McCann (1989); Dierauf (1990); Boyd and Duck (1991); Nowak (1991); Ling (1992); McLaren (1993); Chabot (1994); Silva and Downing (1995); Ferguson et al. (1996); Gallo-Reynoso and Figueroa-Carranza (1996); Ono and Boness (1996)

Phocidae: Lindsey (1937); Crile and Quiring (1940); Laws (1959); Usher and Churcher (1969); Bryden (1972); Robin (1973); Sacher and Staffeldt (1974); Kooyman (1975, 1981a,b,c); Leshko and Nikitenko (1975); Bryden and Erickson (1976); Hofman et al. (1977); Sobolevskij (1977); Sergeant et al. (1978); Bonner (1979b,c,d, 1981a); Boulva (1979a,b); Boulva and McLaren (1979); Brenton (1979a); Ferren and Elsner (1979); Helle (1979); Hofman (1979); Laws and Hofman (1979); Le Boeuf (1979); Sergeant (1979); Bigg (1981); Burns (1981a,b); Eisenberg (1981); Frost and Lowry (1981); Kenyon (1981a); Ling and Bryden (1981, 1992); McGinnis and Schusterman (1981); Ray (1981); Reeves and Ling (1981); Ronald and Healey (1981, 1982); Lavigne et al. (1982); Naito (1982); Popov (1982); Ronald et al. (1982); Finley et al. (1983); King (1983b); Bryden et al. (1984); Stewart and Yochem (1984); Bowen et al. (1985); Kovacs and Lavigne (1985, 1986a); Lydersen and Gjertz (1987); Costa et al. (1988); McCann et al. (1989); Testa et al. (1989); Dierauf (1990); Hammill et al. (1991); Nowak (1991); Smith et al. (1991); Hindell et al. (1992, 1994); Le Boeuf et al. (1992); Slip et al. (1992); McLaren (1993); Stewart and Huber (1993); Skinner and Klages (1994); Silva and Downing (1995); Ferguson et al. (1996)

specific metabolic rates (mBMR; in ml O_2 g^{-1} min^{-1}) by multiplying by species body weight.

15. Body temperature (T_B): resting body temperature (in °C) determined by any method (e.g., rectal thermometers, thermotelemetry).

16. Hematocrit (Hct): proportion of blood composed of red blood cells (%). Because hematocrit is rapidly influenced by numerous factors including physiological condition, activity, and stress levels (Castellini et al. 1996), we only used estimates for animals that were in normal health (e.g., not pregnant) and resting.

17. Hemoglobin concentration (Hb): grams of hemoglobin per 100 ml of blood (in g/100 ml or g%).

18. Red blood cell count (RBC): millions of red blood cells per milliliter of blood (in 10^6 RBC/ml).

19. Heart rate (HR): resting heart rate (in beats min^{-1}).

20. Population density (PD): average number of individuals of all ages found in a given area (in number of individuals/km^2). For pinnipeds, we ensured that these values were not taken from breeding areas, which display unusually high concentrations of individuals.

