THE RELATIONSHIP BETWEEN TWO SPECIES OF FUR SEALS ARCTOCEPHALUS TROPICALIS (GRAY) AND A. GAZELLA (PETERS) ON MARION ISLAND

by

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ABSTRACT

Subantarctic fur seals *Arctocephalus tropicalis* and Antarctic fur seals *A. gazella* are sympatric at the Prince Edward Islands, and appear to be hybridizing. Adult males of both species and the interspecific hybrids can be distinguished using univariate and multivariate analyses of cranial measurements. The two species differed in the electrophoretic mobility of the serum protein, transferrin. The extent of hybridization appears to be limited with the hybrids representing 0,1% of the total fur seal population (34528 *A. tropicalis* and 300-400 *A. gazella*). Although the seasonal haul-out patterns and breeding habitat preferences of these two species do differ, these differences do not appear to be sufficient to prevent hybridization. Differences in suckling periods and pup growth rates may be acting to limit hybridization through pup mortality of hybrids born to *A. gazella* females.

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CHAPTER 1

INTRODUCTION

The Prince Edward Islands, although possibly sighted as early as 1663, were positively located by the French explorer Marion du Fresne in 1772, and named by Cook in 1773. By the beginning of the 1800's the populations of fur seals and elephant seals were being ruthlessly exploited for hides and oil and these populations were soon decimated. Sporadic attempts at sealing continued, with the last recorded fur sealing expedition in 1921 when 785 pelts were collected (Anon. 1921) although the S.S. Kildalkey elephant sealing expedition of 1931 may have collected some fur seals (Marsh 1948).

Rand (1956a) recorded few fur seals on Marion Island in 1952 but did suggest that the population was recovering and even presented possible ideas for their exploitation. Fortunately these ideas were never taken up and by 1971 de Villiers & Ross (1976) could report an appreciable recovery of the Prince Edward Islands fur seal population, which is continuing to this day.

Condy (1978) in 1974 found that there are actually two species of fur seals breeding on the Prince Edward Islands. These were the traditional species, Arctocephalus tropicalis and the normally southerly species A. gazella. The colonization of the Prince Edward Islands by A. gazella is thought to be a function of this species' population expansion at its more southerly breeding grounds and is thought to have occurred relatively recently (Bonner 1981).

This is a unique situation and provided the rare opportunity to investigate species interrelationships in an area of recent sympatry, possibly providing insights into the mechanisms which allow closely related species to either coexist or competitively exclude one another. This study was initiated to investigate the interrelationships between these fur seal species and included both genetic and ecological investigations of these two species at the Prince Edward Islands.

The Study Area

Topography

Marion Island (46° 54'S, 37° 45'E) and Prince Edward Island (46° 38'S, 37° 57'E) together form the Prince Edward Island Group. They are two closely related, coalescing shield volcanoes (Verwoerd 1971). They were originally considered to be extinct but some activity is still occurring (Verwoerd, Russel & Berruti 1981, pers. obs.).

Marion Island is 290 km^2 (Fig. 1) in area, roughly oval shaped with a smooth circumference of 72 km (Verwoerd 1971) and an estimated actual coastline of 120 km or more (Condy 1977). The island has a maximum altitude of 1230 m and can be divided into five physiographic regions: coastline, coastal plain, island slope, central highland and escarpment (Verwoerd 1971).

The coastal plain lies approximately 50m above sea level and varies in width from 0,8 - 2,0 km. It is situated on the western/southwestern portion of the island and is separated from the central highland by the 200 - 300 m high escarpment. The island slope forms the majority of the island and varies in incline, being steeper in the west than the east (Verwoerd 1971).

Two main volcanic stages have been distinguished: the older glaciated grey lava stage of 276000 ± 3000 years ago and the younger black lava stage which is 15000 ± 8000 years old (McDougall 1971). The greater part of the island was inundated by black basaltic lava during the second volcanic stage and the coast formed by the more recent activity is extremely irregular with cliffs about 15 m in height predominating. The coastline formed by the older substrate is more regular although the cliffs are higher, generally about 30 m, but they may be hundreds of metres where the escarpment meets the coast.

