

DOES DIVING LIMIT BRAIN SIZE IN CETACEANS?

LORI MARINO

Neuroscience and Behavioral Biology Program and
Department of Psychology, Emory University,
Atlanta, Georgia 30322, U.S.A.

E-mail: lmarino@emory.edu

and

Living Links Center for the Advanced Study of Ape and Human Evolution,
Yerkes Regional Primate Center,
Atlanta, Georgia 30329, U.S.A.

DANIEL SOL

Department of Biology, McGill University,
1205 Avenue Docteur Penfield,
Montréal, Québec H3A 1B1, Canada

and

Centre de Recerca Ecològica i Aplicacions Forestals (CREAF),
Universitat Autònoma de Barcelona E-08193 Bellaterra,
Catalonia, Spain

KRISTEN TOREN

School of Medicine, Emory University,
Atlanta, Georgia 30322, U.S.A.

LOUIS LEFEBVRE

Department of Biology, McGill University,
1205 avenue Docteur Penfield,
Montréal, Québec H3A 1B1, Canada

ABSTRACT

We test the longstanding hypothesis, known as the dive constraint hypothesis, that the oxygenation demands of diving pose a constraint on aquatic mammal brain size. Using a sample of 23 cetacean species we examine the relationship among six different measures of relative brain size, body size, and maximum diving duration. Unlike previous tests we include body size as a covariate and perform independent contrast analyses to control for phylogeny. We show that diving does not limit brain size in cetaceans and therefore provide no support for the dive constraint hypothesis. Instead, body size is the main predictor of maximum diving duration in cetaceans. Furthermore, our findings show that it is important to conduct robust tests of evolutionary hypotheses by employing a variety of measures of the dependent variable, in this case, relative brain size.

Key words: brain size, diving, oxygenation, cetacean.

The Order Cetacea includes many species with the largest brain sizes of all mammals (Marino 1998, 2002; Marino *et al.* 2004). Brain weights in cetaceans range from 220 g for the Franciscana dolphin (*Pontoporia blainvillei*) to 8,000 g for the sperm whale (Marino 2002, Marino *et al.* 2004). Cetaceans possess the highest encephalization levels next to modern humans once body size allometry is taken into account (Marino 1998). One classical method for expressing relative brain size, encephalization quotient (EQ), can be calculated from mean brain and body weight data for a given species using the equation $EQ = \text{brain weight}/0.12(\text{body weight})^{0.67}$ from Jerison (1973). Modern humans are the most encephalized species with an EQ of 7.0, which means that our brains are approximately seven times larger than one would expect for our body size. Notably, several odontocete species possess EQs in the 4.0–5.0 range, which is significantly higher than any other modern mammal except modern humans.

Large brains incur a heavy metabolic and oxygenation cost (Martin 1981, Armstrong 1983, Harvey and Bennett 1983, Hofman 1983). These costs pose a particular problem to aquatic mammals because diving involves long periods of time when oxygenation of the brain cannot be renewed by respiration. Thus, it has been suggested that the oxygenation demands of diving may limit the absolute and relative size of aquatic mammal brains (Robin 1973, Ferren and Elsner 1979, Hofman 1983). This idea (herein referred to as the “dive constraint hypothesis”) predicts that relative brain size should be negatively associated with dive time. The fact that cetaceans have evolved such large absolute and relative brain sizes despite this potential physiological constraint is all the more intriguing.

There have been three previous tests of the dive constraint hypothesis. Robin (1973) compared maximum diving time with brain weight/body weight ratio in three aquatic mammals, the bottlenose dolphin (*Tursiops truncatus*), the harbor seal (*Phoca vitulina*), and the Weddell seal (*Leptonychotes weddellii*). On the basis of this small sample, Robin concluded that there was an inverse relationship between maximum diving duration and brain weight/body weight ratio. Ridgway (1986) also reported a negative relationship between brain size as a percentage of body size and diving time in six odontocete species. Worthy and Hickie (1986) tested the hypothesis on a much larger sample of 21 species from five different groups of aquatic mammals (Odontoceti, Mysticeti, Pinnipedia, Sirenia, and Ungulata), and found no correlation between relative brain size and either maximum or average diving duration. They concluded that phylogeny is more important than diving in determining brain size.

Previous tests of the dive constraint hypothesis not only provide conflicting evidence, but may also have been affected by two important methodological issues. First, they used ratio measures of relative brain size. Ratios are not normally distributed and may not entirely remove the confounding effects of body size. When relative brain weight is calculated as a fraction of body weight (Robin 1973, Ridgway 1986), the fact that the slope of the brain-body relationship is less than 1 causes small-bodied animals to have overestimated relative brain sizes. When relative brain size is calculated as a fraction of expected brain size derived from allometric regressions (EQ), large-brained species range over a wide spectrum of ratios greater than 1 (*e.g.*, $EQ = 5.1$ for *Lagenorhynchus obliquidens* and 2.8 for *Tursiops truncatus* in Worthy and Hickie 1986), while the EQ levels of small-brained species are confined, as a matter of mathematical definition, to the much narrower range of 0–1. Therefore, the variance for EQ is not symmetrical around 1.

