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PART 3

**GENERAL BIOLOGY**  
**SEXUAL DIMORPHISM**

## **Sexual dimorphism in the adult Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): standard body length and skull morphology**

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### **ABSTRACT**

We examine differences in body size and skull morphology ( $n = 31$  variables) of male and female Cape fur seals, *Arctocephalus pusillus pusillus* ( $n = 55$ ), from the coast of southern Africa. Males were found to be significantly larger than females in standard body length, with K-means cluster analysis successfully identifying 2 relatively homogeneous groups. Principal component analysis (covariance matrix) showed that the underlying data structure for male and female skull variables was different, and that most of this variation was expressed in overall skull size rather than shape. Males were significantly larger than females in 30 of the 31 skull variables. Breadth of brain case was the same for the genders. Relative to condylobasal length, males were significantly larger than females in 13 of the 30 skull variables. These were gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus. In males, these variables were associated with the acquisition and defence of territory (e.g., large head size and mass; increased structural strength of the skull; increased bite capacity). Females were found to be significantly larger than males, relative to condylobasal length, with respect to breadth of brain case and length of upper postcanine row.

**Key words:** Pinnipeds, Otariidae, polygyny, sexual dimorphism, skull morphometrics, standard body length

## INTRODUCTION

Sexual dimorphism is a form of non-geographic variation that can be generated in a species by the process of sexual selection (Schnell, Douglas & Hough, 1995). Highly polygynous species such as fur seals, sea lions, elephant seals, red deer and terrestrial monkeys, generally exhibit a high degree of sexual dimorphism (Schultz, 1969; Ralls, 1977; Clutton-Brock *et al.*, 1982). Differences in reproductive success among males of the species are large, and competition for access to females intense. Therefore, selection pressure appears to favour the development of traits that enhance male fighting ability, including body size, weaponry and skin thickness (Bartholomew, 1970; Selander, 1972; Le Boeuf, 1974; Hausfater, 1975; Alexander *et al.*, 1979; McCann, 1981; Clutton-Brock *et al.*, 1982).

Southern fur seals (*Arctocephalus* spp.) are among the most territorial of animals (Bonner, 1981). They are gregarious, polygynous and sexually dimorphic in body size. Male fur seals generally arrive at the rookeries around November to establish territories. Pregnant females arrive soon after. Once females are present in the male's territory, males guard females until they come into oestrus post-partum. Territorial size varies depending on the extent of competition. Females give birth within 1 week of coming ashore and then mate with the nearest male during the short breeding (pupping/mating) season. Males seldom leave the territory until the breeding season is over (Bonner, 1981). After mating, the territorial system gradually breaks down and males return to sea to replenish their physiological reserves. Males do not care for their young.

When establishing territories, male fur seals threaten each other with stereotyped vocal and visual displays (Bonner, 1968; Stirling, 1970; Miller, 1974). Fights may develop, occasionally resulting in severe injury or death (Rand, 1967; Trillmich, 1984; Campagna & Le Boeuf, 1988). In combat, fur seals usually bite their opponent; jerking or twisting upwards, ripping with their lower canines. In the larger species of fur seals, combat is usually a 'chest to chest pushing contest', with opponents gripping at each other's neck or foreflippers in an attempt to gain positional advantages (Rand, 1967; Miller, 1991).

Adult male fur seals are claimed to be about 3 times heavier and 1/3rd longer than adult females (Stirling, 1983; Boness, 1991). Large body size is advantageous in competitive interactions and enables breeding bulls to remain resident on territory for long periods of time without feeding (Rand, 1967; Miller, 1975; Payne, 1979; Stirling, 1983). Large males have a greater chance of holding territory, hence a greater opportunity to mate with more females. Strong fore-quarters, enlarged jaw and neck muscles, robust canines, increased structural strength of the skull, and long, thick neck hair (protective mane/wig), also appear to be potentially advantageous in the

acquisition and maintenance of territory; quantitative information on these features, however, is lacking (Miller, 1991).

Here we examine morphological differences between skulls ( $n = 31$  variables) of male and female Cape fur seals *Arctocephalus pusillus pusillus* ( $n = 55$  animals), from the coast of southern Africa. Sexual dimorphism in body size is also investigated.

## MATERIALS AND METHODS

### Collection of specimens

Male Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995 (Stewardson *et al.*, 200Ya), and accessioned at the Port Elizabeth Museum (PEM). Routine necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). From this collection, skulls from 44 adults were selected for examination. Animals were aged from incremental lines observed in the dentine of upper canines (Stewardson *et al.*, 200Yb).

The sample was supplemented with measurements from 11 known-aged adults (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town.

Of the 55 animals examined in this study, 37 were adult males and 18 were adult females. All animals had reached full reproductive capacity, i.e., males  $\geq 8$  y (Stewardson *et al.*, 200Ya, 200Yb; Stewardson & Prvan, 200X) and females  $\geq 3$  y (J.H.M. David, pers. comm.). When age was not known, males  $\geq 170$  cm (Stewardson *et al.*, 200Yb) and females  $\geq 135$  cm (J.H.M. David, pers. comm.) were used in analysis. Animals  $> 13$  y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth. Estimated longevity is *c.* 20 y.

### Skull variables

A total of 32 skull measurements was recorded (Table 7.1). However, 1 of these variables, height of sagittal crest, was not examined statistically because there were few measurements for females. Thus, statistical analysis was conducted on 31 of the 32 variables. Skull preparation and measurement procedures follow Stewardson *et al.*, (200Ya).

### Statistical analyses

Four methods of analyses were employed. Firstly, the two sample t-tests (assuming equal variance) were used to test the hypothesis that the mean value of a

skull variable was the same for males and females against an appropriate alternative hypothesis ( $H_0: \mu_{\text{males}} = \mu_{\text{females}}$ ;  $H_1: \mu_{\text{males}} > \mu_{\text{females}}$ ;  $H_1: \mu_{\text{females}} > \mu_{\text{males}}$ ). Since more than 1 skull variable were being considered, the Bonferroni correction was used – the experimentwise error rate was divided by the total number of tests performed.

Secondly, K-means, a non-hierarchical cluster analysis, was used to classify each variable into 1 of 2 groups. Variables from both sexes were pooled so that initially the 2 groups (male and female) were unknown. Clustering was based on the 'similarity' of each variable. All variables were standardised and assigned to the cluster whose centroid (mean) was 'closest' using Euclidean distance (Johnson & Wichern, 1992).

Thirdly, plots of  $\log_e$  of each skull variable against  $\log_e$  of standard body length (SBL) for the genders were examined. 'Robust' regression (Huber M-Regression) was used to fit straight lines ( $\log y = \log a + b \log x$ ) to the transformed data.