Neighbouring Prince Edward Island (22 km NNE, Fig. 2) is much smaller with an area of 44 km^2, a smooth circumference of 29 km and a maximum altitude of 672 m (Verwoerd 1971). The island is bisected by a 500 m high escarpment running NE-SW and has a coastal plain in the northwest, an island slope on the southwest and a central highland. Two stages of volcanic activity, similar to those of Marion Island, can be distinguished (Verwoerd 1971, McDougall 1971).

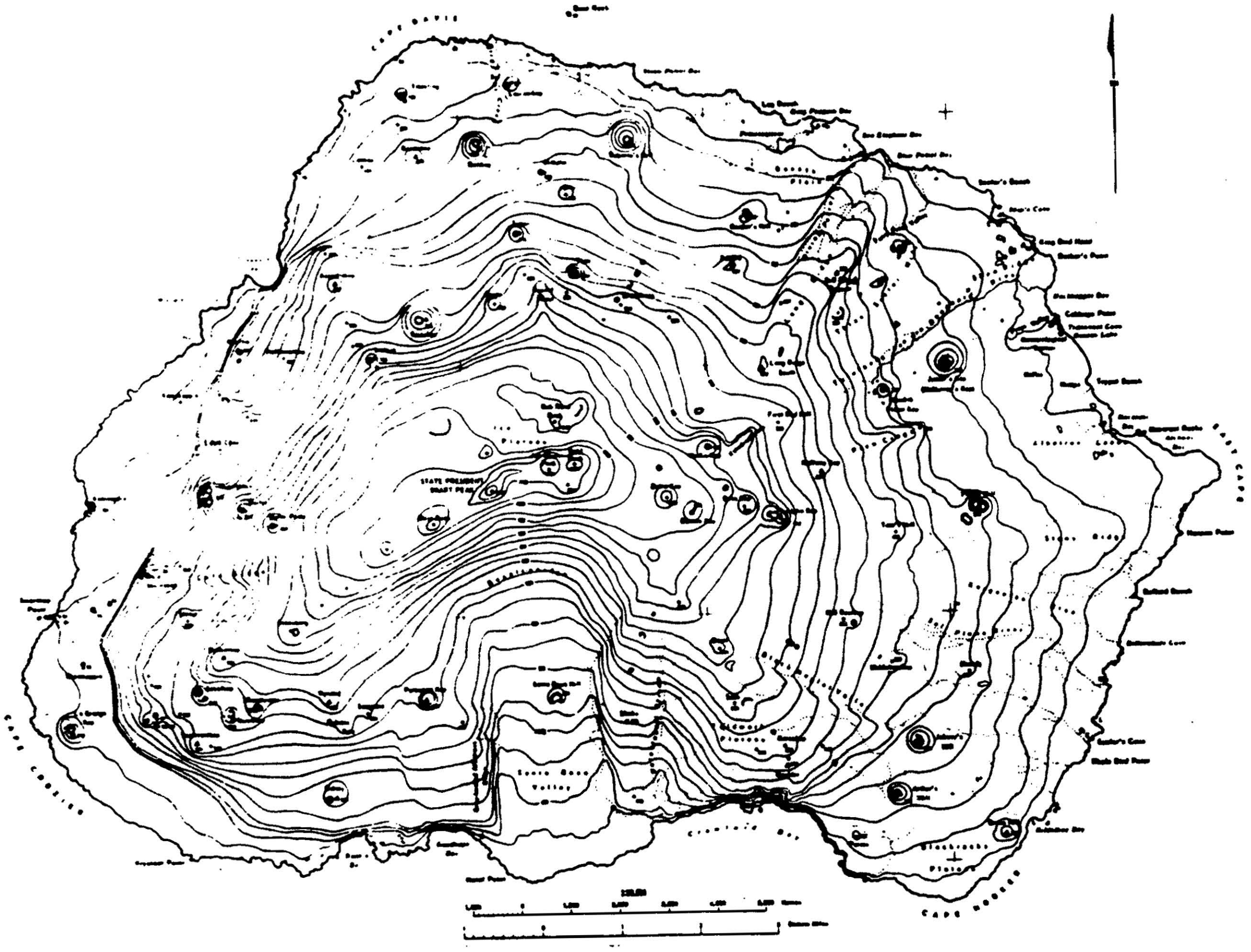


Figure 1: Topographical map of Marion Island (contours in m).

