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PINNIPED BRAIN SIZES

Except for a few scattered estimates in the literature (see Table 1), brain sizes in most pinniped species are unknown. A knowledge of pinniped brain sizes is useful for two reasons. First, comparative and allometric studies require a good estimate of (body) size. Brain size is often a better estimator than other measures (Sacher and Staffeldt 1974, Gittleman 1986*b*) because it is less variable intraspecifically (Economos 1980, Pagel and Harvey 1988). Body weight in particular is highly variable in large species and changes with season, reproductive condition, and physical condition, among other factors (Gittleman 1986*b*). Estimates of size in pinnipeds are especially problematic. Body weight is highly variable due to blubber mass varying both seasonally and individually (McLaren 1993; see also Table 2). Estimates derived from body length tend to be more uniform,[1] but depend on how the measurement was taken, some-

[1] Unpublished data and personal communication from Michael M. Bryden, University of Sydney, Sydney, NSW 2006, Australia, July 1999.

Table 1. Absolute brain weights of adult pinnipeds taken from the literature or personally estimated from volumetric measures of cranial capacities of specimens at Natural History Museum, London. BW = body weight. Nomenclature follows Wozencraft (1993).

	Brain weight (in g)		
	Male	Female	Unknown sex
Otariidae			
Arctocephalus australis			
Present study	350.0	265.0	
Arctocephalus forsteri			
Present study	340.0	300.0	
Arctocephalus galapagoensis			
Present study	302.5	280.0	
Arctocephalus gazella			
Payne (1979)		320, 328 (= 0.95% of BW)	
Present study	360.0	320.0	
Arctocephalus philippii			
Present study	415.0		
Arctocephalus pusillus doriferus			
Present study	425.0	352.5	
Arctocephalus pusillus pusillus			
Present study	377.5	322.5	
Arctocephalus townsendi			
Arctocephalus tropicalis			
Present study	322.5	330.0	
Callorhinus ursinus			
Scheffer (1960)	367 (= 0.20% of BW)		
Sacher and Staffeldt (1974)	355.0		
Present study	335.0	302.5	
Eumetopias jubatus			
Present study	747.5	575.0	

Table 1. Continued

	Brain weight (in g)		
	Male	Female	Unknown sex
Neophoca cinerea			
Present study	440.0	337.5	
Otaria byronia			
Murie (1874)	346 (estimated)		
Vaz-Ferreira (1981)	550		
Present study	542.5	470.0	
Phocarctos hookeri			
Present study	417.5	370.0	
Zalophus californianus			
Sacher and Staffeldt (1974)		363.0	
King (1983)			375
Present study		405.0	360.0
Odobenidae			
Odobenus rosmarus			
Crile and Quiring (1940)	1,126		
Bryden (1972)			1.50% of BW
King (1983)			1,000
Present study	1,480.0	1,340.5	
Phocidae			
Cystophora cristata			
Present study	480.0	430.0	
Erignathus barbatus			
Crile and Quiring (1940)		460	
Present study			420.0
Present study			330.0
Halichoerus grypus			
Present study	342.5	272.5	

Table 1. Continued

	Brain weight (in g)		
	Male	Female	Unknown sex
Hydrurga leptonyx			
Present study	765.0	660.0	
Leptonychotes weddellii			
Robin (1973)			520
Sacher and Staffeldt (1974)			550.0
Kooyman (1975)			0.13% of BW
Ferren and Elsner (1979)			500
Present study	535.0	637.5	
Lobodon carcinophagus			
Bryden and Erickson (1976)	474, 500, 650	530, 480, 550	
Present study	615.0	557.5	
Mirounga angustirostris			
Stewart and Huber (1993)	700	640	
Mirounga leonina			
Bryden (1971)	0.35% of BW	0.36% of BW	
Bryden (1972)			0.12% of BW
Ling and Bryden (1992)	1,350	900	
Present study	1,512.5	897.5	
Monachus monachus			
Present study	480.0	480.0	
Monachus schauinslandi			
Present study	370.0		
Monachus tropicalis			
Present study	460.0		

Table 1. Continued

	Brain weight (in g)		
	Male	Female	Unknown sex
Ommatophoca rossii			
Bryden and Erickson (1976)	430, 350		
Present study	460.0	530.0	
Phoca caspica			
Leshko and Nikitenko (1975)			
Present study	165.0	160.0	
Phoca fasciata			
Present study	257.5	240.0	
Phoca groenlandica			
Sacher and Staffeldt (1974)			442.0
Leshko and Nikitenko (1975)			205.5
Kovacs and Lavigne (1985)			259, 297 (= 0.28%–0.29% of BW)
Present study	297.5	252.5	
Phoca hispida			
Crile and Quiring (1940)	251	255	
Present study	207.5	185.0	
Phoca largha			
Present study	257.5	250.0	
Phoca sibirica			
Present study	185.0	190.0	
Phoca vitulina			
Crile and Quiring (1940)	442		
Ferren and Elsner (1979)			260
King (1983)			275
Present study	282.5	265.0	

Table 2. Brain weights of adult pinnipeds relative to their body weights. Body weights were compiled from numerous literature sources (see Bininda-Emonds 1998 for references; also available from author on request). Summary statistics are not presented for brain weights because they are usually point estimates (see Table 1).