Finally, principal component analysis (PCA) was used. PCA is useful in identifying the most important sources of variation in anatomical measurements for various species (Jolliffe, 1986). Usually the first PC has all positive coefficients and according to Jolliffe (1986) this reflects overall 'size' of the individuals. The other PCs usually contrast some measurements with others and according to Jolliffe (1986) this can often be interpreted as reflecting certain aspects of 'shape' which are important to the species.

Skull measurements were recorded in the same units therefore a covariance matrix was used to calculate PCs (however this gives weight to larger, and hence possibly more variable measurements because the variables are not all treated on equal footing). Genders were examined separately because the grouped PCA was quite different in most cases to either the separate male PCA or female PCA.

PCA and two sample t-tests were calculated in Minitab (Minitab Inc., State College, 1999, 12.23). K-means cluster analyses<sup>1</sup> for skull variables and SBL were calculated in Minitab (Minitab Inc., State College, 1999, 12.23) and in SPSS (SPSS Inc., Chicago, Illinois, 1989–1999, 9.0.1), respectively. The regressions were fitted in S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

## RESULTS

### Standard body length

For available values, standard body length ranged from 157–201 cm in males ( $n = 33^2$ ) and 135–179 cm

in females ( $n = 18$ ). Mean lengths were  $182.9 \pm 2.3$  and  $149.1 \pm 2.5$ , respectively. The two sample t-tests indicated that adult males were significantly larger than adult females (Table 7.1). The ratio of mean female SBL to mean male SBL was 1 : 1.23.

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 7.2). Of the 18 females, 17 (94%) were correctly classified. Of the 33 males, 28 (85%) were correctly classified.

### Skull variables

#### *Absolute skull size: two sample t-tests*

The two sample t-tests indicated that 30 of the 31 mean skull variables were significantly larger in males than in females, i.e., we accept  $H_1: \mu_{\text{male}} > \mu_{\text{female}}$  (Table 7.1, Fig. 7.1). Mean value of breadth of brain case was the same for the genders (Table 7.1).

The coefficient of variation was larger in males, with the following exceptions: least interorbital constriction, breadth of brain case, gnathion to anterior of foramen infraorbital and length of mandibular tooth row (Table 7.1).

Height of sagittal crest was not examined statistically, but was generally larger in most adult males.

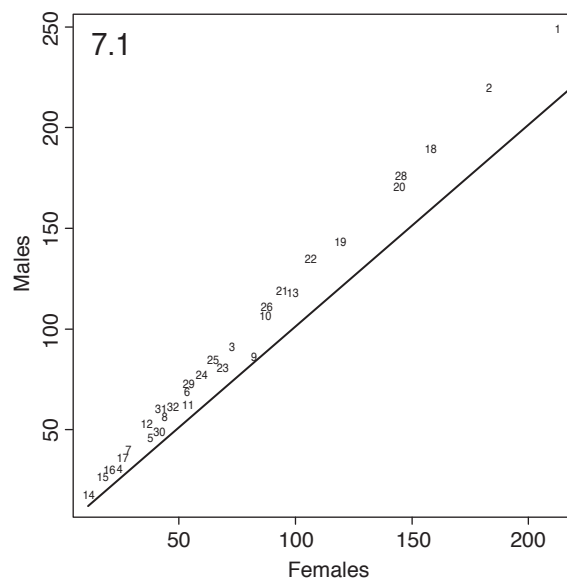


Fig. 7.1 Mean values of 31 skull variables for male and female Cape fur seals.

Numbers correspond to skull variables listed in Table 7.1. Numbers above the line, males > females; numbers on the line, males = females; numbers below the line, females > males.

<sup>1</sup> Minitab could only perform K-means cluster analysis if there was  $\geq 2$  variables, therefore SBL (a single variable) was analysed in SPSS.

<sup>2</sup> SBL was not recorded for 4 of the 37 males (i.e.,  $n = 33$ )

Table 7.1 Summary statistics (mean, S.E., C.V.) for skull measurements (mm) and standard body lengths (cm) from male and female Cape fur seals, and comparison between the mean of the two sexes (two sample t-test). Skull measurements relative to condylobasal length are given in brackets.

Skull variables	Male			Female			Two sample t-test			Size difference		
	mean	S.E.	C.V.	n	mean	S.E.	C.V.	n	T		P	DF
<b>Dorsal</b>												
D1 Condylobasal length	247.1 (0.36)	2.1 (0.003)	5.2 (4.72)	37	212.2 (0.34)	1.8 (0.003)	3.5 (4.26)	18	12.7 (3.96)	0.000 (0.000)	50 (39)	M > F** (M > F**)
D2 Gnathion to middle of occipital crest	217.7 (0.88)	2.8 (0.005)	7.6 (3.43)	35	182.9 (0.86)	1.4 (0.004)	3.2 (2.07)	18	11.5 (2.64)	0.000 (0.011)	50 (49)	M > F** (M = F)
D3 Gnathion to posterior end of nasals	88.9 (0.36)	1.2 (0.003)	8.4 (4.72)	36	72.5 (0.34)	1.0 (0.003)	5.8 (4.26)	18	10.3 (3.96)	0.000 (0.000)	51 (39)	M > F** (M > F**)
D4 Greatest width of anterior nares	28.6 (0.12)	0.5 (0.001)	9.4 (6.98)	36	24.0 (0.11)	0.5 (0.002)	7.8 (6.87)	15	6.9 (0.96)	0.000 (0.345)	37 (27)	M > F** (M = F)
D5 Greatest length of nasals	44.0 (0.18)	0.9 (0.003)	11.7 (8.70)	35	37.5 (0.18)	0.7 (0.003)	7.4 (6.29)	17	5.9 (0.03)	0.000 (0.978)	49 (42)	M > F** (M = F)
D6 Breadth at preorbital processes	68.1 (0.28)	0.9 (0.002)	7.4 (4.61)	33	53.3 (0.25)	1.0 (0.003)	6.9 (5.15)	14	11.2 (5.95)	0.000 (0.000)	33 (24)	M > F** (M > F**)
D7 Least interorbital constriction	37.7 (0.15)	0.5 (0.002)	7.8 (7.12)	32	28.0 (0.13)	0.9 (0.003)	12.4 (10.45)	16	19.7 (5.52)	0.000 (0.000)	26 (24)	M > F** (M > F**)
D8 Breadth at supraorbital processes	56.8 (0.23)	0.9 (0.003)	9.3 (8.35)	33	43.9 (0.21)	1.0 (0.004)	8.9 (7.75)	16	9.6 (4.60)	0.000 (0.000)	38 (35)	M > F** (M > F**)
D9 Breadth of brain case	84.2 (0.34)	0.6 (0.003)	4.5 (5.63)	36	82.0 (0.39)	1.1 (0.005)	5.5 (5.09)	18	1.8 (7.87)	0.089 (0.000)	29 (33)	M = F (F > M**)
<b>Palatal</b>												
P10 Palatal notch to incisors	105.0 (0.42)	1.4 (0.004)	8.1 (5.12)	37	88.0 (0.41)	1.6 (0.007)	7.9 (6.75)	18	7.9 (1.30)	0.000 (0.204)	40 (27)	M > F** (M = F)
P11 Length of upper postcanine row	60.4 (0.24)	0.7 (0.002)	7.4 (6.08)	37	54.9 (0.26)	0.6 (0.003)	4.7 (4.58)	18	5.8 (3.87)	0.000 (0.000)	51 (41)	M > F** (F > M**)
P12 Greatest bicanine breadth	50.9 (0.21)	0.9 (0.002)	10.1 (6.75)	37	37.0 (0.17)	0.8 (0.003)	9.5 (6.80)	18	11.7 (8.72)	0.000 (0.000)	47 (39)	M > F** (M > F**)
P13 Gnathion to posterior end of maxilla	116.4 (0.47)	1.2 (0.002)	6.4 (2.82)	36	99.0 (0.47)	0.9 (0.002)	3.8 (1.71)	17	11.4 (1.83)	0.000 (0.740)	50 (47)	M > F** (M = F)
P14 Breadth of zygomatic root of maxilla	15.7 (0.06)	0.3 (0.001)	13.3 (10.19)	37	12.2 (0.06)	0.3 (0.001)	11.0 (10.27)	18	7.6 (3.49)	0.000 (0.001)	48 (36)	M > F** (M = F)
P15 Breadth of palate at postcanine 1	25.7 (0.10)	0.6 (0.002)	13.4 (11.05)	33	18.7 (0.09)	0.5 (0.002)	12.3 (10.39)	18	8.7 (5.32)	0.000 (0.000)	46 (42)	M > F** (M > F**)
P16 Breadth of palate at postcanine 3	27.8 (0.11)	0.5 (0.002)	10.9 (8.74)	34	21.1 (0.10)	0.3 (0.002)	6.7 (6.45)	17	10.8 (5.37)	0.000 (0.000)	48 (45)	M > F** (M > F**)
P17 Breadth of palate at postcanine 5	33.8 (0.14)	0.5 (0.002)	9.7 (7.71)	36	26.8 (0.13)	0.5 (0.002)	8.0 (8.02)	18	9.4 (3.42)	0.000 (0.002)	48 (35)	M > F** (M = F)
P18 Gnathion to hind border of postgenoid process	187.5 (0.76)	1.9 (0.002)	6.1 (1.56)	35	159.0 (0.75)	1.5 (0.003)	4.0 (1.43)	18	11.6 (2.43)	0.000 (0.020)	50 (37)	M > F** (M = F)
P19 Bizygomatic breadth	141.4 (0.57)	1.7 (0.006)	7.4 (5.88)	37	120.1 (0.57)	1.8 (0.005)	6.5 (4.10)	18	8.5 (0.87)	0.000 (0.388)	44 (46)	M > F** (M = F)