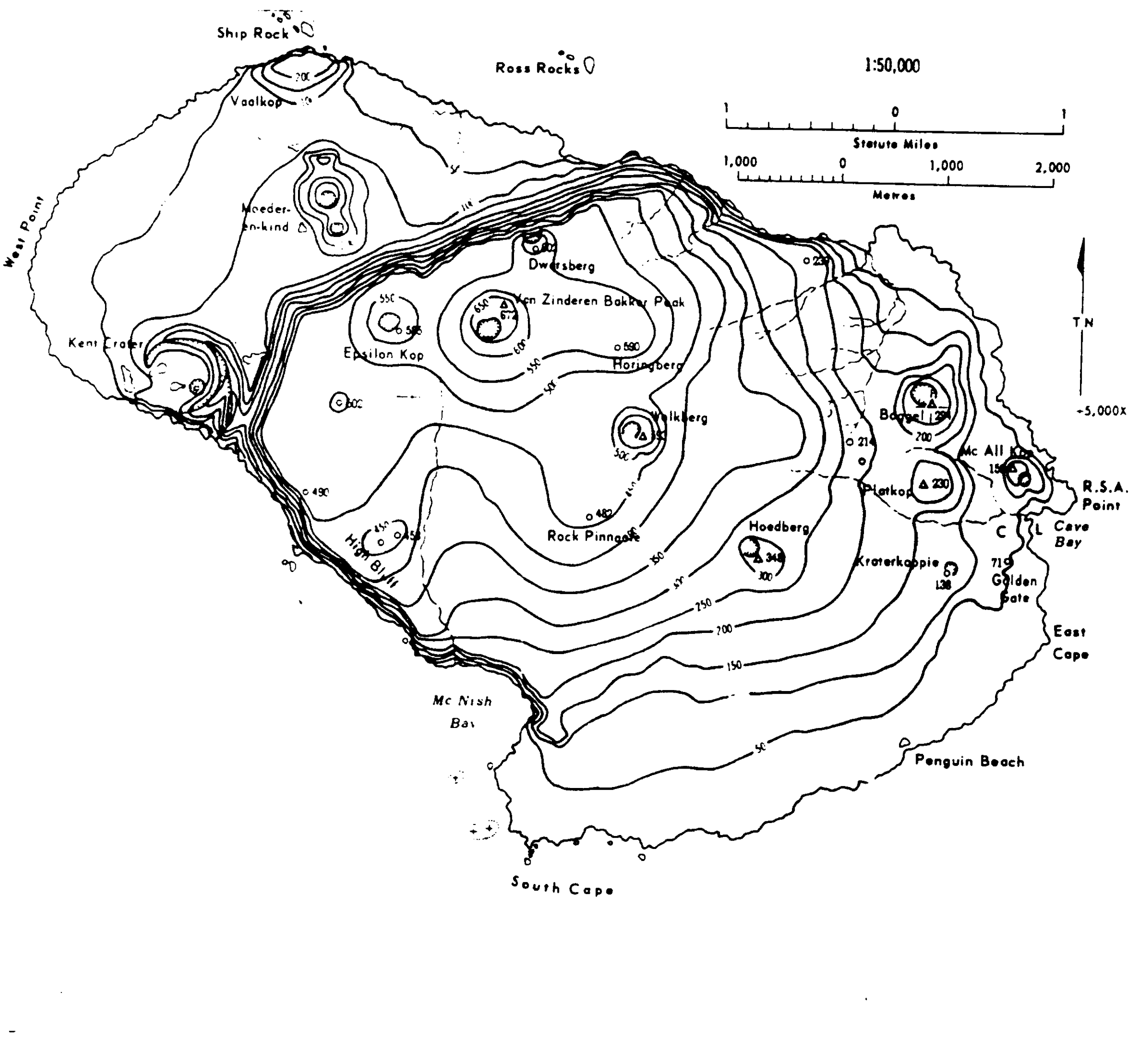


Figure 2: Topographical map of Prince Edward Island (contours in m).