TABLE A2. Values of selected life-history characters for all extant species of pinniped (including *Monachus tropicalis*). See Appendix 1 for identity and descriptions of variables. Sources are given at the bottom of the table.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Odobenidae											
Odobenus rosmarus	1.00	330.00	59090.91	59090.91	720.00	730.00	3285.00	2372.50	24.00	0.00	480.00
Otariidae											
Arctocephalus australis	1.00	236.25	4400.00	4400.00	540.00		2555.00	1095.00	12.00	0.00	252.00
Arctocephalus forsteri	1.00	232.50	3875.00	3875.00	330.00		3650.00	1825.00	12.00	0.00	180.00
Arctocephalus galapagoensis	1.00	210.00	3500.00	3500.00	1080.00	1095.00	2920.00	1460.00	36.00	0.00	264.00
Arctocephalus gazella	1.00	233.25	5433.33	5433.33	118.50		1825.00	1277.50	12.00	0.00	276.00
Arctocephalus philippii	1.00								12.00		
Arctocephalus pusillus	1.00	240.00	6000.00	6000.00	365.00		1460.00	1231.88	12.00	0.00	252.00
Arctocephalus townsendi	1.00				330.00				12.00	0.00	288.00
Arctocephalus tropicalis	1.00	231.75	4900.00	4900.00	330.00		1277.50	1733.75	12.00	0.00	276.00
Callorhinus ursinus	1.00	240.00	5000.00	5000.00	120.00	120.00	1825.00	1460.00	12.00	0.00	420.00
Eumetopias jubatus	1.00	240.00	19500.00	19500.00	365.00		1916.25	1825.00	12.00	0.00	360.00
Neophoca cinerea	1.00	255.00	7000.00	7000.00	540.00		2190.00	1095.00	18.00	0.00	192.00
Otaria byronia	1.00	255.00	12820.00	12820.00	365.00		2007.50	1460.00	12.00	0.00	274.00
Phocarctos hookeri	1.00				300.00	365.00	2190.00		12.00	0.00	
Zalophus californianus	1.00	240.00	6000.00	6000.00	365.00		3285.00	2099.00	12.00	0.00	360.00
Phocidae											
Cystophora cristata	1.00	234.00	22000.00	22000.00	11.00	7.50	1825.00	1095.00	12.00	0.00	420.00
Erignathus barbatus	1.00	270.00	35500.00	35500.00	18.00	18.00	2372.50	2007.75	18.00	0.00	377.43
Halichoerus grypus	1.00	242.00	14468.75	14468.75	19.54	21.00	2190.00	1642.50	12.00	0.00	560.07
Hydrurga leptonyx	1.00	276.00	30000.00	30000.00	28.00	28.00	1460.00	1204.50	12.00	0.00	312.00
Leptonychotes weddellii	1.00	262.75	29000.00	29000.00	45.00	50.00	1642.50	1095.00	12.00	0.00	300.00
Lobodon carcinophagus	1.00	255.00	22000.00	22000.00	31.50	29.75	1460.00	1277.50	12.00	0.00	468.00
Mirounga angustirostris	1.00	229.50	37500.00	37500.00	28.00	27.20	1733.75	1186.25	12.00	0.00	243.50
Mirounga leonina	1.00	225.00	41000.00	41000.00	23.00	24.00	1733.75	1171.04	12.00	0.00	276.00
Monachus monachus	1.00	330.00	20000.00	20000.00	43.00	569.00	1460.00	1460.00	24.00	0.00	284.00
Monachus schauinslandi	1.00	330.00	16250.00	16250.00	38.00	38.00	1460.00	1825.00	15.37	0.00	360.00
Monachus tropicalis	1.00								18.00		
Ommatophoca rossii	1.00	247.50	17000.00	17000.00	28.00	28.00	1277.50	1323.13	12.00	0.00	252.00
Phoca caspica	1.00	330.00	5000.00	5000.00	31.50	31.50	2372.50	1825.00	12.00	0.00	600.00
Phoca fasciata	1.00	234.00	10000.00	10000.00	28.00	28.00	1642.50	1277.75	12.00	0.00	365.26
Phoca groenlandica	1.00	232.50	10150.00	10150.00	12.00	16.50	2463.75	1825.00	12.00	0.00	504.00
Phoca hispida	1.00	225.00	4500.00	4500.00	49.00	49.00	2528.93	2190.00	12.00	0.00	552.00
Phoca largha	1.00	248.00	8300.00	8300.00	28.00	28.00	1642.50	1460.00	12.00	0.00	426.13
Phoca sibirica	1.00	270.00	3050.00	3050.00	70.00	72.50	2007.50	1642.50	12.00	0.00	672.00
Phoca vitulina	1.00	247.75	10150.00	10150.00	38.50	38.50	1916.25	1277.50	12.00	0.00	480.00

Odobenus rosmarus: Laws (1959); Harrison and Kooyman (1968); Harrison (1969); Bryden (1972); Brenton (1979b); Fay (1981, 1982, 1985); King (1983b); Schmitz and Lavigne (1984); Oftedal et al. (1987); Riedman (1990); Walsh et al. (1990); Boyd (1991); Nowak (1991); Hayssen et al. (1993); Ferguson et al. (1996)

Otariidae: Laws (1959); McLaren (1967); Harrison and Kooyman (1968); Harrison (1969); Bryden (1972); Sacher and Staffeldt (1974); Bonner (1979a,e, 1981b, 1982); Crawley and Warneke (1979); King and Marlow (1979); Lander (1979); Marlow and King (1979); Mate (1979); Mate and Gentry (1979); Shaughnessy (1979); Vaz-Ferreira (1979a,b, 1981, 1982a,b); Warneke (1979, 1982); York (1979); Jouventin and Cornet (1980); Trillmich and Arnold (1980); Gentry (1981); Odell (1981); Schusterman (1981); Jones (1982); Shaughnessy (1982a,b); King (1983b); Eibl-Eibesfeldt (1984); Schmitz and Lavigne (1984); Trillmich (1984, 1986); Trillmich and Limberger (1985); Gentry et al. (1986); Croxall and Gentry (1987); Loughlin et al. (1987); Oftedal et al. (1987); Costa and Trillmich (1988); Costa et al. (1988, 1989); Higgins et al. (1988); Boyd and McCann (1989); Mead (1989); Dierauf (1990); Fowler (1990); Riedman (1990); Trites (1990); Boyd (1991); Nowak (1991); Ling (1992); Lunn (1992); Hayssen et al. (1993); Higgins and Gass (1993); Lunn et al. (1993); Trites and York (1993); Wickens (1993); Ferguson et al. (1996)

