Flippers versus feet: comparative trends in aquatic and non-aquatic carnivores

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Summary

1. It is commonly accepted that many adaptations characterize carnivores that live in water. However, no comparative tests have ever shown systematic differences between aquatic and terrestrial carnivore species as a whole. We examine numerous hypotheses that purport to distinguish aquatic and terrestrial carnivores using 20 morphological, life history, physiological and ecological traits.
2. Using the method of independent contrasts with a complete species-level phylogeny of extant carnivores, we found few differences between aquatic and terrestrial species. Compared to terrestrial sister taxa, aquatic carnivores are streamlined (increased head and body length for a given body weight), have larger brains, smaller litter sizes, shorter interbirth intervals, and shorter lifespans.
3. Some of these differences are important functionally. Larger brain size may be related to increased cognitive and sensory needs required for an amphibious lifestyle; smaller litters are likely associated with increased neonatal survival amidst competition for suitable breeding sites and advantages accruing to increased precociality.
4. We conclude that broad differentiation of carnivores into aquatic and terrestrial ecotypes is not useful given that adaptive differences between these groups are limited and seemingly no more numerous than those that occur within each ecological group.

Key-words: aquatic adaptations, comparative method, independent contrasts, phylogeny, terrestrial ecology.

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Introduction

Land and water represent a fundamental physical divide. Many adaptations are consequently found among several groups of higher vertebrates that have returned independently to an aquatic lifestyle (e.g. cetaceans, pinnipeds, otters, penguins, turtles, sea snakes). Within mammals, studies of aquatic adaptations have focused largely on morphological changes, particularly those linked to locomotion: development of flippers, limb restructuring, or the evolution of a streamlined, fusiform body plan are classic examples (e.g. Osburn 1903; Taylor 1914; Howell 1930; Tarasoff 1972; Wyss 1987; Stein 1988, 1989; Fish & Stein 1991; Fish 1993). Certainly, these are striking differences compared to terrestrial mammals; however, a related question is whether other adaptations extend to other functional traits such as physiology (see Williams 1998, 1999), life histories,

ecology or behaviour. Some evidence is suggestive (e.g. Scholander 1940; Bartholomew 1970; Repenning 1976; Hawkey 1977; Estes 1989; Dunstone 1998; Williams 1998) although proper comparative tests have not been performed.

Another issue concerns the relative degree to which differences occur between 'fully aquatic' species and those that only partly exploit aquatic habitats. The latter, 'semi-aquatic' species may need to balance the conflicting demands of aquatic and terrestrial environments (Tarasoff 1972; Dunstone & O'Connor 1979; Stein 1988, 1989; Fish & Stein 1991; Dunstone 1998; Williams 1998, 1999) and thus may represent a qualitatively different ecological strategy. Conversely, semi-aquatic species may merely differ in the degree to which they exhibit aquatic adaptations (Osburn 1903; Churchfield 1998). To determine whether specific traits are needed to exploit aquatic environments in general requires that we demonstrate that these traits occur only, or at least more strongly, in species that use aquatic resources than in closely related, non-aquatic species.

The Carnivora offer an ideal opportunity to study

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Table 1. Summary of the hypotheses under study and the variables used to test them. Predictions refer to the value expected in aquatic forms as compared to non-aquatic forms (+ = increased, − = decreased) and are given for raw variables and ones corrected for size (body or brain weight). Full names for all variables are found in the Appendix

Category	Dependent variable	Independent variable	Raw hypothesis	Size-corrected hypothesis
Allometry	SWt		+	+
	SHB		+	+
	SBr		conflicting	conflicting
	LS		−	none
	GL		+	none
	BWt		+	none
	LWt		+	none
	WA		+	none
	AI	body	+	none
	MMat	weight	+	none
	FMat	or	+	none
	IB	brain	+	none
	EO	weight	none	none
	LY		+	none
	mBMR		+	+
	tBMR		+	+
	T_B		−	−
	Hct		not −	not −
	Hb		+	+
	RBC		−	−
	HR		none	none
	PD		−	−
Dimorphism	MWt	FWt	none	none
	MHB	FHB	none	none
	MBr	FBr	none	none
	MMat	FMat	none	none

these problems. The order is a diverse clade of 271 extant species that includes aquatic (pinnipeds and otters), semi-aquatic (polar bear and mink) and terrestrial forms (most species). The issue of aquatic adaptations across the Carnivora has received some attention (e.g. Repenning 1976; Wyss 1987, 1988, 1989; Flynn 1988; Estes 1989), particularly in the context of the origin and evolution of pinnipeds relative to all other carnivores ('fissipeds'; see Bininda-Emonds & Gittleman 2000). Further, availability of a comparative data base on morphology, life history and ecology of fissipeds (see Gittleman 1984, 1991, 1993) and a complete phylogeny of all extant carnivore species (Bininda-Emonds, Gittleman & Purvis 1999) allows us to perform statistical phylogenetic tests (see Felsenstein 1985; Harvey & Pagel 1991).

Our analyses directly examine hypotheses of aquatic adaptations in carnivores as proposed by Bartholomew (1970), Repenning (1976), Estes (1989) and Dunstone (1998). We evaluate 20 morphological, life history, physiological and ecological traits accounting for both phylogenetic relatedness and allometry. Our goals are: (1) to establish what adaptations characterize aquatic species of carnivorans relative to their terrestrial sister taxa, and (2) to investigate whether a distinction exists between fully and semi-aquatic carnivores.

Comparative hypotheses

We tested three broad categories of traits, plus some miscellaneous ones, previously hypothesized to be important in an aquatic lifestyle (following Bartholomew 1970; Repenning 1976; Estes 1989; Dunstone 1998). Although other potentially key traits and categories exist (see Repenning 1976; Estes 1989; Dunstone 1998), comparative data are lacking. We list the categories below together with associated hypotheses (summarized in Table 1; variables described fully in Appendix). When directionality for a hypothesis is inferred, predictions are given for the value in aquatic forms compared to non-aquatic forms.

HEAT CONSERVATION

Water is effectively a colder environment than air due to its greater thermal conductivity (about 24 times; Williams 1998). Other than decreasing thermal conductance (for which data are scanty) from insulation via blubber or a thicker coat, regional heterothermy or behavioural mechanisms in the more semi-aquatic species (Dunstone 1998), aquatic carnivores can conserve or generate additional body heat in one of three main ways, as follows.
1. Increasing basal metabolic rate (BMR). Although supported by many early physiological studies (e.g. Scholander 1940; Irving 1969, 1973), the assertion that aquatic mammals have proportionately higher BMRs for their mass was disputed recently (see Lavigne *et al.* 1986 and references therein) and may also derive from

the use of invalid cross-species analyses (see Elgar & Harvey 1987). BMR may also scale differently with body mass in aquatic vs. terrestrial animals given that the former are less exposed to gravitational load and therefore not similar geometrically to the latter (Economos 1979; Platt & Silvert 1981).