The second methodological issue that may have affected the conclusions of previous tests is related to phylogenetic autocorrelation. The inclusion of large-brained cetaceans and small-brained aquatic mammals like the manatee (Sirenia) and the

hippopotamus (Ungulata) in a phylogenetically uncontrolled regression means that most of the variance is likely to be taxonomic, which is precisely the explanation suggested by Worthy and Hickie (1986) for their negative results. Thus, phylogenetic effects need to be considered for the potential effect of dive time on brain size to be properly understood.

METHODS

In this study, we test the dive constraint hypothesis on the largest cetacean data set to date, 23 species (Table 1). We limit our sample to only cetaceans to minimize the role of taxonomic variance in our test. We use six different measures of relative brain size to assess the robustness of these techniques in testing evolutionary hypotheses:

1. the brain/body ratio used by Robin (1973) and Ridgway (1986);
2. EQ values based on the equation $EQ = \text{brain weight}/0.12(\text{body weight})^{0.67}$ from Jerison (1973);
3. EQ values based on the equation $EQ = \text{brain weight}/1.77(\text{body weight})^{0.76}$ from Martin (1981);
- 4 and 5. Log transformations of these two EQ measures to normalize their skewness and
6. Residual brain size calculated over the species in our study, a technique that has proven useful in many comparative tests of brain size in birds (Nicolakakis *et al.* 2003, Sol *et al.* 2005).

It is worth noting that body size does not only vary allometrically with brain size (Worthy and Hickie 1986), but it might also have direct effects on dive duration (Noren and Williams 2000). Thus, body size may be a major confounding factor when testing the relationship between dive time and brain size. This is especially true in the tests using brain ratio measures as, for reasons already discussed, ratios do not completely remove the effect of body size. To ensure that the tests are not biased by differences in body size between species we validate the association between dive time and brain size by including body size as a covariate in multiple regressions.

Diving information, brain size, and body weight data were available for 23 cetacean species. Dive data were obtained from published reports using visual observations or time-depth recorders of free-ranging animals. When discernible, we excluded diving records from adult animals accompanied by a calf, from juveniles and calves, and from very early (and probably less reliable) observational reports, as well as extreme outliers. In addition to observations of wild animals, we also included captive diving and breath-hold data for the bottlenose dolphin, *Tursiops truncatus*. This exception was made because of the rigorously established database available on captive bottlenose dolphins. Finally, although we used brain and body weight data for the long-finned pilot whale, *Globicephala melas*, we used diving data for the very closely related short-finned pilot whale, *Globicephala macrorhynchus*, based on the advice of R. Baird in a personal communication of his unpublished data on these sister species.¹

Maximum diving duration was defined as the highest value of all the maximum diving durations across all reports for a given species. We used maximum diving durations instead of average durations because maximum values more accurately reflect the physiological limits of diving for each species. Maximum diving duration,

¹ Personal communication from Robin W. Baird, Ph. D., Cascadia Research Collective, 218½ W. 4th Avenue, Olympia, WA 98501, 21 September 2003.

Table 1. Family name, popular name, Latin name, values for EQ1 based on Jerison (1973), EQ2 based on Martin (1981), mean brain weight in grams, mean body weight in grams, maximum diving duration, and sources for the 23 cetacean species in the present sample.

Family	Popular name	Latin name	EQ1	EQ2	Brain (g)	Body (g)	Max dive (min)	Sources
Delphinidae	Bottlenose dolphin	<i>Tursiops truncatus</i>	4.14	0.093	1,824	209,530	6.8	a, b, c, d
Delphinidae	Common dolphin	<i>Delphinus delphis</i>	4.26	0.107	815	60,170	5.9	e
Delphinidae	Risso's dolphin	<i>Grampus griseus</i>	4.01	0.087	2,387	328,000	30.0	f
Delphinidae	Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>	4.55	0.09	1,148	91,050	6.2	g
Delphinidae	Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	2.25	0.05	1,103	244,667	4.0	h
Delphinidae	Long-finned pilot whale	<i>Globicephala macrorhynchus</i>	2.39	0.047	2,893	943,200	27.0*	i
Delphinidae	Killer whale	<i>Orcinus orca</i>	2.57	0.047	5,059	1,955,450	10.4	j
Delphinidae	Spinner dolphin	<i>Stenella longirostris</i>	3.24	0.081	660	66,200	3.5	k
Delphinidae	Rough-toothed dolphin	<i>Steno bredanensis</i>	4.95	0.117	1,542	124,857	15.0	l
Delphinidae	Tucuxi dolphin	<i>Sotalia fluviatilis</i>	4.56	0.119	688	42,240	1.5	m
Phocoenidae	Harbor porpoise	<i>Phocoena phocoena</i>	2.95	0.08	540	51,193	5.35	n, o, p
Phocoenidae	Dall's porpoise	<i>Phocoenoides dalli</i>	3.54	0.087	866	86,830	5.6	q
Platanistidae	Chinese river dolphin	<i>Lipotes vexillifer</i>	2.17	0.053	510	82,000	2.25	r
Physeteridae	Pygmy sperm whale	<i>Platanista gangetica</i>	1.55	0.039	295	59,630	3.0	s, t
Physeteridae	Dwarf sperm whale	<i>Kogia breviceps</i>	1.78	0.038	1,012	305,000	17.7	u
Physeteridae	Sperm whale	<i>Kogia sima</i>	1.63	0.037	622	168,500	43.0	v
Ziphiidae	Cuvier's beaked whale	<i>Physeter macrocephalus</i>	0.58	0.008	8,028	35,833,330	73.0	w, x, y, z
Monodontidae	Beluga whale	<i>Ziphius cavirostris</i>	0.92	0.017	2,004	2,273,000	68	aa, bb
Monodontidae	Narwhal	<i>Delphinapterus leucas</i>	2.24	0.046	2,083	636,000	18.3	cc, dd, ee, ff
Balaenopteridae	Fin whale	<i>Monodon monoceros</i>	1.76	0.033	2,997	1,578,330	26.2	gg, hh, ii, jj, kk, ll
Balaenopteridae	Blue whale	<i>Balaenoptera physalus</i>	0.49	0.007	7,085	38,421,500	16.0	mm
Balaenopteridae	Humpback whale	<i>Balaenoptera musculus</i>	0.21	0.003	3,636	50,904,000	18.0	nn
Balaenopteridae		<i>Megaptera novaeangliae</i>	0.44	0.006	6,411	39,295,000	21.1	oo