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Skull variables	Male			Female			Two sample t-test			Size difference		
	mean	S.E.	C.V.	n	mean	S.E.	C.V.	n	T		P	DF
<b>Palatal</b>												
<b>P20</b> Basion to zygomatic root (anterior)	168.5 (0.68)	1.5 (0.002)	5.4 (1.70)	36	145.5 (0.69)	1.2 (0.003)	3.6 (1.62)	18	T <sub>11.8</sub> (1.61)	0.000 (0.117)	50 (35)	M > F** (M = F)
<b>P21</b> Calvarial breadth	116.7 (0.47)	1.1 (0.003)	5.5 (3.20)	35	95.2 (0.45)	1.0 (0.003)	4.5 (2.79)	18	T <sub>14.4</sub> (5.73)	0.000 (0.000)	50 (40)	M > F** (M > F**)
<b>P22</b> Mastoid breadth	132.6 (0.54)	1.7 (0.004)	7.6 (4.26)	35	107.5 (0.51)	1.4 (0.005)	5.7 (3.80)	18	T <sub>11.2</sub> (5.13)	0.000 (0.000)	49 (40)	M > F** (M > F**)
<b>P23</b> Basion to bend of pterygoid	79.0 (0.32)	0.6 (0.002)	4.5 (3.23)	35	69.4 (0.33)	0.7 (0.002)	4.1 (3.10)	18	T <sub>10.6</sub> (2.29)	0.000 (0.028)	41 (35)	M > F** (M = F)
<b>Lateral</b>												
<b>L24</b> Gnathion to foramen infraorbital	75.0 (0.30)	0.9 (0.001)	7.0 (3.00)	37	60.8 (0.29)	1.1 (0.004)	7.3 (5.49)	17	T <sub>10.3</sub> (4.06)	0.000 (0.0006)	36 (21)	M > F** (M > F*)
<b>L25</b> Gnathion to hind border of preorbital process	82.2 (0.33)	1.0 (0.002)	7.0 (2.87)	36	65.8 (0.31)	0.9 (0.003)	5.2 (3.36)	16	T <sub>12.8</sub> (6.77)	0.000 (0.000)	45 (26)	M > F** (M > F*)
<b>L26</b> Height of skull at bottom of mastoid	108.7 (0.44)	1.8 (0.005)	10.0 (6.54)	36	88.7 (0.41)	1.5 (0.004)	5.7 (3.59)	11	T <sub>8.5</sub> (3.79)	0.000 (0.0006)	37 (33)	M > F** (M > F**)
<b>L27<sup>a</sup></b> Height of sagittal crest	—	—	—	—	—	—	—	—	—	—	—	—
<b>Mandibular</b>												
<b>M28</b> Length of mandible	173.7 (0.70)	1.7 (0.002)	5.9 (2.09)	36	146.2 (0.69)	1.9 (0.005)	5.5 (2.75)	17	T <sub>10.6</sub> (2.20)	0.000 (0.038)	39 (25)	M > F** (M = F)
<b>M29</b> Length of mandibular tooth row	69.9 (0.29)	0.8 (0.002)	6.0 (4.49)	31	55.2 (0.26)	1.5 (0.007)	10.9 (11.19)	17	T <sub>10.0</sub> (3.70)	0.000 (0.001)	40 (26)	M > F** (M = F)
<b>M30</b> Length of lower postcanine row	47.1 (0.19)	0.4 (0.001)	5.7 (4.55)	35	42.5 (0.20)	0.5 (0.002)	5.0 (4.47)	16	T <sub>6.6</sub> (3.62)	0.000 (0.001)	35 (28)	M > F** (M = F)
<b>M31</b> Height of mandible at meatus	58.3 (0.24)	1.1 (0.003)	11.3 (7.97)	37	44.1 (0.21)	0.9 (0.003)	8.7 (6.64)	17	T <sub>10.0</sub> (6.10)	0.000 (0.000)	48 (41)	M > F** (M > F**)
<b>M32</b> Angularis to coronoideus	58.7 (0.24)	1.0 (0.003)	10.5 (6.70)	35	47.3 (0.22)	0.9 (0.003)	7.4 (6.01)	17	T <sub>8.4</sub> (3.22)	0.000 (0.0026)	48 (37)	M > F** (M = F)
<b>Standard body length</b>	182.9	2.3	7.2	33	149.1	2.5	7.1	18	T <sub>10.0</sub>	0.000	41	(M > F**)

<sup>a</sup> Height of sagittal crest (L27) was not examined statistically because there were few measurements for females. However, in large animals, males crest height was greater than female crest height.