We examined both mass-specific BMR (measured in $mL O_2 g^{-1} min^{-1}$) and total BMR (in $mL O_2 min^{-1}$) to eliminate possible autocorrelative effects with body mass (Elgar & Harvey 1987).

2. Decreasing surface area to volume ratio. To minimize radiative surface to the environment, aquatic carnivores should be larger and less elongate (more spherical) than their non-aquatic sister taxa (e.g. Brown & Lasiewski 1972). Increased size is typical of many aquatic forms (see Estes 1989; Dunstone 1998) and fossil evidence also indicates an increase in size along aquatic lineages (Estes 1989; Wyss 1994).

3. Decreasing body temperature. A slight trend for decreased body temperatures in marine mammals may stem from allometric changes with large body size (Morrison 1962) or be associated with diving ability, as deeper divers have lower temperatures (Hubbard 1968). The relation between temperature and body size is unclear: cross-species analyses suggest that temperature is independent of weight across mammals, although some relationship might occur within 'homogeneous subgroups' such as carnivores (Morrison & Ryser 1952; also Folk, Folk & Craighead 1977). Recently, however, Dunstone (1998) indicated that aquatic vertebrates usually possess elevated core body temperatures relative to their body mass.

OXYGEN CONSERVATION

This category has a greater bearing on the subset of aquatic carnivores that dive, where pressure changes and extended periods of apnea require physiological and morphological adaptations (see Scholander 1940). While these oxygen-related changes, particularly in haematological variables, are more pronounced in deeper divers (Lenfant, Johansen & Torrance 1970; Ridgway 1972; Wickham, Costa & Elsner 1990; Melrose *et al.* 1995), they could still be advantageous to any animal that undergoes immersion frequently (Dunstone 1998). The paucity of data, especially for terrestrial species, restricts our analyses to a few blood parameters. Relative to terrestrial forms, aquatic species are characterized by:

1. Increased haematocrit levels. Haematocrit (or packed cell volume) is the proportion of blood composed of red blood cells (Brannon 1985). Like most haematological variables, haematocrit is a dynamic parameter that can be (rapidly) altered in response to apnea, stress, development, molting, and captivity, in addition to measuring technique (Castellini, Meiselman & Castellini 1996).

2. Increased haemoglobin concentration. Increasing either haematocrit or haemoglobin levels increases

oxygen stores, but Hawkey (1977) indicates both variables to be constant throughout mammals. However, evidence suggests that the hypothesized changes in both variables may occur in phocid seals (Lenfant *et al.* 1970), which are considered the best divers among aquatic carnivores, and possibly also the sea otter and remaining pinnipeds (sea lions, fur seals and walruses) (Lane, Morris & Sheedy 1972).

3. Decreased red blood cell (RBC) count. RBC size and number are inversely related to maintain constant haematocrit. Larger RBCs are beneficial for all diving mammals because the decreased surface area to volume ratio ensures a constant, slower release of oxygen (Hawkey 1977; Wickham *et al.* 1989).

4. Changes in resting heart rate. Apart from hibernators, diving forms are distinguished among mammals by the capacity to greatly reduce their heart rates ('diving bradycardia'). Even on land, heart rates can vary considerably in northern elephant and Weddell seals (Bartholomew 1954; Kooyman 1981, 1985). Correlates of heart rate are poorly known, however, beyond a negative relationship with size (Stahl 1967). We propose no specific hypothesis, but examine if heart rates differ systematically between the groups of interest herein, as this variable is a covariate of other physiological variables.

LIFE HISTORY TRAITS

Although life histories are well studied in both pinnipeds (Harrison 1969; Stirling 1983; Boness & Bowen 1996) and fissipeds (Gittleman 1984, 1986b, 1993), consistent adaptations in relation to the aquatic environment are virtually unknown (Estes 1989). Overall, interspecific differences in fissiped life histories vary significantly with phylogeny (taxonomic families), body size, life history covariants and age-specific mortality rates; exceptions are litter size and age at eye opening (Gittleman 1986b, 1993). If allometry is important, the putatively larger aquatic carnivores (see above) should also have different life history traits (Estes 1989).

MISCELLANEOUS CHARACTERS

1. Brain weight. Two conflicting predictions exist for relative brain size in aquatic mammals. One is that aquatic mammals should have proportionately smaller brains because the high metabolic and energetic demands of neural tissue conflict with the need to conserve oxygen while diving (Robin 1973; Hofman 1983; Worthy & Hickie 1986). Conversely, the complex three-dimensional nature of the aquatic environment might select for larger brains (Estes 1989). Some empirical evidence shows pinnipeds having among the largest indices for various brain regions for carnivores (Wirz 1950; Stephan 1972), except for the olfactory lobes which are reduced, particularly in phocids (Fish 1898; Harrison & Kooyman 1968). Other studies, however,

indicate no difference in overall brain size between aquatic and terrestrial mammals (Gittleman 1986a; Worthy & Hickie 1986). We restrict our analyses to overall brain weight because data on different components in the brain are unavailable for most carnivore species, especially pinnipeds.

2. Sexual dimorphism. Estes (1989) discussed sexual dimorphism in otters but found no empirical trends within the subfamily. In general, factors influencing the degree of sexual dimorphism across species are breeding system, diet and body size, with increasing dimorphism in larger species (Bartholomew 1970; Clutton-Brock, Harvey & Rudder 1977; Ralls 1977; Weckerly 1998). Gittleman & Van Valkenburgh (1997), however, found no allometric pattern within carnivores. We assess sexual dimorphism for body weight, brain weight, head and body length and age at sexual maturity.

3. Population density. The number of individuals residing in an area correlates significantly with resource availability and quality (Gittleman 1984, 1989; Wolff & Guthrie 1985; Estes 1989). If these differences extend to terrestrial vs. aquatic environments in general, then observed differences in population density should be found (e.g. as for water shrews compared to their terrestrial counterparts; Churchfield 1998). For otters, there is increased food availability in marine vs. freshwater environments (Estes 1989). Differences may therefore also exist between aquatic carnivores since pinnipeds are almost exclusively marine while the remaining forms are almost exclusively freshwater.