EQ1 is based on equation from Jerison (1973).

EQ2 is based on equation from Martin (1981).

* Maximum dive value for *Globicephala macrorhynchus* was substituted for *Globicephala melas*.

a = Skrovan *et al.* 1999; b = Ridgway *et al.* 1969; c = Williams *et al.* 1999; d = Lusseau 2003; e = Evans 1975; f = Clarke 1986; g = Black 1994; h = Mate *et al.* 1994; i = Baird *et al.* 2005 and Baird *et al.* 2000; j = Baird *et al.* 2005 and Baird *et al.* 1994; k = Wursig *et al.* 1994; l = Miyazaki and Perrin 1994; m = Edwards and Schnell 2001; n = Otani *et al.* 1998; o = Westgate *et al.* 1995; p = Otani *et al.* 2000; q = Baird and Hanson 1998; r = Peixun 1989; s = Pelletier and Pelletier 1980; t = Pilleri 1970; u = Scott *et al.* 2001; v = Breece and Tershy 1993; w = Miyazaki and Wada 1978; x = Watkins *et al.* 1985; y = Watkins *et al.* 1993; z = Lockyer 1977.

aa = Baird *et al.* 2004; bb = Barlow *et al.* 1997; cc = Martin *et al.* 1993; dd = Martin *et al.* 1998; ee = Martin and Smith 1992; ff = Frost *et al.* 1985; gg = Heide-Jørgensen and Dietz 1995; hh = Martin *et al.* 1994; ii = Vibe 1950; jj = Laird *et al.* 2002; kk = Silverman 1979; ll = Dueck 1989; mm = Croll *et al.* 2001; nn = Lagerquist *et al.* 2000; oo = Dolphin 1987.

however, was almost perfectly correlated with average diving duration ($r = 0.99$), and thus both measures yielded statistically indistinguishable results.

All brain and body mass data (Table 1) were obtained from Marino (1998, 2002) with the exception of those for the rough-toothed dolphin (*Steno bredanensis*) and Atlantic white-sided dolphin (*Lagenorhynchus acutus*), which were calculated from recent cranial volume measurements (using the standard technique of filling and measuring the cranium with plastic beads described in Marino (1998)) and body weight data from the Marine Mammal Collection at the National Museum of Natural History, Smithsonian Institution. For all species in the present study, only data from specimens that possessed normative adult body weights and lengths were included. Because no sex differences in brain and body mass were found (see Marino 1998), we pooled data for the sexes for all analyses. Table 1 presents EQ based on Jerison (1973) and Martin (1981), brain mass, body mass, maximum diving duration, and source of diving data for the entire sample of 23 cetacean species.

We first used extant species in our models to examine present-day trends, then repeated our regressions on phylogenetically controlled independent contrasts (Felsenstein 1985). Independent contrasts remove the effects of common ancestry from present-day variance and yield clues about the possible coevolution of traits. For independent contrasts, we used the program "Compare" (Martins 2003). Our phylogenetic tree was based on Waddell *et al.* (2000), Cassens *et al.* (2000), and Hamilton *et al.* (2001). Branch length information was not available for the species we examined and we thus assumed equal branch lengths for our analyses (Garland *et al.* 1993). Two polytomies were resolved by inserting very short branches (length = 0.0000001) so that the importance of the order of the taxa was minimized. Contrasts were calculated for log brain size, log body size, log maximum dive time, Jerison's EQ, and Martin's EQ. A regression of absolute values of contrasts on their standard deviations revealed that all contrasts were properly standardized by branch lengths (see Harvey and Pagel 1991, Garland *et al.* 1993). We tested the relationship between contrasts with linear regressions forced through the origin.

RESULTS

As predicted by the dive constraint hypothesis, maximum dive duration was negatively correlated with five of our six relative brain size measures calculated from our sample: the brain/body ratios of both Robin (1973) and Ridgway (1986), untransformed EQ calculated according to the regression in Jerison (1973) and EQ calculated according to the regression in Martin (1981; Fig. 1), and log transformed EQ calculated from these two sources (Table 2). Dive duration was also positively correlated with absolute brain size (Fig. 1). In contrast, our sixth estimate, residual brain size, showed no significant correlation with maximum dive duration.

Methodological differences thus seem to affect the conclusions of our test. The key variable here appears to be body size (Fig. 1). Brain/body ratio, Martin's EQ and Jerison's EQ (log transformed or not) all show significant negative correlations with log body size in our sample (Table 2). In contrast, body size is totally removed from the residual brain size measure. When we include both body size and brain size in multiple regressions, the only significant predictor of dive time is body size (partial $r = 0.646$, $P < 0.001$ in all cases). This result is the same regardless of the estimate of relative brain size we use in the multivariate model.