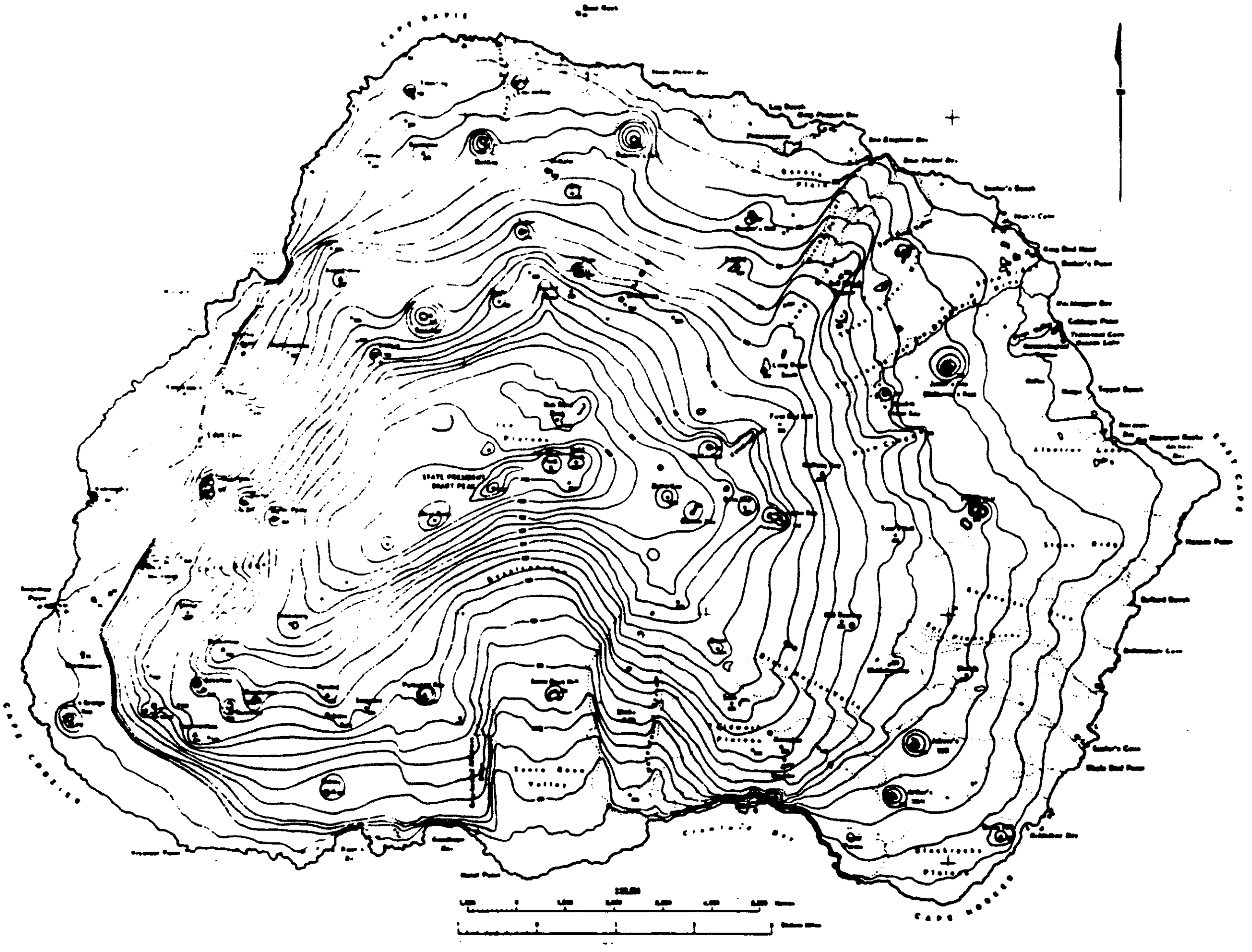


Figure 1: Topographical map of Marion Island (contours in m).