Methods

DEFINING 'AQUATIC'

We consider aquatic carnivores to be those species in which the aquatic habitat inevitably plays a key role in the life-cycle of an individual: pinnipeds; otters; the European and American minks, *Mustela lutreola* and *M. vison*, respectively; the polar bear, *Ursus maritimus*; the marsh mongoose, *Atilax paludinosus*; and the otter and Congo water civets, *Cynogale bennettii* and *Osbornictis piscivora*, respectively. This is a less stringent definition than is commonly used (e.g. those species with an obligate link to water; Estes 1989; Dunstone 1998), but one that permits investigation of whether aquatic adaptations are present, if more weakly, in 'semi-aquatic' species (following Eisenberg 1981; Fish & Stein 1991; Dunstone 1998). In any case, the definition of 'aquatic' for carnivores is highly arbitrary (Dunstone 1998; also compare Wall 1983; Estes 1989; Fish & Stein 1991; Dunstone 1998). Except possibly the sea otter, *Enhydra lutris* (Estes 1980; Kenyon 1981), all carnivores are dependent on land at some point in their life-cycle, usually during mating and parturition. It would perhaps be more accurate to speak of 'amphibious' carnivores.

DATA

The data set consists of 20 morphological, life history, physiological and ecological traits (Table 1). Information on fissipeds was collated largely from Gittleman (1984, 1985, 1986a, 1986b, 1991, 1993; unpublished data), with physiological data being obtained from the recent literature. All information on pinnipeds was drawn from the literature except for most brain size estimates; these values were estimated primarily from volumetric measurements of cranial capacities of adult specimens housed at Natural History Museum, London. 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. However, only two (where possible, one male and one female) rather than 10 or more specimens were measured for each species. Descriptions of all variables and procedures used to compile species values are found in the Appendix. The comparative data set for pinnipeds is given in Bininda-Emonds & Gittleman (2000) and the complete data set is available from the first author (see also Bininda-Emonds 1998).

COMPARATIVE ANALYSES

Correcting for phylogenetic effects

Hierarchical descent with modification during evolution can cause species values in comparative tests to be non-independent: species that share a recent common ancestor are likely to be more similar than distantly related species, rendering cross-species regression invalid (Harvey & Pagel 1991; Pagel 1993; Purvis, Gittleman & Luh 1994). Based on the complete species-level carnivore phylogeny and associated 'best estimate' branch lengths from Bininda-Emonds *et al.* (1999), all variables displayed significant phylogenetic correlation under the Moran's *I* statistic, a measure of spatial autocorrelation implemented in the computer package Phylogenetic Autocorrelation (Gittleman & Kot 1990; Purvis *et al.* 1994). Z-values (standardized relative to values sampled from the *n*! permutations of the raw data) were greater than 1·96 (= $P \leq 0.05$), and were positive and large at the lower taxonomic levels before decaying to negative values at the higher levels (results not shown; see Bininda-Emonds 1998). As an initial analytical step, Moran's *I* is particularly useful because it does not assume any model of trait evolution (Gittleman & Kot 1990) and is appropriate for relatively large sample (taxa) sizes as herein (Martins 1996).

We corrected for this 'phylogenetic inertia' using the method of independent contrasts (Felsenstein 1985) as implemented in the computer package CAIC (Purvis & Rambaut 1995b). Based on a phylogeny, branch length information, and some specified predictor variable, CAIC estimates nodal values for both the predictor

and dependent variables from their values in the node's descendent taxa and then generates 'contrasts' (i.e. differences) between independent nodes or species. The predictor variable can be dichotomous or continuous (implemented in CAIC as either BRUNCH or CRUNCH analyses, respectively).

Analyses were again based on the phylogeny and branch lengths from Bininda-Emonds *et al.* (1999). Both the pattern of relationships and times of divergence for this phylogeny were derived from 177 estimates drawn from the literature using the supertree technique of matrix representation using parsimony analysis (Baum 1992; Ragan 1992). As such, it accounts for estimates derived from different data sources (which are largely non-significant; see Bininda-Emonds, 2000) and represents the best current estimate of carnivore phylogeny. However, because systematic placement of pinnipeds within arctoids remains contentious (for a review, see Bininda-Emonds & Russell 1996), we performed comparative tests using three different tree topologies: (1) a monophyletic Pinnipedia with mustelid (weasel) affinities, (2) a monophyletic Pinnipedia with ursid (bear) affinities or (3) a diphyletic Pinnipedia with phocids (true seals) having a mustelid affinity and otarioids (sea lions, fur seals and walruses) having an ursid affinity (Fig. 1). We excluded the mongooses *Dologale dybowskii* and *Rhynchogale melleri* in the analyses because of uncertainty in their phylogenetic positions (see Bininda-Emonds *et al.* 1999). However, as both species are poorly known for the variables examined herein, the effect of their exclusion should be minimal.

Quantitative variables were log-transformed (base e) to better conform to the underlying random walk model of evolution used in CAIC (Felsenstein 1985; Purvis & Rambaut 1995b). The transformation also often equalizes variances, improves normality and converts allometric relationships into predicted linear ones (Harvey 1982). For the variable 'age of eyes opening', we added one to the raw values before the transformation to eliminate zero values. We determined that these transformations were appropriate, that the branch lengths were adequately standardized (despite CAIC being statistically robust to errors in branch length estimates; Purvis *et al.* 1994), and that the Brownian motion model was appropriate for the data using the diagnostic tests outlined in the CAIC User's Manual (see Purvis & Rambaut 1995a; also Garland *et al.* 1993; Díaz-Uriarte & Garland 1996, 1998).

Allometry

Measurement of size in large-bodied carnivores is problematic (Cattet *et al.* 1997) because body weight is highly variable and changes with season, reproductive condition and physical condition, among other factors (Gittleman 1986b). It has been argued that brain weight is a better estimator of size because neural tissue growth constrains somatic cell proliferation and thus determines development (Sacher & Staffeldt 1974) or, in terms of life history traits, because it may be more closely tied with maternal metabolic rate (Gittleman 1986b). Brain weight often accounts for a greater proportion of the variance in numerous variables than body weight (Sacher & Staffeldt 1974; Gittleman 1986b) because it is less variable intraspecifically (Economos 1980). Here, we are interested in general allometric patterns. Therefore, we tested all variables against both body and brain weight and used the measure that revealed the stronger relationship based on P-values, and secondarily by the one with the higher coefficient of determination (r^2). Multiple regression was not used because the strong collinearity of body and brain weight renders it invalid.