T Normality assumption did not hold (data skewed); therefore the data was transformed using Box-Cox transformation (Myers, 1990).

n, number of animals.

\* Significant at the 5% level, with Bonferroni correction.

\*\* Significant at the 1% level, with Bonferroni correction.

DF were calculated for a two sample t-test assuming unequal variance.

Refer to Stewardson *et al.*, (2009a) for a full description of skull measurement procedures.

The canines were not measured, but were considerably broader in adult males.

### Relative skull size: two sample *t*-tests

When skull variables were analysed relative to condylobasal length (CBL), males were found to be significantly larger than females for 13 (43%) variables: gnathion to posterior end of nasals, breadth at pre-orbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus (Table 7.1, Fig. 7.2). Differences between the genders were highly significant, apart from gnathion to anterior of foramen infraorbital and height of skull at base of mastoid, which were significant at the 5% level (Table 7.1).

Breadth of brain case was the same in 'absolute size' for males and females, but 'relative to CBL' females were larger than males (Table 7.1). Length of upper postcanine row was larger in 'absolute size' in males, but 'relative to CBL' females were larger than males (Table 7.1).

The remaining 15 (50%) variables were equal for the genders (Table 7.1). Since males were larger than females in 'absolute size', this suggested that the 15 variables were proportionate to CBL regardless of sex, i.e., the ratio 'relative to CBL' was the same for the genders.

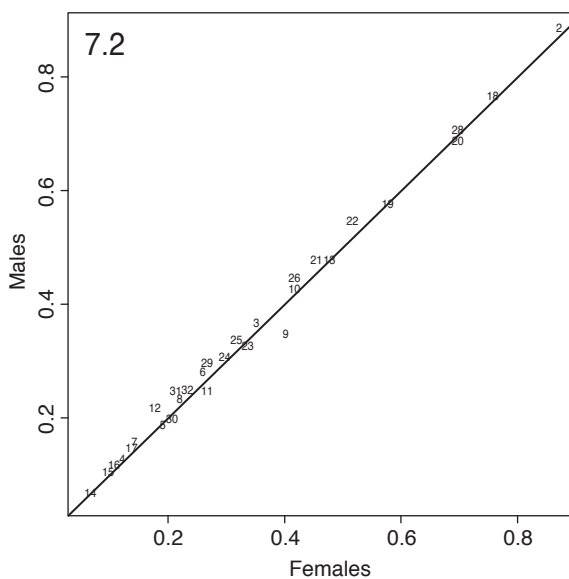


Fig. 7.2 Mean values of 30 skull variables, relative to condylobasal length, for male and female Cape fur seals.

Numbers correspond to skull variables listed in Table 7.1. Numbers above the line, males > females; numbers on the line, males = females; numbers below the line, females > males.

The coefficient of variation for values 'relative to CBL' was larger in males for about 1/3 rd of all variables (Table 7.1). Exceptions were breadth at pre-orbital processes, least interorbital constriction, palatal notch to incisors, breadth of zygomatic root of maxilla, breadth of palate at postcanine 5, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, length of mandible and length of mandibular tooth row. The coefficients of 2 of these variables (least interorbital constriction and length of mandibular tooth row) were considerably larger in females in both 'absolute size' and size 'relative to CBL'.

### *K*-means cluster analysis

*K*-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 7.2). Classification based on dorsal, palatal and mandibular observations was highly successful in recapturing the 2 groups. Classification based on lateral observations was less successful.

Apart from 1 mandibular variable, all females were correctly classified. The majority of males were correctly classified with the following exceptions – 1 dorsal, 2 palatal, 2 mandibular and 7 lateral variables were incorrectly classified as females (Table 7.2). Misclassification occurred in small males only.

### Linear regression

All transformed variables were regressed on  $\log_e$  SBL. Three variables which best depicted maximum discrimination between the sexes, using regression, are given in Fig. 7.1–7.3. These were CBL, greatest

Table 7.2 Classification of skull measurements using *K*-means clusters analysis

Skull variables	Cluster 1	Cluster 2	<i>n</i>
<b>*Dorsal</b>			
male	22 (96%)	1 (4%)	23
female	0	11 (100%)	11
<b>*Palatal</b>			
male	24 (92%)	2 (8%)	26
female	0	17 (100%)	17
<b>*Lateral</b>			
male	28 (80%)	7 (20%)	35
female	0	10 (100%)	17
<b>*Mandibular</b>			
male	25 (93%)	2 (7%)	27
female	1 (6%)	16 (94%)	17
<b>Standard body length</b>			
male	28 (85%)	5 (15%)	33
female	1 (6%)	17 (94%)	18

*n*, number of animals.

\* Standardised variables.

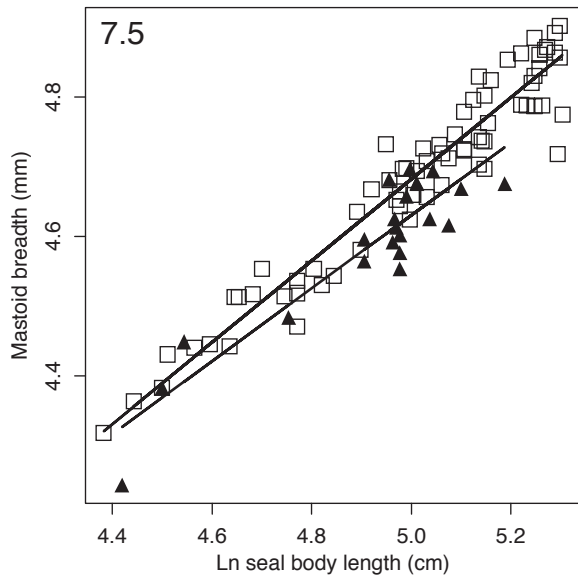
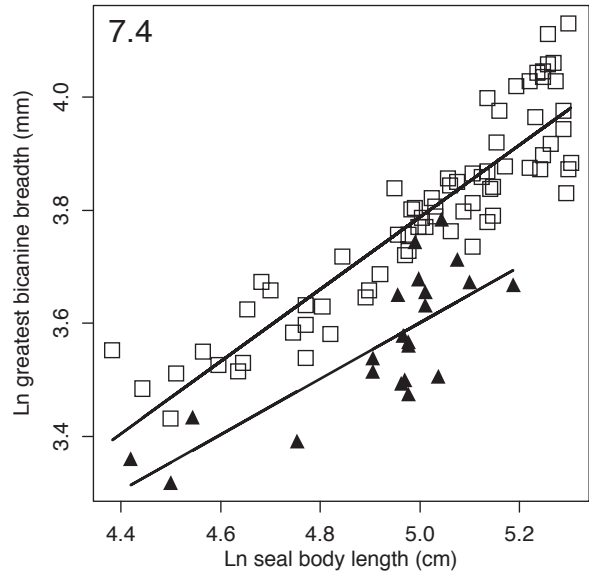
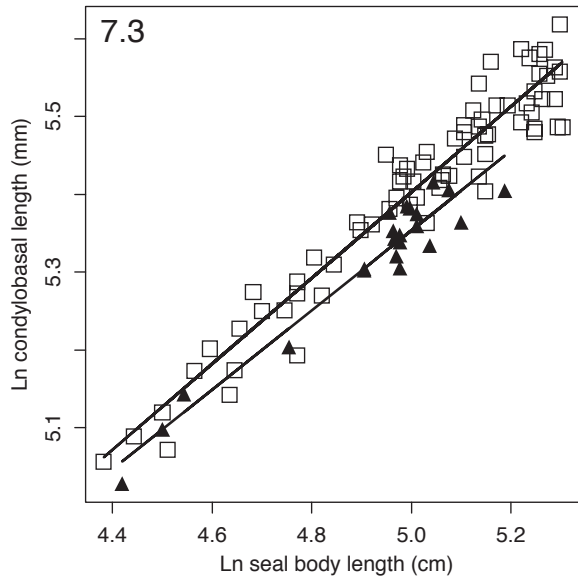