Climate

Systematic observations have been made at the Meteorological Station on the leeward east coast since 1948. The climate is basically cool oceanic with the following characteristics:

(a) Strong, predominantly westerly winds, with the highest velocities during the day and gales most frequent in the winter.
(b) Relatively low air temperatures, with a mean annual temperature of 5,5°C; with little annual or diurnal variation.
(c) Abundant precipitation in the form of rain, snow or graupel (ice-rain) with a mean annual precipitation of 2576 mm.
(d) High relative humidity, with little annual or diurnal variation from 80%.
(e) A high degree of cloudiness, with only 20 - 33% of the possible amount of sunshine reaching the island surface. Sunshine duration is 15 h in summer and 9 h in winter (Schulze 1971).

Sea surface temperatures measured at the Station are low (annual mean = 5,0°C) with little annual variation. Mean sea surface temperatures are higher than the mean air temperatures during the winter months, from May to September (Schulze 1971).

Identity of the fur seals on the Prince Edward Islands

The Antarctic fur seal (*A. gazella*) was long regarded as conspecific with the subantarctic fur seal (*A. tropicalis*) and both referred to as *A. gazella*. They were separated on the basis of cranial and dental characters at the subspecific level by King (1959a), who recognized *A. tropicalis gazella* as the southern subspecies and *A. t. tropicalis* as the northern subspecies (King 1959b), with their ranges separated by the Antarctic Convergence, although the collection of a skull (Rand 1956a, no. 3791) on Marion Island typical of the southern subspecies led to some confusion. Bonner (1968) considered that the differences between the two taxa rated recognition at the species level but did not revise the nomenclature. However Repenning, Peterson & Hubbs (1971) in the most recent taxonomic review of the genus *Arctocephalus* distinguished between these two taxa at the specific level as *A. gazella* from islands south of the Antarctic Convergence and *A. tropicalis* from islands north of the Convergence.

Repenning et al. (1971) proposed the vernacular name of "Amsterdam Island fur seal" for A. tropicalis as the type specimen was thought to have been collected in the vicinity of that island and that population was the best studied (Paulian 1964). The name "subantarctic fur seal" has also been used for this species (Shaughnessy 1976a, Bonner 1981) and as this name is appropriate to their distribution it will be used in this text. The name "Kerguelen fur seal" was proposed by Repenning et al. (1971) for A. gazella, as the type specimen was collected at Kerguelen. However, the name "Antarctic fur seal" is more appropriate (Bonner 1976, Shaughnessy 1976a) and will be used here.

Rand (1956a) provisionally concluded that the fur seals at the Prince Edward Islands were A. gazella (the species were not separated yet), while van Zinderen Bakker, Jr. (1967) and de Villiers & Ross (1976) referred to them as A. tropicalis. It was not until 1976 that Condy (1978) showed that both A. tropicalis and A. gazella occur and breed on the Prince Edward Islands.

A single vagrant Cape fur seal A. pusillus pusillus was recorded at Cape Davis on Marion Island in January 1982 (Kerley 1983).

Distribution

A. tropicalis

A. tropicalis breeds on islands north of the Antarctic Convergence (Fig.3) including Gough Island (Bester 1980), Nightingale and Inaccessible Islands (Wace & Holdgate 1976), Tristan da Cunha (Bester 1980), Amsterdam Island (Paulian 1964), Saint Paul Island (Segonzac 1972), the Crozet Archipelago (Jouventin, Stahl & Weimerskirch 1982), Macquarie Island (P.D. Shaughnessy pers. comm.) and Marion and Prince Edward Islands (Condy 1978). Isolated vagrants have been recorded from the South African coast (Shaughnessy & Ross 1980), South Georgia (Payne 1979a) and the South American Coast (Castello & Pinedo 1977).

The largest population of A. tropicalis is at Gough Island (200 000 in 1977 - Bester 1980) followed by Amsterdam Island and the Prince Edward Islands (both with approximately 35000 in 1981 - Hes & Roux 1983, this study). The remaining populations are small and poorly studied (Bonner 1981).