Previous studies have shown that most comparative traits examined in our study are related to size (see above). To investigate allometric relations, we plotted contrasts of each variable vs. contrasts of size (the predictor variable in CAIC's CRUNCH analysis) using least squares regression through the origin. In all cases,
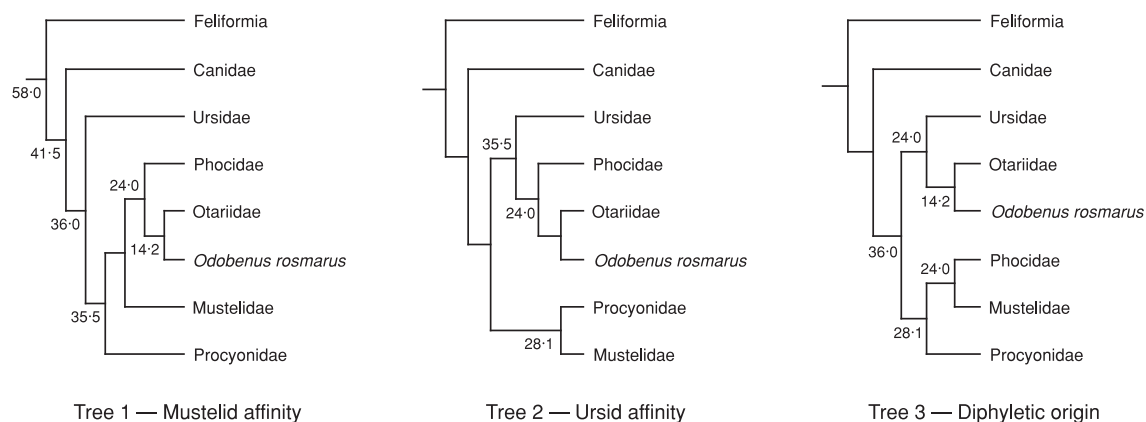
Fig. 1. The major competing hypotheses for the placement of the pinnipeds within the arctoids as tested herein. Numbers are relevant divergence times in millions of years. We consider the composite phylogeny of Bininda-Emonds *et al.* (1999) to be a variant of Tree 1 (mustelid affinity).

we used species values of size except for life history traits in which we used female values (or male values for age at male sexual maturity; following Gittleman 1986b). We produced size-corrected residuals, when appropriate, by fitting the least squares regression equation so determined to the species (not contrast) data points (Purvis & Rambaut 1995a).

Aquatic vs. non-aquatic comparisons

We tested for any distinction between aquatic and non-aquatic carnivores by generating contrasts using a dichotomous habitat variable (aquatic vs. terrestrial) as the predictor variable in CAIC (a BRUNCH analysis). Analyses of sexual dimorphism used ratios calculated as ln (male value/female value), which we did not correct for allometric effects.

If a distinction between aquatic and non-aquatic carnivores exists, the resulting contrasts will be predominantly in the same direction. Unfortunately, the small number of contrasts (nine maximum) limit statistical power. A sign test in particular will be unusually stringent: significant results will usually require all contrasts to be in the same direction and even this might not always be sufficient. This methodological necessity also makes the assumption that all aquatic species will adopt the same solution to a general problem such as heat conservation. In reality, different equally effective solutions may be employed in different lineages (e.g. increased size, increased insulation or increased metabolic rate; see Dunstone 1998; Losos *et al.* 1998). Unfortunately, it is not possible to test this. Therefore, we employed one- and two-tailed *t*-tests coupled with examining for the presence of trends in the data. 'Weak' trends are those where a clear majority of contrasts are in one direction; 'strong' trends are those where all contrasts are in the same direction. The limited number of contrasts also means that the alternative topologies examined herein to account for systematic placement of pinnipeds could greatly affect our results. Note that Tree 3 yields an extra contrast relative to Trees 1 and 2 because phocids and otarioids each possess a non-aquatic sister taxon (Fig. 1).

Results

REGRESSION ANALYSES

Most variables revealed significant allometric relationships to either body or brain weight except age of independence, age of eyes opening, body temperature, haematocrit and haemoglobin concentration (Table 2). Variables typically regressed significantly on both body and brain weight, and usually slightly stronger on the latter; only total BMR and RBC count were slightly more closely related to body weight. The correction for multiple comparisons meant that some variables correlated with only one size measure: litter size, age of weaning, interbirth interval (all with brain size) and

Table 2. Results of least squares regression analyses through the origin of independent contrasts with size (body or brain weight) as the independent variable. *Indicates slopes significantly different than zero at the 0·05 level (corrected for multiple comparisons using a sequential Bonferroni correction; Rice 1989). The size estimator yielding the stronger relationship is indicated in bold type. Full names for all variables are found in the Appendix

Variable	Versus body weight			Versus brain weight		
	n	slope	*r*²	*n*	slope	*r*²
SW	NA	NA	NA	**187**	**1·479***	**0·718**
SHB	198	0·204*	0·533	**189**	**0·481***	**0·726**
SBr	**187**	**0·462***	**0·714**	NA	NA	NA
LS	151	0·010	0·001	**118**	**−0·131***	**0·075**
GL	133	0·062*	0·060	**109**	**0·205***	**0·176**
BWt	117	0·531*	0·440	**97**	**1·245***	**0·747**
LWt	117	0·550*	0·480	**97**	**1·172***	**0·736**
WA	118	0·118	0·044	**101**	**0·283***	**0·070**
AI	78	0·160	0·075	70	0·195	0·043
MMat	95	0·153*	0·163	**85**	**0·385***	**0·322**
FMat	116	0·106*	0·069	**98**	**0·405***	**0·324**
IB	117	0·082	0·052	**101**	**0·249***	**0·139**
EO	114	−0·063	0·020	96	−0·184	0·045
LO	145	0·148*	0·121	**142**	**0·356***	**0·216**
mBMR	55	−0·123*	0·147	**55**	**−0·231***	**0·171**
tBMR	**56**	**0·941***	**0·926**	56	1·409*	0·819
T_B	51	0·001	0·000	51	0·010	0·047
Hct	65	−0·018	0·020	65	−0·019	0·007
Hb	66	0·019	0·016	66	0·041	0·024
RBC	**63**	**−0·076***	**0·120**	63	−0·132*	0·117
HR	**35**	**−0·166***	**0·237**	36	−0·212	0·128
PD	68	−0·733*	0·197	**66**	**−1·597***	**0·290**

Table 3. Results of least squares regression analyses of size-corrected independent contrasts testing hypotheses relating to sexual dimorphism. *Indicates slopes significantly different than zero at the 0·05 level (corrected for multiple comparisons using a sequential Bonferroni correction; Rice 1989). Full names for all variables are found in the Appendix

Dependent	Independent	*n*	Slope	*r*²
MWt	FWt	143	0·930*	0·886
MHB	FHB	78	0·870*	0·809
MBr	FBr	118	0·945*	0·902
MMat	FMat	95	0·463*	0·244

heart rate (with body weight). Except for litter size, uncorrected *P*-values were less than 0·05 for regressions of these variables with the other size estimator. With respect to sexual dimorphism, all four variables estimated in males (body weight, head and body length, brain weight and age of sexual maturity) showed strong, significant relationships with their female analogues (Table 3).

