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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 1986b) 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 1986b); 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¹ Unpublished data and personal communication from Michael M. Bryden, University of Sydney, Sydney, NSW 2006, Australia, July 1999.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			
<i>Arctocephalus australis</i>			
Present study	350.0	265.0	
<i>Arctocephalus forsteri</i>			
Present study	340.0	300.0	
<i>Arctocephalus galapagoensis</i>			
Present study	302.5	280.0	
<i>Arctocephalus gazella</i>			
Payne (1979)		320, 328 (= 0.95% of BW)	
Present study	360.0	320.0	
<i>Arctocephalus philippii</i>			
Present study	415.0		
<i>Arctocephalus pusillus doriferus</i>			
Present study	425.0	352.5	
<i>Arctocephalus pusillus pusillus</i>			
Present study	377.5	322.5	
<i>Arctocephalus townsendi</i>			
<i>Arctocephalus tropicalis</i>			
Present study	322.5	330.0	
<i>Callorhinus ursinus</i>			
Scheffer (1960)	367 (= 0.20% of BW)		
Sacher and Staffeldt (1974)	355.0		
Present study	335.0	302.5	
<i>Eumetopias jubatus</i>			
Present study	747.5	575.0	

Table 1. Continued

	Brain weight (in g)		
	Male	Female	Unknown sex
<i>Neophoca cinerea</i>			
Present study	440.0	337.5	
<i>Otaria byronia</i>			
Murie (1874)	346 (estimated)		
Vaz-Ferreira (1981)	550		
Present study	542.5	470.0	
<i>Phocartos bookeri</i>			
Present study	417.5	370.0	
<i>Zalophus californianus</i>			
Sacher and Staffeldt (1974)		363.0	
King (1983)			375
Present study		405.0	360.0
Odobenidae			
<i>Odobenus rosmarus</i>			
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			
<i>Cystophora cristata</i>			
Present study	480.0	430.0	
<i>Erignathus barbatus</i>			
Crile and Quiring (1940)		460	
Present study			420.0
Present study			330.0
<i>Halichoerus grypus</i>			
Present study	342.5	272.5	

Table 1. Continued

	Brain weight (in g)		
	Male	Female	Unknown sex
<i>Hydrurga leptonyx</i>			
Present study	765.0	660.0	
<i>Leptonychotes weddellii</i>			
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	
<i>Lobodon carcinophagus</i>			
Bryden and Erickson (1976)	474, 500, 650	530, 480, 550	
Present study	615.0	557.5	
<i>Mirounga angustirostris</i>			
Stewart and Huber (1993)	700	640	
<i>Mirounga leonina</i>			
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	
<i>Monachus monachus</i>			
Present study	480.0	480.0	
<i>Monachus schauinslandi</i>			
Present study	370.0		
<i>Monachus tropicalis</i>			
Present study	460.0		

Table 1. Continued

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

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	<i>n</i>	(in g)	(as % of body weight)
Otariidae						
<i>Arctocephalus australis</i>						
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
<i>Arctocephalus forsteri</i>						
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
<i>Arctocephalus galapagoensis</i>						
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
<i>Arctocephalus gazella</i>						
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
<i>Arctocephalus philippii</i>						
male	140.00	(140.00–159.00)	9.5	4	415.00	0.30
female	50.00	(40.00–50.00)	5.8	3		
<i>Arctocephalus pusillus</i>						
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
<i>Arctocephalus townsendi</i>						
male	145.00	(136.00–165.00)	12.9	4		
female	49.55	(45.00–136.36)	44.2	4		
<i>Arctocephalus tropicalis</i>						
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	<i>n</i>	(in g)	(as % of body weight)
<i>Callorhinus ursinus</i>						
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
<i>Eumetopias jubatus</i>						
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
<i>Neophoca cinerea</i>						
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
<i>Otaria byronia</i>						
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
<i>Phocarctos hookeri</i>						
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
<i>Zalophus californianus</i>						
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						
<i>Odobenus rosmarus</i>						
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	<i>n</i>	(in g)	(as % of body weight)
<i>Phocidae</i>						
<i>Cystophora cristata</i>						
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
<i>Erignathus barbatus</i>						
male	265.00	(250.00–340.00)	42.4	4		
female	276.36	(250.00–340.00)	34.3	8	460.00	0.17
<i>Halichoerus grypus</i>						
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
<i>Hydrurga leptonyx</i>						
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
<i>Leptonychotes weddellii</i>						
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
<i>Lobodon carcinophagus</i>						
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
<i>Mirounga angustirostris</i>						
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
<i>Mirounga leonina</i>						
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	<i>n</i>	(in g)	(as % of body weight)
<i>Monachus monachus</i>						
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
<i>Monachus schauinslandi</i>						
male	173.00	(172.40–250.00)	34.5	5	370.00	0.21
female	265.00	(172.00–273.00)	36.2	7		
<i>Monachus tropicalis</i>						
male				0	460.00	
female	160.00	(160.00)		1		
<i>Ommatophoca rossii</i>						
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
<i>Phoca caspica</i>						
male	70.50	(55.00–86.00)	21.9	2	165.00	0.23
female	55.00	(55.00)		1	160.00	0.29
<i>Phoca fasciata</i>						
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
<i>Phoca groenlandica</i>						
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
<i>Phoca hispida</i>						
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	<i>n</i>	(in g)	(as % of body weight)
<i>Phoca largha</i>						
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
<i>Phoca sibirica</i>						
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
<i>Phoca vitulina</i>						
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 (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. 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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