	Body weight (in kg)				Brain weight	
	Median	Range	SD	*n*	(in g)	(as % of body weight)
Otariidae						
Arctocephalus australis						
male	159.00	(135.00–180.00)	14.4	7	350.00	0.22
female	48.50	(45.00–60.00)	5.1	7	265.00	0.55
Arctocephalus forsteri						
male	164.38	(137.50–200.00)	27.4	4	340.00	0.21
female	55.00	(32.00–90.00)	22.6	7	300.00	0.55
Arctocephalus galapagoensis						
male	64.50	(63.70–70.00)	2.9	4	302.50	0.47
female	27.40	(27.00–39.50)	5.2	8	280.00	1.02
Arctocephalus gazella						
male	155.00	(117.00–200.00)	23.9	11	360.00	0.23
female	38.20	(33.00–50.00)	6.9	13	322.00	0.84
Arctocephalus philippii						
male	140.00	(140.00–159.00)	9.5	4	415.00	0.30
female	50.00	(40.00–50.00)	5.8	3		
Arctocephalus pusillus						
male	279.50	(36.00–447.20)	154.6	14	401.25	0.14
female	78.00	(50.00–122.00)	24.9	13	337.50	0.43
Arctocephalus townsendi						
male	145.00	(136.00–165.00)	12.9	4		
female	49.55	(45.00–136.36)	44.2	4		
Arctocephalus tropicalis						
male	152.50	(76.00–165.00)	32.6	8	322.50	0.21
female	50.00	(32.00–55.00)	9.4	9	330.00	0.66

Table 2. Continued

	Body weight (in kg)				Brain weight	
	Median	Range	SD	*n*	(in g)	(as % of body weight)
Callorhinus ursinus						
male	227.00	(95.60–300.00)	54.8	10	355.00	0.16
female	44.75	(34.50–63.64)	8.6	12	302.50	0.68
Eumetopias jubatus						
male	1,000.00	(900.00–1,120.00)	74.7	8	747.50	0.07
female	287.55	(270.00–350.00)	37.0	10	575.00	0.20
Neophoca cinerea						
male	300.00	(272.50–355.00)	34.6	4	440.00	0.15
female	78.55	(60.00–82.75)	8.3	6	337.50	0.43
Otaria byronia						
male	300.00	(237.10–350.00)	38.5	6	546.25	0.18
female	144.00	(126.75–160.00)	10.6	6	470.00	0.33
Phocarctos hookeri						
male	364.00	(318.00–400.00)	41.1	3	417.50	0.11
female	183.00	(136.00–230.00)	47.0	3	370.00	0.20
Zalophus californianus						
male	300.00	(200.00–392.50)	71.3	7	405.00	0.14
female	91.00	(75.00–110.60)	13.1	11	361.50	0.40
Odobenidae						
Odobenus rosmarus						
male	1,232.95	(900.00–1,900.00)	250.2	10	1,303.00	0.11
female	811.50	(560.00–1,000.00)	129.9	11	1,340.50	0.17

Table 2. Continued

	Body weight (in kg)				Brain weight	
	Median	Range	SD	*n*	(in g)	(as % of body weight)
Phocidae						
Cystophora cristata						
male	343.18	(272.00–410.00)	57.1	10	480.00	0.14
female	222.50	(160.00–350.00)	76.0	14	430.00	0.19
Erignathus barbatus						
male	265.00	(250.00–340.00)	42.4	4		
female	276.36	(250.00–340.00)	34.3	8	460.00	0.17
Halichoerus grypus						
male	233.00	(220.00–314.00)	31.6	7	342.50	0.15
female	155.00	(145.50–220.00)	22.4	9	272.50	0.18
Hydrurga leptonyx						
male	324.00	(270.00–655.00)	162.4	5	765.00	0.24
female	367.00	(367.00–450.00)	47.9	3	660.00	0.18
Leptonychotes weddellii						
male	360.00	(322.00–425.00)	39.9	8	501.50	0.14
female	376.00	(320.00–425.00)	33.5	11	563.15	0.15
Lobodon carcinophagus						
male	220.50	(204.67–225.00)	7.4	6	578.17	0.26
female	224.00	(220.00–242.00)	7.5	7	538.75	0.24
Mirounga angustirostris						
male	2,275.00	(2,250.00–2,700.00)	222.1	6	700.00	0.03
female	700.00	(363.00–900.00)	244.5	11	640.00	0.09
Mirounga leonina						
male	3,510.00	(900.00–4,000.00)	1,063.9	14	1,431.25	0.04
female	503.00	(346.00–900.00)	188.4	16	898.75	0.18