COMPARISONS OF AQUATIC VS. NON-AQUATIC TAXA

Few significant differences were found between aquatic and non-aquatic carnivores, and most that did would disappear if corrected for multiple comparisons (Table 4;

Table 4. Functional differences in aquatic carnivores as compared to their terrestrial sister species for three alternative tree topologies (see Fig. 1). For both the *t*-test and sign test ('Direction'), a positive sign indicates larger values in aquatic carnivores. For the sign test, a question mark denotes no clear trend, while multiple signs indicate that all independent contrasts (*n*) were in the same direction. *Indicates those comparisons that are significant at the 0·05 level using the *t*-test (uncorrected for multiple comparisons); probabilities take into account whether a hypothesis was ventured (see Table 1). The 'best estimate' for each variable is based on the outcome of the allometric analysis. Full names for all variables are found in the Appendix

Variable	Tree 1 (mustelid affinity)				Tree 2 (bear affinity)				Tree 3 (pinniped diphyly)			
	n	*t*	*P*	Direction	*n*	*t*	*P*	Direction	*n*	*t*	*P*	Direction
Uncorrected for body size												
SWt	8	1·51	0·0876	+	8	1·23	0·1288	+	9	1·68	0·0661	+
SHB	8	3·78	0·0046*	+ +	8	3·56	0·0059*	+ +	9	3·50	0·0050*	+ +
SBr	7	0·56	0·2951	+ +	7	0·66	0·5290	+ +	8	0·17	0·8688	+ +
LS	8	0·36	0·6320	–	8	0·12	0·5449	–	9	0·97	0·8161	–
GL	6	2·40	0·0307*	+	6	2·66	0·0224*	+	7	2·69	0·0180*	+
BWt	6	2·92	0·0166*	+	6	3·61	0·0077*	+	7	3·05	0·0112*	+
LWt	6	1·00	0·1822	+	6	0·61	0·2857	+	7	0·63	0·2772	+
WA	6	1·04	0·1778	+	6	0·62	0·2852	+	7	0·11	0·4587	?
AI	5	1·49	0·0978	?	5	1·00	0·1823	?	6	1·64	0·0761	+
MMat	6	2·89	0·0223*	+	6	1·88	0·0666	+	7	2·59	0·0245*	+
FMat	5	1·18	0·1459	+	5	0·80	0·2298	?	6	0·95	0·1897	+
IB	5	–1·51	0·9044	?	5	–1·55	0·9096	?	6	–1·91	0·9478	?
EO	6	1·31	0·2379	?	6	0·95	0·3770	?	7	1·34	0·2234	?
LY	7	–0·82	0·7701	?	7	–0·31	0·6155	?	8	–0·56	0·7011	?
mBMR	4	1·34	0·1362	–	4	0·78	0·2450	?	5	1·20	0·1479	?
tBMR	4	1·17	0·1636	+ +	4	1·17	0·1629	+ +	5	1·14	0·1586	+ +
T_B	4	0·57	0·6993	?	4	0·42	0·6515	?	5	0·89	0·7936	?
Hct	4	1·91	0·0761	?	4	1·84	0·0817	?	5	2·17	0·0479*	?
Hb	4	–0·77	0·7519	+	4	–0·68	0·7281	+	5	–1·29	0·8675	?
RBC	4	0·26	0·5948	–	4	0·97	0·7989	–	5	0·07	0·5252	– –
HR	4	–1·03	0·3796	?	4	0·09	0·9370	?	5	0·39	0·7184	?
PD	5	–1·36	0·1114	– –	5	–1·46	0·0971	–	6	–1·33	0·1129	–
SDWt	7	–0·27	0·8002	?	6	–0·30	0·7738	?	8	–0·26	0·8067	?
SDHB	7	–0·74	0·4859	–	7	–0·81	0·4475	–	8	–0·87	0·4118	–
SDBr	6	0·79	0·4760	+	6	0·76	0·4880	+	7	0·75	0·4858	?
SDMat	5	0·03	0·9793	+	5	0·03	0·9793	+	6	0·03	0·9793	+
Corrected for body size using body weight												
SWt												
SHB	8	2·24	0·0298*	+ +	8	2·00	0·0429*	+ +	9	2·32	0·0243*	+ +
SBr	7	1·99	0·0942	+	7	1·69	0·1422	+	8	2·20	0·0640	+
LS												
GL	6	1·22	0·2764	+	6	1·17	0·2962	+	7	1·69	0·1422	+
BWt	6	1·98	0·1041	+	6	1·96	0·1074	+	7	2·20	0·0705	+
LWt	6	1·05	0·3409	+	6	1·11	0·3158	+	7	1·55	0·1729	+
WA												
AI												
MMat	6	1·63	0·1643	+	6	1·24	0·2716	+	7	1·64	0·1528	+
FMat	5	1·99	0·1180	+	5	1·35	0·2493	?	6	1·92	0·1127	+
IB												
EO												
LY	7	–1·44	0·1987	–	7	–1·52	0·1801	–	8	–1·42	0·1973	–
mBMR	4	0·69	0·2693	+	4	0·84	0·2321	+	5	0·88	0·2139	+
tBMR	4	0·08	0·4689	–	4	0·44	0·3459	?	4	0·33	0·3802	?
T_B												
Hct												
Hb												
RBC	4	–0·07	0·4727	–	4	–0·16	0·4403	–	5	–0·41	0·3519	–
HR	3	0·15	0·1479	+ +	3	1·76	0·1761	+ +	5	2·11	0·1027	+ +
PD	5	–0·30	0·3892	+	5	–0·28	0·3972	+	6	0·38	0·6408	+
SDWt												
SDHB												
SDBr												
SDMat												
Corrected for body size using brain weight												
SWt	7	–0·45	0·6669	?	7	–0·57	0·7061	–	8	–0·54	0·6973	–
SHB	7	0·98	0·3661	?	7	0·94	0·3828	?	8	0·32	0·1600	?