Phocidae: Lindsey (1937); Laws (1959, 1977, 1979a,b); Smith (1965); McLaren (1967); Harrison and Kooyman (1968); Harrison (1969); Stirling (1969, 1971, 1977, 1979); Bryden (1972); Bigg and Fisher (1974); Sacher and Staffeldt (1974); Potelov (1975); Elsner et al. (1977); Reiter et al. (1978); Sergeant et al. (1978); Bonner (1979b,c,d, 1981a); Boulva (1979a,b); Boulva and McLaren (1979); Brenton (1979a); DeMaster (1979); Helle (1979); Hofman (1979); Lavigne (1979); Laws and Hofman (1979); Le Boeuf (1979); Popov (1979a,b,c, 1982); Sergeant (1979); Stirling and Archibald (1979); Stirling and Calvert (1979); Jouventin and Cornet (1980); Stewart and Lavigne (1980); Bigg (1981); Bowen et al. (1981); Burns (1981a,b); Frost and Lowry (1981); Kenyon (1981a); Kooyman (1981a,b,c,d); Ling and Bryden (1981, 1992); McGinnis and Schusterman (1981); Ray (1981); Reeves and Ling (1981); Ronald and Healey (1981, 1982); Capstick and Ronald (1982); Jones (1982); Lavigne et al. (1982); Naito (1982); Ronald et al. (1982); Thomas et al. (1982); Warneke (1982); Hennemann (1983); King (1983b); Thomas and DeMaster (1983); Worthy and Lavigne (1983); Bryden et al. (1984); Schmitz and Lavigne (1984); Stewart and Yochem (1984); Bowen et al. (1985); Kovacs and Lavigne (1985, 1986a,b,c); Huber (1987); Little et al. (1987); Lydersen and Gjertz (1987); Oftedal et al. (1987, 1993); Costa et al. (1988); Heide-Jørgensen and Härkönen (1988); Hindell and Little (1988); Le Boeuf et al. (1989); McCann et al. (1989); Mead (1989); Shaughnessy and Kerry (1989); Riedman (1990); Boyd (1991); Guinet (1991); Hammill et al. (1991); Nowak (1991); Reiter and Le Boeuf (1991); Smith et al. (1991); Sydeman et al. (1991); Rea and Costa (1992); Arnbom et al. (1993); Campagna et al. (1993); Hayssen et al. (1993); Iverson et al. (1993); Muelbert and Bowen (1993); Stewart and Huber (1993); Skinner and Klages (1994); Teilmann and Dietz (1994); Stirling and Øritsland (1995); Ferguson et al. (1996); Haller et al. (1996)

APPENDIX 2

Pinniped Species Values

We restrict presentation of the dataset to the pinnipeds; species values for fissipeds can be derived from Gittleman (1984, 1985, 1986a,b, 1991, 1993) and are also found in Bininda-Emonds (1998). The sources used to compile the species values follow each data table; citations match those found in Bininda-Emonds (1998), which contains the complete references. The latter are also available from O. R. P. Bininda-Emonds on request. For presentation purposes, we divide the variables into three data tables: morphology, life history, and physiology/miscellany (Tables A.1–A.3, respectively).

TABLE A3. Values of selected physiological and miscellaneous characters for all extant species of pinniped (including *Monachus tropicalis*). See Appendix 1 for identity and descriptions of variables. Sources are given at the bottom of the table.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Odobenidae								
Odobenus rosmarus			36.60	46.00	16.48	3.27	55.00	1.27
Otariidae								
Arctocephalus australis				49.30	16.80			
Arctocephalus forsteri				47.60	16.90	5.41		
Arctocephalus galapagoensis	4.51	207.23	37.70					
Arctocephalus gazella								22.01
Arctocephalus philippii								
Arctocephalus pusillus			37.50	39.00	13.60	4.04	85.00	
Arctocephalus townsendi								
Arctocephalus tropicalis								
Callorhinus ursinus			37.70	46.58	15.64	4.58	100.00	18.00
Eumetopias jubatus			38.50	40.20	14.68	3.95		
Neophoca cinerea				56.29	19.00	5.53	120.00	
Otaria byronia								
Phocarctos hookeri								
Zalophus californianus			37.50	45.00	15.30	4.40	95.00	0.50
Phocidae								
Cystophora cristata	3.71	1049.85	36.50	63.00	26.40	4.80	100.00	0.00
Erignathus barbatus			37.13	56.40				0.02
Halichoerus grypus	3.32	643.43	36.50	56.00	19.03	5.13	127.50	
Hydrurga leptonyx					19.60	4.40		0.12
Leptonychotes weddellii	5.15	1895.20	36.70	58.72	23.70	3.73	60.00	0.13
Lobodon carcinophagus					18.20	4.41		1.01
Mirounga angustirostris			34.90	57.00	24.33	3.25	59.63	
Mirounga leonina			36.30	60.60	22.85	2.85	39.60	
Monachus monachus								
Monachus schauinslandi			36.20	54.70				
Monachus tropicalis								
Ommatophoca rossii			37.80				151.00	0.17
Phoca caspica								1.47
Phoca fasciata				66.80	24.48	4.49		
Phoca groenlandica	3.10	410.02	36.00	59.00	22.10	5.11	116.75	0.10
Phoca hispida	3.09	213.55	38.25	61.80	24.45	5.24	85.00	0.95
Phoca largha	6.53	597.42		54.45	18.00	4.70		
Phoca sibirica				62.93	18.00	5.50		1.59
Phoca vitulina	6.18	539.18	37.50	53.00	18.35	5.36	98.75	5.68