When common ancestry is controlled for by the use of independent contrasts, the relationship between contrasts in Jerison's EQ (log transformed or not) and maximum dive time failed to reach statistical significance, but all other conclusions were the

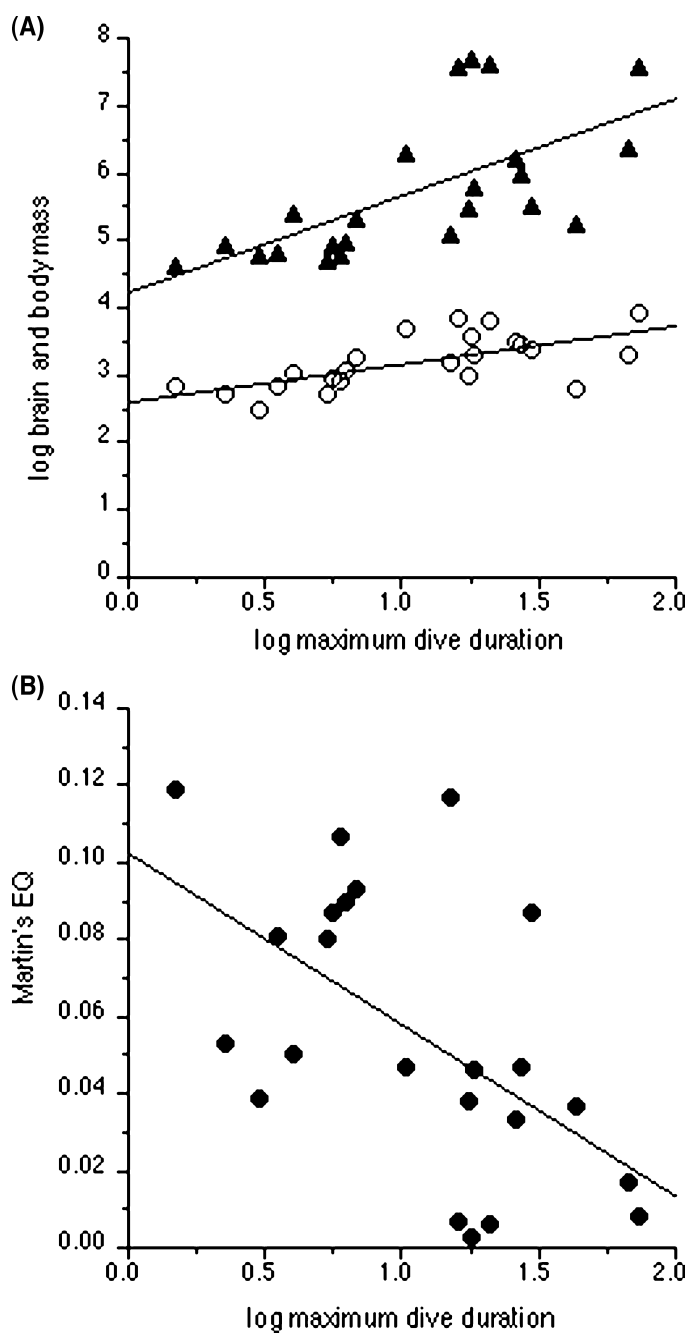


Figure 1. (A) Body mass (closed triangles), brain mass (open circles) as a function of dive duration, log transformed, $P < 0.01$ (B) Martin's EQ (closed circles) as a function of dive duration, log transformed, $P < 0.01$.

Table 2. Correlation between different measures of relative brain size and log maximum dive duration and log body weight. *P* values are given in parentheses. Partial correlations with dive time are given in the case of multiple regressions, where log body size is the only significant predictor.

	With dive time	With body weight	Partial correlation
Brain/body	-0.657 (0.001)	-0.807 (0.001)	-0.309 (0.161)
Jerison EQ	-0.491 (0.017)	-0.763 (0.001)	-0.004 (0.986)
Contrasts Jerison EQ	-0.256 (0.239)	-0.571 (0.004)	0.221 (0.337)
Martin EQ	-0.565 (0.005)	-0.806 (0.001)	-0.098 (0.665)
Contrasts Martin EQ	-0.414 (0.050)	-0.688 (0.001)	0.101 (0.664)
Log Jerison EQ	-0.481 (0.020)	-0.872 (0.001)	0.220 (0.325)
Contrasts log Jerison	-0.364 (0.096)	-0.742 (0.001)	0.287 (0.207)
Log Martin EQ	-0.526 (0.010)	-0.918 (0.001)	0.221 (0.323)
Contrasts log Martin	-0.478 (0.024)	-0.862 (0.001)	0.292 (0.198)
Residual brain size	0.170 (0.439)	0.015 (0.947)	0.235 (0.293)
Absolute brain size	0.653 (0.001)	0.892 (0.001)	0.235 (0.293)
Contrasts abs. Brain	0.712 (0.001)	0.940 (0.001)	0.046 (0.842)

same (Table 2, Fig. 2A, B). Body size is still the only predictor of maximum diving duration in multiple regressions that include the brain size measures along with it (partial $r = 0.680$, $P < 0.001$ in all cases). Furthermore, our results are not due to the inclusion of the very large-bodied Mysticetes and sperm whales with smaller-bodied species in the same regressions. Exclusion of the four larger-bodied species (three Mysticetes and *Physeter macrocephalus*) leads to the same conclusions as their inclusion.