Fig. 7.3–7.5 Bivariate plot of: (3) log CBL (mm) on log SBL (cm); (4) log greatest bicanine breadth (mm) on log SBL (cm); (5) log mastoid breadth (mm) on log SBL (cm).

Squares, males. Solid triangles, females.

by each PC. The variances of corresponding PCs for the 2 genders do vary and interpretations are dissimilar for most pairs of PCs.

### Can you determine the gender of an isolated skull without measuring it?

It is possible to visually determine the gender of an isolated Cape fur seal skull, provided the skull is from an adult animal. However, visual identification based on morphology of the skull alone can be misleading, e.g., young adult males can be mistaken for older females. Therefore, before examining the skull, it is advisable to age the specimen first (i.e., count the GLGs in the upper canine).

bicanine breadth and mastoid breadth. These plots clearly show pronounced sexual dimorphism in adult Cape fur seals, supporting findings of the two sample t-test and K-means cluster analysis.

### Principal component analysis

The first 3 PCs accounted for most of the variation. The first PC (PC1) can be interpreted as a measure of overall skull size while PC2 and PC3 define certain aspects of shape (Table 7.3). Interpretations for the first 3 PCs for the 2 genders are given in Table 7.4, together with the percentage of total variation given

The skull of an adult male  $\geq 10$  y is larger (CBL  $\geq 248$  mm; mastoid breadth  $\geq 134$  mm) and more robust than the skull of a similar aged female. In males, the canines are considerably broader, and the sagittal/occipital crests are more pronounced (but variable in height). In adult males, bony deposits occur throughout the parietal region which become more prominent with increasing age (Stewardson *et al.*, 200Ya; present study, Rand, 1949a, b). Mean size of sexually dimorphic traits, according to age (y), have been summarised elsewhere (Stewardson *et al.*, 200Ya).



Table 7.3 *Principal component analysis of covariance matrix for adult male and adult female Arctocephalus pusillus pusillus, showing principal components, eigenvalues, proportions and cumulative proportions of the first three principal components*

Skull variable	PC I	PC II	PC III	PC I	PC II	PC III
<b>Dorsal</b>	<b>Males (n = 23)</b>			<b>Females (n = 10)</b>		
D1 Condylbasal length	-0.58	-0.35	-0.50	-0.61	0.48	0.38
D2 Gnathion to middle of occipital crest	-0.71	-0.06	0.52	-0.28	-0.001	-0.32
D3 Gnathion to posterior end of nasals	-0.28	0.30	-0.28	-0.24	-0.49	0.09
D4 Greatest width of anterior nares	-0.10	0.16	0.03	-0.16	0.28	0.06
D5 Greatest length of nasals	-0.16	0.34	0.02	-0.08	-0.25	0.04
D6 Breadth at preorbital processes	-0.19	0.30	-0.28	-0.41	0.15	-0.17
D7 Least interorbital constriction	-0.08	0.29	0.09	-0.37	-0.15	-0.14
D8 Greatest breadth at supraorbital processes	-0.08	0.49	0.38	-0.36	-0.39	-0.43
D9 Breadth of brain case	-0.03	-0.48	0.41	-0.15	-0.44	0.71
<b>Eigenvalue</b>	<b>444.9</b>	<b>36.1</b>	<b>15.7</b>	<b>93.7</b>	<b>17.7</b>	<b>12.7</b>
<b>Proportion</b>	<b>0.84</b>	<b>0.07</b>	<b>0.03</b>	<b>0.68</b>	<b>0.13</b>	<b>0.09</b>
<b>Cumulative</b>	<b>0.84</b>	<b>0.91</b>	<b>0.94</b>	<b>0.68</b>	<b>0.81</b>	<b>0.91</b>
<b>Palatal</b>	<b>Males (n = 26)</b>			<b>Females (n = 16)</b>		
P10 Palatal notch to incisors	-0.31	-0.21	0.82	-0.34	0.83	0.32
P11 Length of upper postcanine row	-0.13	-0.13	0.10	-0.08	-0.06	-0.02
P12 Greatest bicanine breadth	-0.19	0.03	-0.01	-0.20	-0.08	-0.19
P13 Gnathion to posterior end of maxilla	-0.30	-0.34	-0.06	-0.24	0.04	0.10
P14 Breadth of zygomatic root of maxilla	-0.07	-0.01	-0.003	-0.03	-0.04	0.04
P15 Breadth of palate at postcanine 1	-0.10	0.03	-0.14	-0.11	0.08	-0.21
P16 Breadth of palate at postcanine 3	-0.08	0.04	-0.08	-0.03	0.09	-0.24
P17 Breadth of palate at postcanine 5	-0.10	0.05	-0.14	-0.02	0.08	-0.24
P18 Gnathion to posterior border of postglenoid process	-0.50	-0.18	-0.06	-0.41	-0.16	-0.21
P19 Bizygomatic breadth	-0.30	0.86	0.23	-0.53	-0.15	0.27
P20 Basion to zygomatic root	-0.41	-0.11	-0.13	-0.30	0.13	-0.66
P21 Calvarial breadth	-0.25	0.13	-0.31	-0.26	-0.15	0.19
P22 Mastoid breadth	-0.39	0.05	-0.28	-0.37	-0.42	0.17
P23 Basion to bend of pterygoid	-0.13	-0.08	-0.13	-0.13	0.14	0.26
<b>Eigenvalue</b>	<b>507.1</b>	<b>84.4</b>	<b>35.0</b>	<b>155.5</b>	<b>44.4</b>	<b>13.9</b>
<b>Proportion</b>	<b>0.73</b>	<b>0.12</b>	<b>0.05</b>	<b>0.62</b>	<b>0.18</b>	<b>0.06</b>
<b>Cumulative</b>	<b>0.73</b>	<b>0.85</b>	<b>0.90</b>	<b>0.62</b>	<b>0.79</b>	<b>0.85</b>
<b>Lateral</b>	<b>Males (n = 35)</b>			<b>Females (n = 10)</b>		
L24 Gnathion to anterior of foramen infraorbital	0.39	-0.56	0.73	0.24	-0.71	0.66
L25 Gnathion to posterior border of preorbital process	0.43	-0.59	-0.68	0.33	-0.58	-0.74
L26 Height of skull at base of mastoid	0.82	0.58	0.01	0.91	0.40	0.09
L27 <sup>a</sup> Height of sagittal crest	-	-	-	-	-	-
<b>Eigenvalue</b>	<b>153.8</b>	<b>14.5</b>	<b>0.7</b>	<b>31.4</b>	<b>6.3</b>	<b>0.8</b>
<b>Proportion</b>	<b>0.91</b>	<b>0.09</b>	<b>0.004</b>	<b>0.82</b>	<b>0.16</b>	<b>0.02</b>
<b>Cumulative</b>	<b>0.91</b>	<b>0.996</b>	<b>1.00</b>	<b>0.82</b>	<b>0.98</b>	<b>1.00</b>
<b>Mandibular</b>	<b>Males (n = 26)</b>			<b>Females (n = 16)</b>		
M28 Length of mandible	-0.73	0.38	-0.41	-0.86	-0.20	-0.35
M29 Length of mandibular tooth row	-0.19	0.45	0.57	-0.13	0.96	-0.23
M30 Length of lower postcanine row	-0.12	0.47	0.13	-0.15	-0.09	-0.37
M31 Height of mandible at meatus	-0.49	-0.48	0.63	-0.37	0.05	0.50
M32 Angularis to coronoideus	-0.42	-0.46	-0.31	-0.30	0.14	0.66
<b>Eigenvalue</b>	<b>145.2</b>	<b>13.9</b>	<b>8.0</b>	<b>88.5</b>	<b>27.2</b>	<b>9.1</b>
<b>Proportion</b>	<b>0.84</b>	<b>0.08</b>	<b>0.05</b>	<b>0.70</b>	<b>0.21</b>	<b>0.07</b>
<b>Cumulative</b>	<b>0.84</b>	<b>0.92</b>	<b>0.97</b>	<b>0.70</b>	<b>0.91</b>	<b>0.98</b>