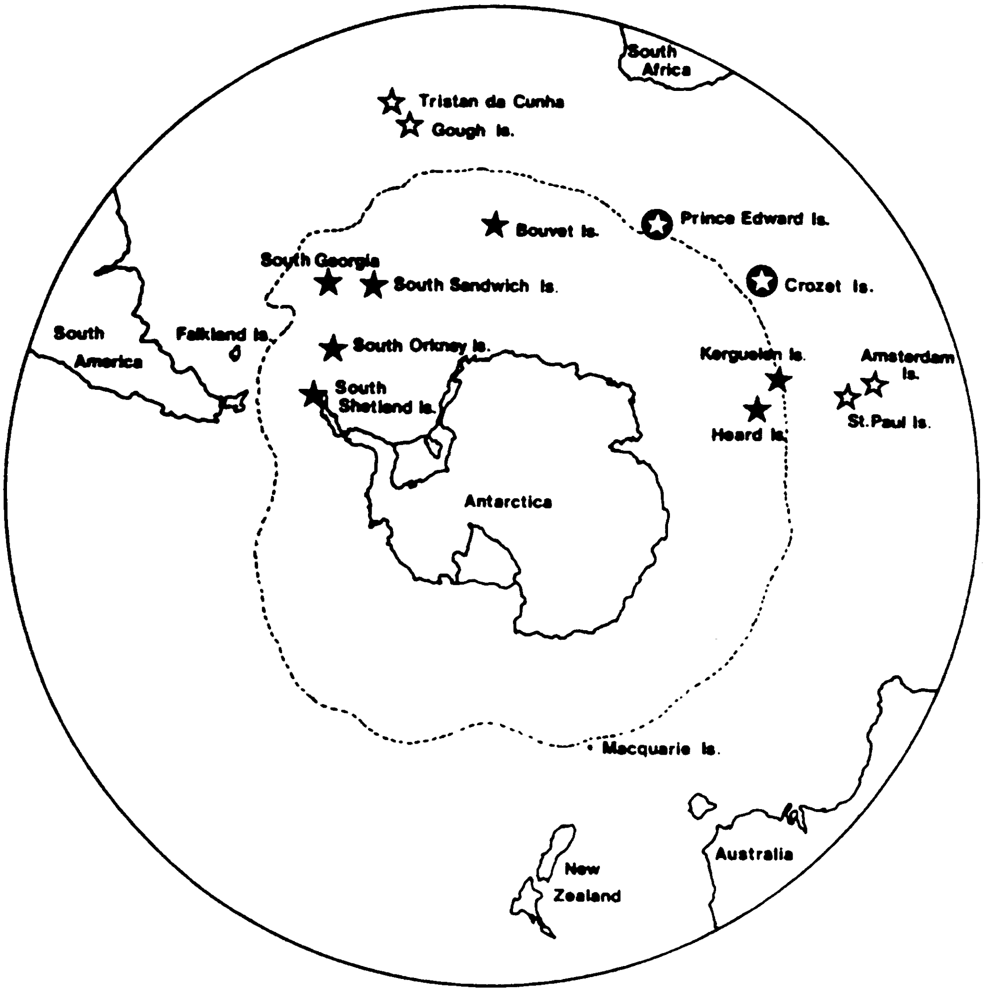


Fig 3: Map showing the distribution of breeding localities of *Arctocephalus tropicalis* (open stars) and *A. gazella* (solid stars) and of those where sympatry (circled stars) has been observed. The broken line represents the position of the Antarctic Convergence.

A. gazella

A. gazella breeds on islands south of the Antarctic Convergence (Fig. 3) including South Georgia (Bonner 1968), South Orkney Islands (Oritsland 1960), South Shetland and South Sandwich Islands (O'Gormon 1961), Bouvet Island (Haftorn, Somme & Gray 1981), Heard and McDonald Islands (Budd 1970, 1972) the Kerguelen Archipelago (Jouventin *et al*. 1982), and possibly Marquarie Island (P.D. Shaughnessy pers. comm.). *A. gazella* also breeds at two localities north of the Antarctic Convergence, the Prince Edward Islands (Condy 1978) and the Crozet Archipelago (Jouventin *et al*. 1982). A single individual has been recorded in Tierra de Fuego (Payne 1979a) and a group of five has been recorded in South Atlantic pack ice (Bester 1979). The largest population of *A. gazella* is located at South Georgia where the population was estimated at $1,2 \times 10^6$ in 1984 (McCann & Doidge in press).