DISCUSSION

The present findings provide a more definitive answer to the question of whether diving limits brain size because, unlike previous tests of the “dive constraint hypothesis,” we have included body size as a covariate and also taken phylogeny into account. The results show that diving does not limit brain size and therefore provides no support for the “dive constraint hypothesis.”

Our results have important implications for theoretical and methodological issues in brain evolution. The evolution of very large brains in the Order Cetacea does not seem to have been constrained by the possible oxygenation costs of prolonged dives. Brains only appear to be constrained by diving costs when estimates of their relative size include the confounding effects of body size. Large muscle mass appears to be the main correlate of long dives. Cetaceans possess a number of adaptations for diving. These include increased myoglobin levels in muscle, increased blood volume, and a higher concentration of hemoglobin than in terrestrial mammals (Castellini and Somero 1981, Kooyman *et al.* 1981, Kooyman 1989). In addition, dive limits are also dictated by the rate of oxygen utilization. Large bodies are able to store more oxygen through large muscle mass and also utilize oxygen more slowly because of lower mass-specific metabolic rate (Williams 1999). Therefore, the present results are consistent with previous findings that body mass (and myoglobin content) accounts for much of the variation in cetacean diving performance (Noren and Williams 2000).

Our results also support those of Worthy and Hickie, using a data set that, for taxonomic reasons, is less likely than theirs to favor type 2 error. The positive relationship

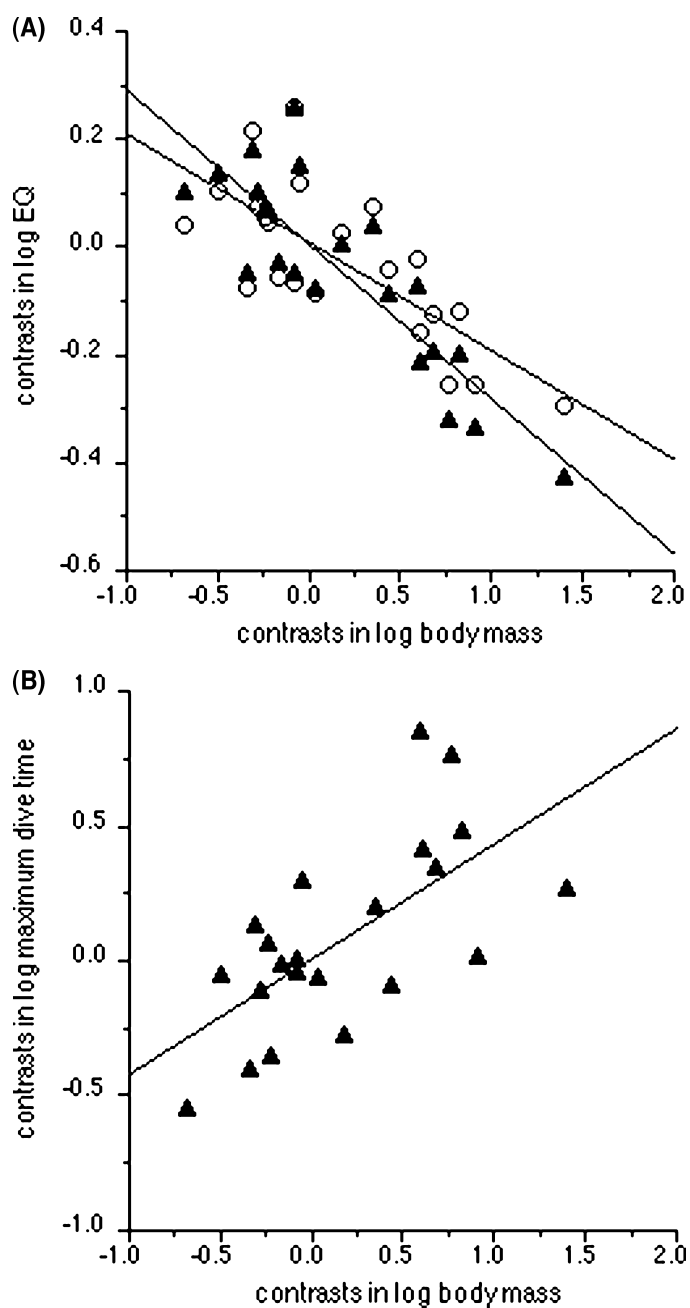


Figure 2. (A) Contrasts in EQ based on Jerison (s) and EQ based on Martin (1981) *vs.* contrasts in log body weight for the present sample. (B) Contrasts in log maximum dive duration *vs.* contrasts in log body weight for the present sample.

between body size and dive time in extant cetaceans is not due to common ancestry and remains highly significant when we use phylogenetically independent contrasts.