Proportion gives the amount of the total variation that the PC accounted for.

Cumulative gives the amount the first PC accounted for, then the amount that the first two PCs accounted for and finally the amount of total variation the first three PCs accounted for.

<sup>a</sup> Height of sagittal crest (L27) was not examined statistically because there were few measurements for females.

Table 7.4 Interpretations for the first 3 principal components for adult male and adult female *Arctocephalus pusillus pusillus*

Male	Female
<b>Dorsal</b>	
<i>Component 1 (male 84%, female 68%)</i>	
CBL and gnathion to middle of occipital crest measure overall size.	CBL, breadth at preorbital processes, least interorbital constriction and greatest breadth at supraorbital processes measures overall size.
<i>Component 2 (male 7%, female 13%)</i>	
Contrasts greatest breadth at supraorbital processes with CBL and breadth of brain case.	Contrasts CBL with gnathion to posterior end of nasals, greatest breadth at supraorbital processes and breadth of brain case.
<i>Component 3 (male 3%, female 9%)</i>	
Contrasts CBL with gnathion to middle of occipital crest, greatest breadth at supraorbital processes and breadth of brain case.	Contrasts greatest breadth at supraorbital processes with CBL and breadth of brain case.
<b>Palatal</b>	
<i>Component 1 (male 73%, female 62%)</i>	
Gnathion to posterior border of postglenoid process, basion to zygomatic root and mastoid breadth measure overall size.	Gnathion to posterior border of postglenoid process, bizygomatic breadth and mastoid breadth measure overall size.
<i>Component 2 (male 12%, female 18%)</i>	
Bizygomatic breadth dominates.	Contrasts palatal notch to incisors with mastoid breadth.
<i>Component 3 (male 5%, female 6%)</i>	
Palatal notch to incisors dominates.	Basion to zygomatic root dominates.
<b>Lateral*</b>	
<i>Component 1 (male 91%, female 82%)</i>	
Height of skull at base of mastoid, gnathion to posterior border of preorbital process and gnathion to anterior of foramen infraorbital measure overall size.	Height of skull at base of mastoid measures overall size
<i>Component 2 (male 9%, female 16%)</i>	
Contrasts height of skull at base of mastoid with gnathion to anterior of foramen infraorbital and gnathion to posterior border of preorbital process.	Contrasts height of skull at base of mastoid with gnathion to anterior of foramen infraorbital and gnathion to posterior border of preorbital process.
<b>Mandibular</b>	
<i>Component 1 (male 84%, female 70%)</i>	
Length of mandible, height of mandible at meatus and angularis to coronoideus measure overall size.	Length of mandible and height of mandible at meatus measure overall size.
<i>Component 2 (male 8%, female 21%)</i>	
Contrasts height of mandible at meatus and angularis to coronoideus with others (length of mandible, length of mandibular tooth row, length of lower postcanine row).	Length of mandibular tooth row dominates.
<i>Component 3 (male 5%, female 7%)</i>	
Contrasts length of mandible with length of mandibular tooth row and height of mandible at meatus.	Contrasts length of mandible and length of lower postcanine row with height of mandible at meatus and angularis to coronoideus.

Covariance matrix used.

Variables that contributed predominantly to size and/or shape are listed above, i.e., variables with loadings  $\geq 0.36$  (absolute value).

\* Only 2 PCs considered.

## DISCUSSION

### Possible bias

Several factors must be taken into consideration when interpreting the data. Firstly, there may be an over representation of either larger or smaller individuals in the data set which may possibly bias the results. Secondly, although identical variables were taken from PEM and MCM animals, PEM variables were recorded by the first author whereas MCM variables were recorded by the third author, introducing possible inter-observer error.

### Principal component analysis: skull size and shape

For both genders, CBL, mastoid breadth, height of skull at base of mastoid, gnathion to posterior border of postglenoid process and length of mandible contributed the most to overall skull size. Gnathion to middle of occipital crest and basion to zygomatic root were predominant in males but not in females. Bizygomatic breadth was predominant in females but not in males.