CHAPTER 2

METHODS

The present study is divided into discrete sections, each presented in the form of a chapter with the relevant detailed techniques and materials used. General methods which are relevant to most sections are presented here.

The fieldwork on Marion Island was carried out during two consecutive austral summers, from September 1980 to May 1981 and October 1981 to May 1982. During the first phase, fieldwork was centred at the Cape Davis *A. tropicalis* colony on the north-west coast and during the second phase field work was centered at the Rook's Bay *A. gazella* colony (Fig. 1). Prince Edward Island was visited on three occasions: 5 - 7 May 1981; 28 April - 2 May 1982 and 12 - 13 May 1982.

Fur seal pups were double tagged with monel metal tags on the posterior edge of the foreflippers (Condy & Bester 1975) during the 1981/82 austral summer. Tagged pups were used for mark-recapture experiments and to monitor growth and will also contribute to the pool of known age identifiable individuals.

Species identification

Species identification in the field was based on characteristic external features following Bonner (1968), Bester (1977), and Condy (1978). Features used were coat colour, presence or absence of the crest, and relative body proportions as well as vocalizations. Adult males were classified as hybrids when they could not be positively classed as either *A. gazella* or *A. tropicalis* (Condy 1978), however females and subadults could not be classified with absolute certainty.

Age and sex classification

For the purposes of this study fur seals were classified into general age and sex classes, based on features such as body size, coat colouration, development of the crest, appearance of the mystacial vibrissae, and behaviour. Observations of specific features such as erect nipples in adult females and the presence of the penial opening in males aided classification. The classification used here follows Bester (1977) and consists of: adult males (AM), adult females (AF), subadults of both sexes (SAU), underyearlings (U) and pups (P). The subdivisions of the SAU class used by Bester (1977) were not used here. Pups of the year were classified as pups until they moulted their black natal coats to become underyearlings.

Similar classifications were used by Rand (1956b) for *A. p. pusillus*, Bonner (1968) for *A. gazella* and Stirling (1971 a,b) for *A. fosteri*.

Colony types

Fur seal colonies were classified according to the age and sex specific composition during the December breeding season peak haul-out and the breeding success in terms of the final pup yield, after Bester (1982). The four colony types are:

Idle colony: comprised mainly of idle, nonbreeding adult males with few subadults. Adult females were rare, although isolated births were recorded.

Nonbreeding colony: comprised of equal proportions of adult and subadult males. Adult females relatively common and in excess of the number of pups born.

Breeding colony: subadults predominate with more adult females than adult males but a low pup yield (AM : P = 1,4 : 1).

Established breeding colony: Adult females predominate (AM : AF = 1 : 4,4) with few subadults and a high pup yield (AM : P = 1 : 5,3).

Specimen collection

Fur seals were shot in the neck with a .22 calibre rifle for specimen collection. Standard measurements were taken following the recommendations of the American Society of Mammalogists (1967). When bodyweight of the intact animal could not be determined, the correction factor for piecemeal mass determinations found by Kerley & Bester (1983) was used.

The skull, baculum, skin, blood samples, stomach contents (if any) and endo- and ectoparasites were collected from each specimen, which was allocated a Marion fur seal (MFS) number. Skulls and bacula were boiled in water and cleaned by hand. Material from stomach contents, regurgitations and faeces are being identified by the Prey Identification Service, Port Elizabeth Museum.

CHAPTER 3

COMPARATIVE SKULL MORPHOMETRICS

Introduction

Although the taxonomy of the fur seals has been well delineated by Repenning et al. (1971), it was necessary to develope an objective method to distinguish between A. tropicalis and A. gazella which would in turn allow an objective assessment of the status of the putative interspecific hybrids. Univariate and multivariate morphometric analyses are extremely useful taxonomic tools for the assessment of inter- and intraspecific relationships (see Swanepoel & Genoways 1978, Yates, Genoways & Jones 1979, Robinson & Dippenaar 1983), and were used in the present investigation.