Table 4. *continued*

Variable	Tree 1 (mustelid affinity)				Tree 2 (bear affinity)				Tree 3 (pinniped diphyly)			
	n	*t*	*P*	Direction	*n*	*t*	*P*	Direction	*n*	*t*	*P*	Direction
SBr												
LS	6	−2·03	0·0979	−−	6	−1·98	0·1050	−−	7	−2·45	0·0496*	−
GL	6	1·05	0·3427	?	6	1·12	0·3137	?	7	1·59	0·1639	?
BWt	6	1·05	0·3411	+	6	1·09	0·3270	+	7	1·45	0·1972	+
LWt	6	−0·38	0·7216	+	6	0·03	0·9804	+	7	0·42	0·6922	?
WA	6	0·25	0·8118	+	6	0·19	0·8602	+	7	−0·22	0·8357	+
AI												
MMat	6	0·65	0·5431	+	6	0·46	0·6621	?	7	0·58	0·5822	+
FMat	5	1·09	0·3365	+	5	0·79	0·7910	?	6	0·93	0·3965	+
IB	6	−3·06	0·0280*	−−	6	−2·99	0·0303*	−−	7	−3·59	0·0114*	−−
EO												
LY	7	−2·82	0·0302*	−	7	−2·68	0·0366*	−	8	−2·89	0·0232*	−
mBMR	4	0·83	0·2337	+	4	0·91	0·2144	+	5	1·03	0·1811	+
tBMR	4	0·18	0·4360	?	4	0·21	0·4236	?	5	0·09	0·4657	?
T_B												
Hct												
Hb												
RBC	4	0·00	0·4994	−	4	−0·12	0·4562	−	5	−0·38	0·3602	−
HR												
PD	5	0·42	0·6535	+	5	0·34	0·6258	+	6	0·99	0·8159	+
SDWt												
SDHB												
SDBr												
SDMat												
Best estimate												
SWt	7	−0·45	0·6669	?	7	−0·57	0·7061	−	8	−0·54	0·6973	−
SHB	7	0·98	0·3661	?	7	0·94	0·3828	?	8	0·32	0·1600	?
SBr	7	1·99	0·0942	+	7	1·69	0·1422	+	8	2·20	0·0640	+
LS	6	−2·03	0·0979	−−	6	−1·98	0·1050	−−	7	−2·45	0·0496*	−
GL	6	1·05	0·3427	?	6	1·12	0·3137	?	7	1·59	0·1639	?
BWt	6	1·05	0·3411	+	6	1·09	0·3270	+	7	1·45	0·1972	+
LWt	6	−0·38	0·7216	+	6	0·03	0·9804	+	7	0·42	0·6922	?
WA	6	0·25	0·8118	+	6	0·19	0·8602	+	7	−0·22	0·8357	+
AI	5	1·49	0·0978	?	5	1·00	0·1823	?	6	1·64	0·0761	+
MMat	6	0·65	0·5431	+	6	0·46	0·6621	?	7	0·58	0·5822	+
FMat	5	1·09	0·3365	+	5	0·79	0·7910	?	6	0·93	0·3965	+
IB	6	−3·06	0·0280*	−−	6	−2·99	0·0303*	−−	7	−3·59	0·0114*	−−
EO	6	1·31	0·2379	?	6	0·95	0·3770	?	7	1·34	0·2234	?
LY	7	−2·82	0·0302*	−	7	−2·68	0·0366*	−	8	−2·89	0·0232*	−
mBMR	4	0·83	0·2337	+	4	0·91	0·2144	+	5	1·03	0·1811	+
tBMR	4	0·08	0·4689	−	4	0·44	0·3459	?	4	0·33	0·3802	?
T_B	4	0·57	0·6993	?	4	0·42	0·6515	?	5	0·89	0·7936	?
Hct	4	1·91	0·0761	?	4	1·84	0·0817	?	5	2·17	0·0479*	?
Hb	4	−0·77	0·7519	+	4	−0·68	0·7281	+	5	−1·29	0·8675	?
RBC	4	−0·07	0·4727	−	4	−0·16	0·4403	−	5	−0·41	0·3519	−
HR	3	0·15	0·1479	+ +	3	1·76	0·1761	+ +	5	2·11	0·1027	+ +
PD	5	0·42	0·6535	+	5	0·34	0·6258	+	6	0·99	0·8159	+
SDWt	7	−0·27	0·8002	?	6	−0·30	0·7738	?	8	−0·26	0·8067	?
SDHB	7	−0·74	0·4859	−	7	−0·81	0·4475	−	8	−0·87	0·4118	−
SDBr	6	0·79	0·4760	+	6	0·76	0·4880	+	7	0·75	0·4858	?
SDMat	5	0·03	0·9793	+	5	0·03	0·9793	+	6	0·03	0·9793	+

complete statistical results available from first author; see also Bininda-Emonds 1998). In the following, a positive vs. negative trend refers to a variable having a greater or lesser value, respectively, in aquatic carnivores compared to their terrestrial sister taxa.

Differences between alternative tree topologies were minimal (Table 4; also Table 5) and restricted to variables displaying equivocal or weak trends such that a change in a single contrast could affect the directionality of results. However, the *P*-value for a given variable was usually the lowest on Tree 3 (pinniped diphyly), possibly because of the larger number of contrasts this phylogeny allowed.

Inferred differences between aquatic and non-aquatic carnivores were influenced strongly by whether and how we accounted for possible allometric effects. Without size correction, most variables showed no

Table 5. Frequency of each taxon to be the 'discrepant taxon' for the best estimate of each variable (see text). Presented as the number of variables the taxon was discrepant/total number of variables it supplied a contrast for. 'Within viverrids' refers to a contrast at the root of the viverrid tree that could not be ascribed to either *Cynogale* or *Osbornictis*

Taxon	Tree 1 (mustelid affinity)	Tree 2 (bear affinity)	Tree 3 (pinniped diphyly)
Atilax	5/15	4/15	6/15
Cynogale	2/4	2/4	2/4
Mustela lutreola	5/21	4/21	3/21
Mustela vison	9/25	8/25	10/25
Osbornictis	1/1	0/1	0/1
Otters	6/26	6/26	5/26
Pinnipeds	5/26	6/26	NA
Otarioids	NA	NA	4/26
Phocids	NA	NA	4/26
Ursus maritimus	7/26	6/26	4/26
'Within viverrids'	0/1	0/1	0/1

clear trend or a weak to occasionally strong tendency to increased values in aquatic species. Head and body length, gestation length, birth weight and possibly age at male maturity and haematocrit were significantly larger in aquatic species. All distinct trends were in the same direction as hypothesized in Table 1. Of the variables that scaled with body weight, most retained their weak tendency to increased values when we used body weight to correct for size; head and body length remained significantly larger in aquatic species. Only one reversal was seen, that of a weak negative trend in population density to a weak positive trend (contradicting the hypothesis in Table 1), although total BMR did change from a strong positive trend to no clear trend when corrected for body size. When brain weight was used to correct for size, a number of weakly positive trends remained; however, some variables were 'muted' to show no clear patterns whatsoever and interbirth interval, longevity and possibly litter size displayed significant negative trends. Again, the only clear reversal from no size correction was for population density. This goes against the prediction in Table 1, as does the negative trend for body weight.