More generally, our results suggest that some estimates of encephalization in cetaceans can lead to type 1 statistical error (finding a correlation between brain size and diving when there is in fact none) because they are confounded with body size. In the case of brain/body ratios, the problem stems from the well-known overestimation of the small-bodied end of the distribution because the slope of the relationship is smaller than 1. In the case of EQ, whether it is calculated from Jerison's equation or Martin's and whether or not log transformations normalize its inherent skewness, the problem is caused by the difference between regression slopes calculated over higher *vs.* lower taxonomic levels. This problem, pointed out by Martin and Harvey (1984), causes a body size confound when values estimated from a higher taxonomic level are used to test a prediction at a lower taxonomic level. For example, the EQ of a dolphin is routinely expressed as the ratio of its observed absolute brain size divided by that expected for the average mammal of a dolphin body weight, as determined by the best fit log-log regression line for all mammals. However, because the slope of the brain-body regression for cetaceans is lower than that of all mammals calculated together (as are all slopes calculated within Orders), EQ values will, by definition, be correlated with body size.

Different ways of calculating relative brain size are also known to affect other tests of brain evolution, particularly in primates. For example, Deaner *et al.* (2000) have shown that the relationship between social group size and relative neocortex size depends on the method used to calculate the latter. Reader and Laland (2002) obtained significant correlations between neocortex size and rates of innovation, social learning and tool use only when the neocortex is expressed in terms of absolute volume or executive brain ratio (neocortex + striatum/brainstem), but not as a residual from a prior regression against brainstem size as an allometric control. *A priori* justification is sometimes made for choosing one method over another (*e.g.*, Byrne and Corp 2004), but there is at present no strong independent theory for choosing a specific technique. Until there is, the most prudent solution to testing ideas such as the "dive constraint hypothesis" is to do as in the present study, employ several techniques, identify possible confounding variables, and favor robust conclusions that are reproducible using different methods. When this approach was used in the present study we were able to conclude that brain size is not limited by diving duration in cetaceans and we were able to make that conclusion more confidently than ever before.

ACKNOWLEDGMENTS

The authors wish to thank Robin Baird for assistance on obtaining and verifying many of the dive durations used in the present study. We also wish to thank Jim Mead and Charles Potter, Marine Mammal Program, The Smithsonian Institution, for access to their collection of extant cetaceans.

LITERATURE CITED

- ARMSTRONG, E. 1983. Relative brain size and metabolism in mammals. *Science* 200:1302–1304.
- BAIRD, R. W., AND M. B. HANSON. 1998. A preliminary analysis of the diving behavior of Dalls porpoise in the transboundary waters of British Columbia and Washington. Pages

- 99–110 in Marine Mammal Protection Act and Endangered Species Act Implementation Program 1997. AFSC Processed Report 98-10.
- BAIRD, R. W., D. J. MCSWEENEY, A. D. LIGON AND D. L. WEBSTER. 2004. Tagging feasibility and diving of Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) in Hawai'i. Report prepared under Order No. AB133F-03-SE-0986 to the Hawai'i Wildlife Fund, Volcano, HI, from the Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, CA.
- BAIRD, R. W., M. B. HANSON AND L. M. DILL. 2005. Factors influencing the diving behaviour of fish-eating killer whales: Sex differences and diel and interannual variation in diving rates. *Canadian Journal of Zoology* 83:257–267.
- BARLOW, J., K. FORNEY, A. VON SAUNDER AND J. URBAN-RAMIREZ. 1997. A report of cetacean acoustic detection and dive interval studies (CADDIS) conducted in the southern Gulf of California, 1995. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service, Southwest Fisheries Science Center La Jolla, CA.
- BLACK, N. A. 1994. Behavior and ecology of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in Monterey Bay, California. M.S. thesis, San Francisco State University, San Francisco, CA. 133 pp.
- BREESE, D., AND B. R. TERSHY. 1993. Relative abundance of Cetacea in the Canal de Ballenas, Gulf of California. *Marine Mammal Science* 9:319–324.
- BYRNE, R. W., AND N. CORP. 2004. Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London* 271:1693–1699.
- CASSENS, I., S. VICARIO, V. H. WADDELL, H. BALCHOWSKY, D. VAN BELLE, W. DING, C. FAN, R. S. LAI MOHAN, P. C. SIMOES-LOPES, R. BASTIDA, A. MEYER, M. J. STANHOPE AND M. C. MILINKOVITCH. 2000. Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages. *Proceedings of the National Academy of Sciences, USA* 97:11343–11347.
- CASTELLINI, M. A., AND G. N. SOMERO. 1981. Buffering capacity of vertebrate muscle: Correlations with potentials for anaerobic function. *Journal of Comparative Physiology B* 143:191–198.
- CLARKE, M. R. 1986. Cephalopods in the diet of odontocetes. Pages 281–321 in M. M. Bryden and R. Harrison, eds. *Research on dolphins*. Clarendon Press, Oxford, UK.
- ROLL, D. A., A. ACEVEDO-GUTIERREZ, B. R. TERSHY AND J. URBAN-RAMIREZ. 2001. The diving behavior of blue and fin whales: Is dive duration shorter than expected based on oxygen stores? *Comparative Biochemistry and Physiology A-Molecular Integrative Physiology* 129:797–809.
- DEANER, R. O., C. L. NUNN AND C. P. VAN SCHAİK. 2000. Comparative tests of primate cognition: Different scaling methods produce different results. *Brain, Behavior and Evolution* 55:44–52.
- DOLPHIN, W. F. 1987. Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. *Canadian Journal of Zoology* 65:83–90.
- DUECK, L. 1989. The abundance of the narwhal (*Monodon monoceros* L.) in Admiralty Inlet, Northwest Territories, Canada, and implications of behavior for survey estimates. M.S. thesis, University of Manitoba, Winnipeg, Manitoba. viii + 81pp.
- EDWARDS, H. H., AND G. D. SCHNELL. 2001. Body length, swimming speed, dive duration, and coloration of the dolphin *Sotalia fluviatilis* (Tucuxi) in Nicaragua. *Caribbean Journal of Science* 37:271–272.
- EVANS, W. E. 1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* in the Northeastern Pacific. Ph.D. dissertation. University of California, Los Angeles, CA. 145 pp.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- FERREN, H., AND R. ELSNER. 1979. Diving physiology of the ringed seal: Adaptations and implications. *Proceedings of the Alaska Science Conference* 29:379–387.