Odobenus rosmarus: Harrison and Kooyman (1968); Lenfant et al. (1970); Irving (1973); Estes and Gilbert (1978); King (1983b); Fedoseev (1984); Fay (1985); Gilbert (1989); Bossart and Dierauf (1990); Dierauf (1990); Walsh et al. (1990); Little (1995)

Otariidae: Bartholomew and Wilke (1956); Harrison and Kooyman (1968); Hubbard (1968); Irving (1969, 1973); Lenfant (1969); Ronald et al. (1969); Lenfant et al. (1970); Lane et al. (1972); Ridgway (1972); Sobolevskij (1977); Wells (1978); Needham et al. (1980); Gentry (1981); Odell (1981); Kooyman and Sinnett (1982); Thurman et al. (1982); King (1983b); Hunt et al. (1986); Limberger et al. (1986); Trillmich et al. (1986); Bonnell and Ford (1987); Jablonski et al. (1987); Costa and Trillmich (1988); Bossart and Dierauf (1990); Dierauf (1990); Williams et al. (1990); Hedrick and Duffield (1991); Nowak (1991); Butler et al. (1992); Hunt et al. (1992); Little (1995); Castellini et al. (1996)

Phocidae: Bartholomew (1954); Pugh (1959); Tyler (1960); Morrison (1962); Harrison and Kooyman (1968); Hubbard (1968); Bryden and Lim (1969); Irving (1969, 1973); Lenfant (1969); Ronald et al. (1969, 1977, 1982); Lenfant et al. (1970); Geraci (1971); Stirling (1971); Lane et al. (1972); Ridgway (1972); Kerem and Elsner (1973); Altman and Dittmer (1974); Geraci and Smith (1975); Hawkey (1975); Kooyman (1975, 1981a,c,d, 1985); Øritsland and Ronald (1975); Folk et al. (1977); Gilbert and Erickson (1977); Laws (1977); Sobolevskij (1977); Stirling et al. (1977, 1982); St. Audin et al. (1978); Ashwell-Erickson et al. (1979, 1986); Ferren and Elsner (1979); Finley (1979); Gallivan and Ronald (1979); Kenny (1979); Popov (1979a,b, 1982); Stirling and Calvert (1979); Kooyman et al. (1980); Needham et al. (1980); Bigg (1981); Burns (1981b); Eisenberg (1981); Frost and Lowry (1981); Kenyon (1981a); Ray (1981); Reeves and Ling (1981); Ronald and Healey (1981); Sinnett et al. (1981); Kooyman and Sinnett (1982); Lapennas and Reeves (1982); Lavigne et al. (1982); Worthy and Lavigne (1982); Erickson et al. (1983, 1989); Finley et al. (1983); Hennemann (1983); King (1983b); Erickson (1984); Schmitz and Lavigne (1984); Davis et al. (1985); Kingsley et al. (1985); Fedak (1986); Hedrick et al. (1986); Kovacs and Lavigne (1986a); Keiver et al. (1987); Castellini et al. (1988, 1996); Wickham et al. (1989, 1990); Bossart and Dierauf (1990); Dierauf (1990); Erickson and Hanson (1990); Hammill and Smith (1990); Härkönen and Heide-Jørgensen (1990); Olesiuk et al. (1990); Williams et al. (1990); Hedrick and Duffield (1991); Nowak (1991); Harwood and Stirling (1992); Ling and Bryden (1992); Lydersen et al. (1992); Castellini and Castellini (1993); Gales and Renouf (1993); Ponganis et al. (1993); Stewart and Huber (1993); Gelatt et al. (1994); Renouf and Gales (1994); Stenson and Kavanagh (1994); Bester et al. (1995); Boily and Lavigne (1995); Little (1995); Melrose et al. (1995); Stirling and Øritsland (1995); Mathews and Kelly (1996)