We base further discussion on the 'best estimate' for each variable (Table 4), which accounts for whether a variable was size-independent or regressed more strongly with body or brain weight. Most variables displayed either no clear trend or a weakly positive one. Morphologically, aquatic species showed weak tendencies to be relatively smaller in body size (compared to brain weight) and, equivalently, to have relatively larger brains for their body weight; neither trend was significant however, under a *t*-test. There was no clear pattern in morphological sexual dimorphism with aquatic species being more (brain weight) or less (head and body length) sexually dimorphic or displaying no difference (body weight). With life histories, aquatic species showed significantly reduced interbirth intervals, longevity and possibly litter size. Although the latter trend was only significant on Tree 3 (pinniped diphyly), the contrasts were usually all negative, a strong trend. Weak trends existed for most other variables (birth and litter weights, weaning age, and age at male and female sexual maturity), all of which were positive with respect to non-aquatic species. Aquatic species may also be more dimorphic in terms of age at sexual maturity. Last, aquatic species showed significantly increased haematocrit values (on Tree 3 only), a strong tendency to higher heart rates and weak tendencies to higher haemoglobin levels and population densities and to lower RBC counts than terrestrial forms. Only the results for body weight and population density run contrary to the hypothesized directions in Table 1.

All taxa revealed an equal tendency to display a trend opposite to the hypothesized direction or, when no hypothesis was presented, to the clear majority of the remaining forms (Table 5). Again, differences between the tree topologies were negligible. Except for the otter civet (*Cynogale*) and aquatic genet (*Osbornictis*) where the data were too scant to render a fair assessment, frequencies for being the 'discrepant taxon' ranged between 19 and 32%, with no apparent correlation to whether a taxon was fully or semi-aquatic.

Discussion

COMPARING CROSS-SPECIES REGRESSION TO INDEPENDENT CONTRASTS

Comparisons with previous studies are difficult because the data bases and especially comparative methodologies are fundamentally different. Most earlier studies used simple cross-species regression and thus may overestimate the strength of a relationship by failing to distinguish similarity due to common ancestry from that due to similar selection pressures (Harvey & Pagel 1991). Such was the case when we re-examined the allometric relationships using cross-species regression. Except for age of independence and haematocrit, all variables displayed a significant relationship with size (either body or brain weight), with uncorrected *P*-values often less than 0·0001 (see Bininda-Emonds & Gittleman

2000). Throughout the discussion, we assume our use of independent contrasts at least in part explains any different findings compared to the literature and will instead concentrate on other, more case specific causes.

Results from studies of the Carnivora using cross-species analysis vs. those using some form of phylogenetic correction (e.g. Gittleman 1986b, 1993, 1994; Elgar & Harvey 1987; Ferguson, Virgl & Larivière 1996) are not substantially different. This arises partly because many early 'taxonomic corrections' resemble cross-species techniques more than current ones, which account more effectively for phylogenetic effects. Also, although cross-species regression is theoretically invalid (Purvis *et al*. 1994), it can still give approximately correct answers when the comparative relationship is strong (Pagel 1993) and largely independent of phylogeny.

ADAPTATIONS IN AQUATIC CARNIVORES

Relative to their terrestrial sister taxa, aquatic carnivores possess increased (absolute) head and body lengths, decreased interbirth intervals, shorter lifespans and possibly smaller litter sizes. There were few other differences in the 20 variables we examined.

Smaller litter sizes are characteristic of K-selected species, which otters and pinnipeds are often considered to be (McLaren 1967; Hennemann, Thompson & Konecny 1983; Stirling 1983; Schmitz & Lavigne 1984). This life history trait is also associated with a tendency towards larger neonates (only weakly supported herein) and generally precocial young (Eisenberg 1981). Together, this suite of life histories provides advantages for both mother and offspring in dealing with an amphibious lifestyle. Given that dens or rookeries are often close to the water, suitable breeding sites are at a premium (Bartholomew 1970; Repenning 1976), thus competitively limiting the number of offspring that can be raised. Precociality is advantageous because of the greater risks the aquatic environment places on newborns (e.g. risk of drowning, problems with flotation) and the increased complexity of dealing with both terrestrial and aquatic habitats (only sea otter offspring will potentially never set foot on land; Kenyon 1981).

Functional explanations for the remaining two strong trends are not apparent. The result for interbirth interval may be an artefact. With few exceptions, carnivores give birth at approximately 12-month intervals. Many viverrids have shorter interbirth intervals than this and many large carnivores have longer intervals. Together, these two exceptions are sufficient to produce a positive correlation between interbirth interval and brain weight. Thus, although most aquatic species have 12-month interbirth intervals like their sister taxa, their intervals appear shorter when scaled to their relatively large brain size (see below); comparisons uncorrected for size showed no trend (Table 4). Comparative statements about interbirth interval are also often suspect due to rounding errors in the raw data (Gittleman 1989)

and because the values given in the literature often do not account for the true interval where successful rearing of offspring occurs. The decreased longevity of aquatic species could derive from the truly amphibious nature of these organisms. Aquatic carnivores are therefore at greater risk from predators and other dangers associated with two very different environments, neither of which they are ideally adapted to. However, because the longevity estimates we used represent maximum, rather than average lifespans, and were often obtained from captive animals, such a functional explanation seems unlikely. Differences in animal husbandry techniques may be a partial explanation; however, in pinnipeds at least, captive vs. wild longevity values were usually comparable.

Size differences between aquatic and terrestrial carnivores influence numerous functional traits. Despite being advantageous for thermodynamic reasons, aquatic carnivores are absolutely larger than their terrestrial sister taxa for only head and body length, and generally not proportionately larger when we accounted for allometry. The significant increase in head and body length, which remains even when we corrected for size using body weight, is actually detrimental thermodynamically by making these animals less spherical, but is beneficial for locomotion due to streamlining (see Fish 1993). Therefore, other mechanisms such as increased insulation (see also Wolff & Guthrie 1985) are apparently sufficient to meet the thermoregulatory demands of the aquatic environment without changes to basal metabolic rate (BMR). The assertion that aquatic mammals have proportionately higher BMRs apparently stems from incompatible data (Lavigne *et al*. 1986). Early physiological studies of marine mammals used more manageably sized juveniles, whereas those of most terrestrial mammals used adults in accordance with Kleiber's (1975) criteria (adults that are postabsorptive, non-reproductive, at rest and in thermoneutral conditions). Juveniles have elevated BMRs compared to adults (Ashwell-Erickson, Elsner & Wartzok 1979; Little 1995). Metabolic data for marine mammals meeting Kleiber's criteria do not show elevated BMRs (Lavigne *et al*. 1986; but see Williams 1998).