Predominant variables contributing to shape in both genders were CBL, breadth at supraorbital

processes, breadth of brain case, palatal notch to incisors, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid, length of mandible, length of mandibular tooth row, length of lower postcanine row, height of mandible at meatus and angularis to coronoideus.

Bizygomatic breadth contributed predominantly to skull shape in males but not in females. Gnathion to posterior end of nasals, basion to zygomatic root and mastoid breadth contributed predominantly to skull shape in females but not in males.

These findings indicate that the underlying data structure for males and females was different. Differences occurred in the combination of predominant variables, and in their magnitude and sign.

### General pattern of growth

Although male Cape fur seals are slightly heavier than females (4.5–6.4 kg) at birth, growth patterns for the genders are similar up until puberty. Males attain puberty between 3 and 4 y (Stewardson *et al.*, 1998) and females between 3 and 5 y (J.H.M David, pers. comm.).

Although males are sexually mature at an early age, they are physically unable to hold a harem until much latter. Full reproductive status (social maturity) is deferred until full size and competitive vigour are developed. Females approximate adult size at *c.* 5 y, while males approximate adult size between 8 and 10 y (Stewardson *et al.*, 200Yb; Stewardson & Prvan, 200X). Adult males may weigh up to 353 kg (mean, 250 kg), while females may weigh up to 122 kg (mean, 58 kg) (J.H.M David, pers. comm.). Similar growth patterns in body size have been reported in other polygynous breeding pinnipeds which exhibit pronounced size dimorphism, e.g., *Callorhinus ursinus*, northern fur seals (McLaren, 1993).

Development of the skull also differs between the genders, with male Cape fur seals exhibiting monophasic growth in some variables and biphasic growth in others, while females exhibit only monophasic growth (Stewardson *et al.*, 200Ya). In males, biphasic growth is associated with territorial acquisition and maintenance (Stewardson *et al.*, 200Ya). Similar growth patterns have been reported in the skulls of other southern fur seals, e.g., *A. p. doriferus*, Australian fur seal, and *A. forsteri*, New Zealand fur seal (Brunner, 1998).

Differences in growth patterns between the genders support our findings of pronounced sexual dimorphism in this species.

### Variation among adult males

The coefficient of variation for most skull variables was larger in males than in females (present study). Variability in adult males at least partly reflects

differences in social status. Considering that only a small percentage of males become breeding bulls, we suggest that secondary sexual characteristics may not fully develop in non-breeding males, of similar age, that do not hold territories. Differences in physical appearance will be most noticeable before and during the breeding season when breeding bulls build up their body reserves.

## Loci of sexual dimorphism

### Dorsal

Males were significantly larger than females 'relative to CBL' in 44% ( $n = 4$ ) of dorsal variables (gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes). In both genders, these variables form part of the splanchnocranium (gnathion to posterior end of nasals) and the frontal region (least interorbital constriction and breadth at supraorbital processes), and are associated with respiration/vocalisation (gnathion to posterior end of nasals) and feeding (breadth at supraorbital processes).

In males, at least 2 of these variables have obvious functional significance with respect to territorial acquisition and defence. Least interorbital constriction and breadth at supraorbital processes contribute to the structural strength of the skull, and shield the animal against blows to the head (especially the eyes) during combat with rival males.

### Palatal

Males were significantly larger than females 'relative to CBL' in 36% ( $n = 5$ ) of palatal variables (greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth and mastoid breadth). In both genders, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, form part of the palatal region and are associated with feeding (greatest bicanine breadth, breadth of palate at postcanine 1 and 3) and respiration/vocalisation (greatest bicanine breadth). Calvarial breadth and mastoid breadth form part of the basicranium and are associated primarily with auditory function (calvarial breadth, mastoid breadth).

Enlargement of the canines (greatest bicanine breadth) enables males to inflict a potentially lethal bite during combat. The rostrum is broad (palatal breadth at postcanine 1 and 3), accommodating the large canines. Enlargement of calvarial breadth and mastoid breadth increases physical appearance and structural strength of the skull (large head size/mass).

### Lateral

Males were significantly larger than females 'relative to CBL' in all lateral variables (gnathion to anterior of foramen infraorbital, gnathion to posterior border of

preorbital process, height of skull at base of mastoid). In both genders, gnathion to anterior of foramen infraorbital and gnathion to posterior border of preorbital process form part of the splanchnocranium and are associated with respiration/vocalisation.

Enlargement of skull height and facial length in males, increases overall head size. Large size is advantageous in territorial acquisition and maintenance.

### **Mandible**

Males were significantly larger than females 'relative to CBL' in only 1 mandibular variable (height of mandible at meatus). This variable is associated with auditory function and feeding in both genders. Enlargement of this variable in males, increases gape and provides a larger surface area for muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in territorial combat.

Sexual dimorphism of the skull in southern fur seals has been reported for *A. p. doriferus* and *A. forsteri* (Brunner, 1998). As with the Cape fur seal, sexually dimorphic traits are mainly those characteristics that increase the ability of males to acquire and defend territory.

### **Significance of the dimorphism**

In male Cape fur seals, there appears to be strong selection pressure for the development of certain morphological traits associated with fighting ability. Development of these traits is not evident in female Cape fur seals, hence dimorphism between the genders.

Firstly, in male Cape fur seals, selection pressure appears to favour large body size. For the range of available values in this study, males (mean, 183 cm) were shown to be significantly larger in standard body length than females (mean, 149 cm). Large males in breeding condition may be 4–5 times heavier than adult females (David, 1989). These large males have an advantage over their smaller rivals in gaining high social rank through fighting. Furthermore, large males in breeding condition have a well developed fat store. This thick blubber layer enables males to remain resident on territory for long periods (up to 40 days) without feeding. If a male abandons his territory to feed, this may result in a rival male mating with his females and/or increase the risk of injury when re-claiming his territory, thus decrease his opportunity of multiple matings.

Secondly, selection pressure appears to favour the development of certain skull traits that appear to be

associated with fighting ability. In the present study, traits which are significantly larger in males appear to be associated with bite force (e.g., broad canines, increased surface area for muscle attachment, large gape), large head size/mass (e.g., increased mastoid and calvarial breadth) and/or structural strength of the skull (shields against direct blows to the head during combat).

As with other male fur seals, selection pressure favours traits associated with fighting ability because the length of time a male can hold territory among breeding females is critical to his genetic success (Bartholomew, 1970). Large body size and the development of weaponry would increase social rank in this polygynous breeding species, hence, increase the opportunity of multiple matings. Large, dominant male Cape fur seals may mate with 10–30 adult females during the short (6–8 weeks) breeding season.