- FROST, K. J., L. F. LOWRY AND R. R. NELSON. 1985. Radiotagging studies of Belukha whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. *Marine Mammal Science* 1:191–202.
- GARLAND, T., JR., A. W. DICKERMAN, C. M. JANIS AND J. A. JONES. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* 42:265–292.
- HAMILTON, H., S. CABALLERO, A. G. COLLINS AND R. L. BROWNELL, JR. 2001. Evolution of river dolphins. *Proceedings of the Royal Society of London B* 268:549–556.
- HARVEY, P. H., AND P. M. BENNETT. 1983. Brain size, energetics, ecology, and life history patterns. *Nature* 306:314–315.
- HARVEY, P. H., AND M. PAGEL. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- HEIDE-JORGENSEN, M. P., AND R. DIETZ. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. *Canadian Journal of Zoology* 73:2120–2132.
- HOFMAN, M. A. 1983. Energy metabolism, brain size and longevity in mammals. *Quarterly Review of Biology* 58:496–512.
- JERISON, H. J. 1973. *Evolution of the brain and intelligence*. Academic Press, New York.
- KOOYMAN, G. L. 1989. *Diverse divers: Physiology and behaviour*. Springer-Verlag, Berlin.
- KOOYMAN, G. L., M. A. CASTELLINI, AND R. W. DAVIS. 1981. Physiology of diving in marine mammals. *Annual Review of Physiology* 43:343–356.
- LAGERQUIST, B. A., K. M. STAFFORD AND B. R. MATE. 2000. Dive characteristics of satellite-monitored blue whales (*Balaenoptera musculus*) off the central California coast. *Marine Mammal Science* 16:375–391.
- LAIDRE, K. L., M. P. HEIDE-JORGENSEN AND R. DIETZ. 2002. Diving behavior of narwhals (*Monodon monoceros*) at two coastal localities in the Canadian high arctic. *Canadian Journal of Zoology* 80:624–635.
- LOCKYER, C. 1977. Observations on diving behaviour of the sperm whale *Physeter catodon*. Pages 591–609 in M. Angel, ed. *A voyage of discovery*. Pergamon Press, New York, NY.
- LUSSEAU, D. 2003. Male and female bottlenose dolphins (*Tursiops* spp.) have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecological Progress Series* 257:267–274.
- MARINO, L. 1998. A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, Behavior and Evolution* 51:230–238.
- MARINO, L. 2002. Brain size evolution. Pages 158–162 in W. F. Perrin, B. Wursig and H. Thewissen, eds. *Encyclopedia of marine mammals*. Academic Press, San Diego.
- MARINO, L., D. MCSHEA AND M. D. UHEN. 2004. The origin and evolution of large brains in toothed whales. *The Anatomical Record* 281A:1247–1255.
- MARTIN, R. D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293:57–60.
- MARTINS, E. P. 2003. COMPARE, version 4.5. Computer programs for the statistical analysis of comparative data. Distributed by the author at <http://compare.bio.indiana.edu/>. Department of Biology, Indiana University, Bloomington, IN.
- MARTIN, R. D., AND P. H. HARVEY 1984. Brain size allometry: Ontogeny and phylogeny. Pages 147–173 in W. L. Jungers, ed. *Size and scaling in primate biology*. Plenum Press, London, UK.
- MARTIN, A. R., AND T. G. SMITH. 1992. Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. *Canadian Journal of Fisheries and Aquatic Science* 49:462–466.
- MARTIN, A. R., T. G. SMITH AND O. P. COX. 1993. Studying the behavior and movements of high Arctic belugas with satellite telemetry. *Symposium of the Zoological Society of London* 66:195–210.
- MARTIN, A. R., M. C. S. KINGSLEY AND M. A. RAMSAY. 1994. Diving behavior of narwhals (*Monodon monoceros*) on their summer grounds. *Canadian Journal of Zoology* 72:118–125.
- MARTIN, A. R., T. G. SMITH AND O. P. COX. 1998. Dive form and function in belugas *Delphinapterus leucas* of the eastern Canadian high arctic. *Polar Biology* 20:218–228.