Overall, the large lack of differences among aquatic and non-aquatic carnivores is striking. Within fissipeds, life history traits are independent of ecological factors such as diet, zonation, habitat and activity pattern (Gittleman 1986b, 1993). With few exceptions (see above; also delayed ages at sexual maturity in some otters compared to terrestrial mustelids; Gittleman 1984, 1986b), our comparative tests provide another example of how little ecological factors influence carnivore life history patterns.

The similarity in haematology between aquatic and non-aquatic taxa might occur because these variables are interdependent and vary within narrow limits across all mammals to maintain optimal oxygen transport (Hawkey 1977). A more critical adaptation for aquatic species may be increasing oxygen stores

through either increased blood volume or increased oxygen capacity of both blood and haemoglobin (Lenfant 1969; Lapennas & Reeves 1982; Hochachka 1992). However, there were insufficient data, particularly for terrestrial species, to test this hypothesis.

In conclusion, the effects of aquatic living as a general selective force is often a simplification and may obscure important functional differences within terrestrial (e.g. cursorial vs. arboreal species) and aquatic forms (Gittleman 1986b; Boness & Bowen 1996). Further comparative analyses are needed to isolate which key factors led to the transition between terrestrial and aquatic living and why these factors were so important.

BRAIN SIZE

We interpret two findings as indirect support for aquatic species also possessing proportionately larger brains for their size (see Wirz 1950; Stephan 1972). First, when corrected for body weight, brain weight showed a weak trend to increased values in aquatic forms (with *P*-values generally below 0·10), whereas correcting for brain weight indicated a weak trend to decreased body weight. Secondly, opposing patterns were seen in the size-corrected analysis depending on whether body or brain weight was used as the size estimator. Correcting for body weight revealed the same trends as the uncorrected analysis, but correcting for the proportionately larger brain weight caused most of the positive trends to disappear or occasionally reverse. In other words, using brain weight as a size estimator makes aquatic carnivores appear larger than they really are (in terms of body size), thereby causing variables displaying allometric effects to appear smaller.

The adaptive explanation for relatively larger brains in aquatic carnivores relates to the need for such species to process information in a complex three-dimensional environment (see Estes 1989), a form of the perceptual complexity hypothesis (see Eisenberg & Wilson 1978; Mace, Harvey & Clutton-Brock 1980; Harvey & Krebs 1990). Consistent with this is that aquatic carnivores are actually amphibious. Relatively larger brains may help to process information in two very different environments, each with specific sensory cues and cognitive demands. The amphibious nature of aquatic carnivores also explains why they retain small olfactory lobes (Fish 1898; Hubbard 1968; Gittleman 1991), structures that are absent or nearly so in the fully aquatic cetaceans (Jerison 1973). For example, in all pinnipeds, and otariids in particular, identification of newborns and pups by their mothers is based primarily on smell (King 1983; Boness & Bowen 1996). Further comparative work is needed on whether olfactory bulbs and possibly other brain components are transitional characters representing key evolutionary shifts from terrestrial to amphibious to aquatic forms (see also Barton, Purvis & Harvey 1995).

BEYOND CARNIVORES

Although only a limited number of aquatic–terrestrial comparisons exist within the Carnivora, the ecological and morphological variability found in this group makes our study a valuable initial test of the questions we seek to answer: (1) to identify adaptations characterizing aquatic carnivores (relative to their terrestrial sister taxa) and (2) to determine if adaptation to an aquatic lifestyle is gradual or discrete. Our inclusion of 'semi-aquatic' species in order to test our second question supported the idea that exploitation of aquatic resources at even partial levels correlates with possession of what have been previously thought of as 'aquatic adaptations' (Stein 1988, 1989; Fish & Stein 1991). The semi-aquatic species did not display a greater tendency to contradict the proposed hypotheses or display a contrary trend to the remaining forms than did the fully aquatic pinnipeds and otters.

Increases in sample size within carnivores are not possible (beyond obtaining more information for the poorly known aquatic civets *Cynogale* and *Osbornictis*). Similar comparative analyses should test how well the 'aquatic adaptation' hypotheses apply across other mammals and vertebrates in general. Unfortunately, answering this question may not be easy. For instance, there are many aquatic mammals: cetaceans, sirenians, hippopotamus, platypus, some shrews, some marsupials and numerous rodents. However, the identity of their non-aquatic sister taxa is often unknown or contentious, particularly for rodents (see Parker 1990; Nowak 1991). Furthermore, even when the sister taxa are well agreed upon, such as artiodactyls for cetaceans or proboscideans for sirenians (Irwin, Kocher & Wilson 1991; Novacek 1992; Arnason & Gullberg 1996; Stanhope *et al*. 1996), the age of both divergences (≥ 60 million years; Novacek 1992; Arnason & Gullberg 1996; Lavergne *et al*. 1996) presents special problems. In each case, the accuracy of the contrast depends on obtaining extensive species data and well-resolved phylogenies for both sister groups. As well, the long divergence times mean that any differences might have accrued for selective forces other than the adaptations to an aquatic environment.

Acknowledgements

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Appendix

COMPARATIVE TRAITS

The present data set, including selection and definitions of traits, is similar to that employed in Gittleman (1984, 1985, 1986a, 1986b, 1991, 1993) for comparative studies of the behaviour, ecology and morphology of fissipeds. Unless otherwise noted, species values for a variable are medians. In the case of large discrepancies between sources (including species values in the Gittleman papers), preference was given to those articles with larger sample sizes or employing a more robust methodology.

1. Body weight (SWt, MWt and FWt): average weight of the body (in 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. The species value (SWt) was calculated as the median of weight estimates that did not specify a gender and the average of 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 (in 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 1967). Despite including the tail, standard length is a roughly equivalent measure since 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 and FBr): weight of the brain (in g). When only the brain volume or cranial capacity was given, 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 of sexual maturity (MMat and FMat): age at first conception (in days). Unlike Gittleman (1985, 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 post absorptive, at rest and in a thermoneutral environment. Total metabolic rates (tBMR; in mL O_2 min^{-1}) were derived from mass-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 determined by any method (e.g. rectal thermometers, thermotelemetry) (in °C).

16. Haematocrit (Hct): proportion of blood composed of red blood cells (%). Because haematocrit 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. Haemoglobin concentration (Hb): grams of haemoglobin per 100 mL of blood (in g per 100 mL or g%).

18. Red blood cell count (RBC): millions of red blood cells per mL of blood (in 10^6 RBC mL^{-1}).

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.