Table 2. Continued

	Body weight (in kg)				Brain weight	
	Median	Range	SD	*n*	(in g)	(as % of body weight)
Monachus monachus						
male	260.00	(220.00–375.00)	62.3	5	480.00	0.18
female	301.00	(182.25–375.00)	69.2	5	480.00	0.16
Monachus schauinslandi						
male	173.00	(172.40–250.00)	34.5	5	370.00	0.21
female	265.00	(172.00–273.00)	36.2	7		
Monachus tropicalis						
male				0	460.00	
female	160.00	(160.00)		1		
Ommatophoca rossii						
male	173.80	(170.00–205.00)	11.3	8	425.00	0.24
female	185.00	(166.67–205.00)	11.2	7	530.00	0.29
Phoca caspica						
male	70.50	(55.00–86.00)	21.9	2	165.00	0.23
female	55.00	(55.00)		1	160.00	0.29
Phoca fasciata						
male	94.80	(74.00–95.45)	10.2	5	257.50	0.27
female	80.36	(74.00–95.00)	8.4	6	240.00	0.30
Phoca groenlandica						
male	135.00	(105.62–140.00)	11.6	7	297.50	0.22
female	129.50	(118.18–140.00)	10.2	12	252.50	0.19
Phoca hispida						
male	71.67	(33.00–96.60)	20.5	13	229.25	0.32
female	66.50	(39.74–92.90)	15.6	16	220.00	0.33

Table 2. Continued

	Body weight (in kg)				Brain weight	
	Median	Range	SD	*n*	(in g)	(as % of body weight)
Phoca largha						
male	97.00	(90.00–129.00)	16.0	5	257.50	0.27
female	86.00	(65.00–104.55)	13.5	7	250.00	0.29
Phoca sibirica						
male	89.50	(85.00–94.00)	6.4	2	185.00	0.21
female	89.50	(85.00–94.00)	6.4	2	190.00	0.21
Phoca vitulina						
male	97.13	(87.00–154.00)	26.4	14	362.25	0.37
female	77.50	(56.70–148.00)	25.2	19	265.00	0.34

thing for which there is no clear consensus for pinnipeds (American Society of Mammalogists 1967, McLaren 1993).

Second, there has been disagreement about the size of pinniped brains compared to other mammals. Anatomical studies report relatively larger brains (as measured by various brain indices) in the few pinniped species examined (Wirz 1950, Stephan 1972). However, more recent theoretical papers have argued that pinnipeds, and aquatic mammals in general, should possess relatively smaller brains because the high metabolic demands of neural tissue conflict with the need to conserve oxygen while submerged (Robin 1973, Hofman 1983), or because large animals have proportionately smaller brains, and diving species are large to maximize oxygen-storage capabilities (Worthy and Hickie 1986). Finally, an empirical study based on the limited information available concluded that there was no difference in relative brain size between aquatic and non-aquatic mammals (Worthy and Hickie 1986). The conflicting conclusions from these studies in part reflect the limited information available and should be regarded as tenuous.

To provide an initial estimate of brain size for most pinniped species (Table 1), I measured the cranial capacity of specimens (generally one male, one female) housed at the Natural History Museum, London, following the protocol of Gittleman (1986*a*). 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. The generally close agreement in Table 1 between values derived using this technique and the literature values based on more direct techniques indicates that indirect volumetric measures are reasonable estimates of brain size (see also Radinsky 1967, Jerison 1973).

Although the sample sizes are admittedly small (and often point estimates), I present average brain weights for each species (based on both my measurements and literature estimates) together with brain sizes as a percentage of body weight in Table 2. Relative brain size ranges from 0.03% of body weight in male southern elephant seals (*Mirounga leonina*) to 1.02% of body weight in female Galapagos fur seals (*Arctocephalus galapagoensis*). It can be quickly seen that relative brain size tends to be smaller in heavier species. This trend also holds within strongly sexually dimorphic species (*i.e.*, the smaller females have relatively larger brains). This suggests that brain size in pinnipeds is bounded within relatively narrow limits, possibly due to functional constraints on skull size.

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A DESIGN FOR A TWO-DIMENSIONAL BOAT-BOUND HYDROPHONE ARRAY FOR STUDYING HARBOR SEALS, *PHOCA VITULINA*

Hydrophone arrays have many applications for studying marine mammal acoustic behavior (Watkins and Wartzok 1985, Clark *et al.* 1986, Spiesberger and Fristrup 1990), but the design of these arrays is frequently constrained by the site and equipment available, as well as by the distribution and behavior of animals. For this study we built an array to determine the spatial distribution of male harbor seals making low-frequency vocalizations (mean of 665 Hz) during the breeding season (Van Parijs *et al.* 1997). Our aim was to use male harbor vocalizations to map distribution at sea (Van Parijs *et al.*, in press *a*). Male harbor seals perform vocal and dive displays at display sites for male/male competition and/or to attract females (Hanggi and Schusterman 1994, Bjørge *et al.* 1995, Van Parijs *et al.* 1997). The infrequent vocalizations of males (Van Parijs *et al.* 1997; Van Parijs *et al.*, in press *b*) made the use of a directional hydrophone impractical.

The wide distribution of male display areas (Van Parijs *et al.* 1997; Van