- MATE, B., K. M. STAFFORD, R. NAWOJCHIK AND J. L. DUNN. 1994. Movements and dive behavior of a satellite-monitored Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in the Gulf of Maine. *Marine Mammal Science* 10:116–121.
- MIYAZAKI, N., AND W. F. PERRIN. 1994. Rough-toothed dolphin *Steno bredanensis* (Lesson, 1828). Pages 1–21 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Volume 5. The first book of dolphins. Academic Press, London, UK.
- MIYAZAKI, N., AND S. WADA. 1978. Observation of cetacean during whale marking cruise in the western tropical Pacific, 1976. *Scientific Reports of the Whales Research Institute, Tokyo* 30:179–195.
- NICOLAKAKIS, N., D. SOL AND L. LEFEBVRE. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour* 65:445–452.
- NOREN, S. R., AND T. M. WILLIAMS. 2000. Body size and skeletal muscle myoglobin of cetaceans: Adaptations for maximizing dive duration. *Comparative Biochemistry and Physiology Part A* 126:181–191.
- OTANI, S., Y. NAITO, A. KAWAMURA, M. KAWASAKI, S. NISHIWAKI AND A. KATO. 1998. Diving behavior and performance of harbor porpoises, *Phocoena phocoena*, in Funka Bay, Hokkaido, Japan. *Marine Mammal Science* 14:209–220.
- OTANI, S., Y. NAITO, A. KATO AND A. KAWAMURA. 2000. Diving behavior and swimming speed of a free-ranging harbor porpoise, *Phocoena phocoena*. *Marine Mammal Science* 16:811–814.
- PEIXUN, C. 1989. Bajji – *Lipotes vexillifer* Miller, 1918. Pages 25–43 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Volume 4. River dolphins and the larger toothed whales. Academic Press, London, UK.
- PELLETIER, C., AND F. X. PELLETIER. 1980. Rapport sur l'expédition delphinasi (Septembre 1977–Septembre 1978). *Annales de la Société des sciences naturelles de la Charente-Maritime* 6:647–679.
- PILLERI, G. 1970. Observations on the behaviour of *Platanista gangetica* in the Indus and Brahmaputra rivers. *Investigations on Cetacea* 2:27–60.
- READER, S. M., AND K. N. LALAND. 2002. Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, USA* 99:4436–4441.
- RIDGWAY, S. H. 1986. Diving by cetaceans. Pages 33–62 in A. O. Brunakk, J. W. Kanwisher and G. Sundness, eds. *Diving in animals and man*. The Royal Norwegian Society of Science and Letters, Trondheim, Norway.
- RIDGWAY, S. H., B. L. SCRONCE AND J. KANWISHER. 1969. Respiration and deep diving in the bottlenose porpoise. *Science* 166:1651–1654.
- ROBIN, E. D. 1973. The evolutionary advantages of being stupid. *Perspectives in Biology and Medicine* 16:369–379.
- SCOTT, M. D., A. A. HOHN, A. J. WESTGATE, J. R. NICOLAS, B. R. WHITAKER AND W. B. CAMPBELL. 2001. A note on the release and tracking of a rehabilitated pygmy sperm whale (*Kogia breviceps*). *Journal of Cetacean Research and Management* 3:87–94.
- SILVERMAN, H. B. 1979. Social organization and behaviour of the narwhal, *Monodon monoceros* L. in Lancaster Sound, Pond Inlet and Tremblay Sound, Northwest Territories. M.S. thesis, McGill University, Montreal, Quebec. xi + 147 pp.
- SKROVAN, R. C., T. M. WILLIAMS, P. S. BERRY, P. W. MOORE AND R. W. DAVIS. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*): II. Biomechanics and changes in buoyancy at depth. *Journal of Experimental Biology* 202:2749–2761.
- SOL, D., R. P. DUNCAN, T. M. BLACKBURN, P. CASSEY AND L. LEFEBVRE. 2005. Big brains, enhanced cognition and response of birds to novel environments. *Proceedings of the National Academy of Sciences, USA* 102: 5460–5465.
- VIBE, C. 1950. The marine mammals and the marine fauna in the Thule district (northwest Greenland) with observations on the ice conditions in 1939–1941. *Meddelelser om Gronland Bioscience* 124:1–42.

- WADDELL, V. G., M. C. MILINKOVITCH, M. BÉRUBÉ AND M. J. STANHOPE. 2000. Molecular phylogenetic examination of the Delphinoidea trichotomy: Congruent evidence from three nuclear loci indicates that porpoises (Phocoenidae) share a more recent common ancestry with white whales (Monodontidae) than they do with true dolphins (Delphinidae). *Molecular Phylogenetics and Evolution* 15:314–318.
- WATKINS, W. A., K. E. MOORE AND P. TYACK. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. *Cetology* 49:1–15.
- WATKINS, W. A., M. A. DAHER, K. M. FRISTRUP AND T. J. HOWALD. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. *Marine Mammal Science* 9:55–67.
- WESTGATE, A. J., A. J. READ, P. BERGGREN, H. N. KOOPMAN AND D. E. GASKIN. 1995. Diving behaviour of harbor porpoises, *Phocoena phocoena*. *Canadian Journal of Fisheries and Aquatic Science* 52:1064–1073.
- WILLIAMS, T. M. 1999. The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Philosophical Transactions of the Royal Society of London (B)* 354:193–201.
- WILLIAMS, T. M., J. E. HAUN AND W. A. FRIEDL. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*): I. Balancing the demands of exercise for energy conservation at depth. *Journal of Experimental Biology* 202:2739–2748.
- WORTHY, G. A., AND J. P. HICKIE. 1986. Relative brain size in marine mammals. *American Naturalist* 128:445–459.
- WURSIG, B., R. S. WELLS, K. S. NORRIS AND M. WURSIG. 1994. A spinner dolphin's day. Pages 65–102 in K. S. Norris, B. Würsig, R. S. Wells and M. Würsig, eds. *The Hawaiian spinner dolphin*. University of California Press, Berkeley, CA.

Received: 6 May 2005

Accepted: 27 October 2005