### **CONCLUSIONS**

Information presented in the study demonstrates that there is pronounced sexual dimorphism in adult Cape fur seals with respect to body size, skull size and skull shape. Male Cape fur seals were significantly larger than females in SBL, and 43% of skull variables were found to be significantly larger in males 'relative to CBL'. These variables were associated with fighting ability, e.g., large head size/mass, increased structural strength of the skull and/or increased bite capacity. Principal component analysis showed that the underlying data structure for males and females was different, and that most variation between the sexes was expressed in overall skull size rather than shape. Condylbasal length, height of skull at base of mastoid and length of mandible contributed considerably to overall size, with gnathion to middle of occipital crest predominating in males only.

Further studies are required to test the suggestion that secondary sexual characteristics may not fully develop in non-breeding males that do not hold territories.

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## REFERENCES

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- ALEXANDER RD, HOOGLAND JL, HOWARD RD, NOONAN KM & SHERMAN PW (1979) Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In *Evolutionary biology and human social behaviour* (ed. Chagnon NA, Irons W). North Scituate, Mass.: Duxbury Press.
- BARTHOLOMEW GA (1970) A model for the evolution of pinniped polygyny. *Evolution* **24**, 546–559.
- BONESS DJ (1991) Determinants of mating systems in the Otariidae (Pinnipedia). In *Behaviour of pinnipeds* (ed. Renouf D), pp. 1–65. London: Chapman and Hall.
- BONNER WN (1968) 'The fur seal of South Georgia', British Antarctic Survey Scientific Reports. No. 56. 1–81, London.
- BONNER WN (1981) Southern fur seals *Arctocephalus* (Geoffroy Saint-Hilaire and Cuvier, 1826). In *Handbook of Marine Mammals, vol. 1: The walrus, sea lions, fur seals and sea otter* (ed. Ridgway SH, Harrison, RJ), pp. 161–208. London: Academic Press.
- BRUNNER S (1998) Skull development and growth in the southern fur seals *Arctocephalus forsteri* and *A. pusillus doriferus* (Carnivora: Otariidae). *Australian Journal of Zoology* **46**, 43–66.
- CAMPAGNA C, Le BOEUF BJ (1988) Reproductive behaviour of southern sea lions. *Behaviour* **104**, 233–261.
- CLUTTON-BROCK TH, GUINNESS FE, ALBON SD (1982) *Red Deer. Behaviour and ecology of two sexes*. Chicago: University of Chicago.
- COMMITTEE ON MARINE MAMMALS, AMERICAN SOCIETY OF MAMMALOGISTS (1967) Standard variables of seals. *Journal of Mammalogy* **48**, 459–462.
- DAVID JHM (1989) Seals. In *Oceans of life off southern Africa* (ed. Payne AIL, Crawford RJM), pp. 288–302. South Africa: Vlaeberg Publishers.
- HAUSFATER G (1975) *Dominance and reproduction in baboons (Papio cynocephalus): a quantitative analysis*. (Contributions to primatology, 7) Basel: Karger.
- JACKSON JE (1991) *A User's Guide to Principal Components*. USA: John Wiley & Sons, Inc.
- JOLLIFFE IT (1986) *Principal Component Analysis*. USA: Springer-Verlag New York Inc.
- JOHNSON RA, WICHERN D (1992) *Applied multivariate statistical analysis*. 3rd edn. Prentice Hall: Englewood Cliffs.
- Le BOEUF BJ (1974) Male-male competition and reproductive success in elephant seals. *American Zoology* **14**, 163–176.
- McCANN TS (1981) Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *Journal of Zoology (London)* **195**, 295–310.
- McLAREN IA (1993) Growth in pinnipeds. *Biological Review* **79**, 1–79.
- MILLER EH (1974) Social behaviour between adult male and female New Zealand fur seals *Arctocephalus forsteri* (Lesson) during the breeding season. *Australian Journal of Zoology* **22**, 155–173.
- MILLER EH (1975) Annual cycle of fur seals, *Arctocephalus forsteri* (Lesson) on the Open Bay Islands, New Zealand. *Pacific Science* **29** (2), 139–152.
- MILLER EH (1991) Communication in pinnipeds, with special reference to non-acoustic signalling. In *Behaviour of pinnipeds* (ed. Renouf D), pp. 128–235. London: Chapman and Hall.
- MYERS RH (1990) *Classical and modern regression with applications*. 2nd edn. Boston: PWS-Kent publishing Company.
- PAYNE MR (1979) Growth in the Antarctic fur seal *Arctocephalus gazella*. *Journal of Zoology (London)* **187**, 1–20.
- RALLS K (1977) Sexual dimorphism in mammals; avian models and unanswered questions. *American Naturalist* **111**, 917–938.
- RAND RW (1949a) Studies on the Cape fur seal *Arctocephalus pusillus pusillus* 1. Age grouping in the female. Progress report submitted June 1949.
- RAND RW (1949b) Studies on the Cape fur seal *Arctocephalus pusillus pusillus* 3. Age grouping in the male. Progress report submitted November 1949.
- RAND RW (1967) The Cape fur seal *Arctocephalus pusillus pusillus* 3. General behaviour on land and at sea. *Sea Fisheries Research Institute Investigational Report, South Africa* **60**, 1–39.
- SCHNELL GD, DOUGLAS ME, HOUGH DJ (1995) Sexual dimorphism in spotted dolphins (*Stenella attenuata*) in the Eastern Tropical Pacific Ocean. *Marine Mammal Science* **1**, 1–14.
- SCHULTZ AH (1969) *The life of primates*. Great Britain: Unwin Bros. Ltd.

SELANDER RK (1972) Sexual selection and dimorphism in birds. In *Sexual selection and the descent of man 1871–1971* (ed. Campbell B) Chicago: Aldine.

STEWARDSON CL, BESTER MN, OOSTHUIZEN WH (1998) Reproduction in the male Cape fur seal *Arctocephalus pusillus pusillus*: age at puberty and annual cycle of the testis. *Journal of Zoology (London)* **246**, 63–74.

STEWARDSON CL & PRVAN T (200X). Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part three, baculum. *Journal of Anatomy (Cambridge)* (submitted 2001).

STEWARDSON CL, PRVAN T, MEYER M (200Ya). Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part two, skull. *Journal of Anatomy (Cambridge)* (submitted 2001).

STEWARDSON CL, PRVAN T, MEYER M (200Yb). Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part one, external body measurements. *Journal of Anatomy (Cambridge)* (submitted 2001).

STIRLING I (1970) Observations on the behaviour of the New Zealand fur seal, (*Arctocephalus forsteri*). *Journal of Mammalogy* **51**(4), 766–778.

STIRLING I (1983) The evolution of mating systems in pinnipeds. In *Recent Advances in the study of mammalian behaviour* (ed. Eisenberg JF, Kleiman DG), pp. 489–527. *Special publication No 7, American Society of Mammalogists*.

TRILLMICH F (1984) Natural history of the Galapagos fur seal (*Arctocephalus galapagoensis*, Heller). In *Key environments – Galapagos* (ed. Perry R), pp. 215–223 Oxford: Pergamon Press.