Materials and Methods

Skulls of 47 Arctocephalus spp. fur seals (Table 1) were examined and 34 cranial measurements recorded for each specimen. Measurements were taken to the nearest 0,1mm with a vernier caliper, except for the facial angle measurement (Repenning et al. 1971) which was taken to the nearest 1^{o} with an engineer's protractor. Measurements used corresponded to those used in other otariid studies (Sivertsen 1954, King 1959a, Orr, Schonewald & Kenyon 1970, Repenning et al. 1971). External body measurements, which were available only for the Marion Island specimens, were excluded from the analyses.

As fur seals exhibit sexual dimorphism, with adult males being more than twice the size of adult females (Bonner 1981), this source of variation was excluded by including only males in the present study. A second source of variation, that of age, was reduced by using only adult specimens. Sivertsen's (1954) suture index was used for ageing and only specimens with an index of 19 or more (corresponding to an age of 8 years or older - M.N. Bester pers.comm.) were included in the analyses.

Table 1: Reference numbers, species, source localities and sample sizes for the *Arctocephalus* specimens used in this study.

Reference number (OTU's)	*Arctocephalus* Species	Source locality	n
1 - 15	*A. gazella*	South Georgia	15
16 - 19	*A. gazella*	Marion Island	4
20 - 42	*A. tropicalis*	Marion Island	23
43 - 47	Hybrid	Marion Island	5

Measurement trials for both species were carried out for all the cranial measurements (five repetitions, n=5) and all measurements were found to be highly repeatable. Individual variation, as expressed by the Coefficient of Variation (CV), was determined for all variables. The Operational Taxonomic Units (OTU's) for the analyses were individual specimens.

Univariate analyses yielding standard statistics (mean, range, standard deviation, standard error, variance, among others) were performed using the CONDESCRIPTIVE subprogramme of the Statistical Package for Social Sciences (Statistical Package for Social Sciences 1983).

The Marion Island and South Georgia *A. gazella* subsamples were tested for significant differences using the ONEWAY subprogramme of the SPSS package. This is a single classification analysis of variance (ANOVA).

Multivariate statistical analyses were performed using selected subroutines of the Numerical Taxonomy System of Multivariate Statistical Programmes (NT-SYS)(Rohlf, Kispaugh & Kirk 1974). Matrices of Pearson's product-moment correlation and taxonomic distance co-efficients were computed. Cluster analyses were performed utilising the unweighted pair group method using arithmetic averages (UPGMA) on the correlation and distance matrices and phenograms were generated for both.

The NT-SYS principal component analysis (PCA) allows an objective assessment of data without prior grouping of material. The PCA is based on correlation coefficients among characters. Two dimensional projections of the pairwise comparisons of the first three components generated by the programme were analysed. Factor matrices indicating the character loadings in these components and the percentage of variation accounted for by them were computed. A minimum spanning tree (MST) was superimposed on the two dimensional projections of the PCA. This shows the affinities of the OTU's to each other and indicates the degree of distortion created by representing the OTU's in a two dimensional projection.

Two group discriminant function analysis using the DISCRIMINANT subprogramme of the SPSS package was used for checking species integrity. Discriminant analysis is a statistical technique in which linear combinations of variables are used to distinguish between two or more categories of cases (OTU's). The variables "discriminate" between groups of cases and predict into which category or group a case falls, based upon the values of these variables.

An indepth review of the theory, underlying assumptions and methods of multivariate analyses for systematics is given by Neff & Marcus (1980).

Computer analyses using the NT-SYS and SPSS packages were conducted on the University of Pretoria IBM 370 computer.

Results

Individual variation

Individual variation, as expressed by the coefficient of variation (CV), was determined for all 34 variables and found to be relatively high. Nineteen variables (Fig. 4, Table 2) with relatively low variation (CV $\leqslant 8{,}0$) or little or no interspecific overlap were included in the analyses. Of the ten variables considered by King (1959a) and Bonner (1968, p 17) to differentiate between A. tropicalis and A. gazella, four were excluded from the analyses as these variables exhibited either high individual variation or species overlap or both of these (Table 3, Fig. 4).)

Geographic variation in A. gazella

Analyses of variance showed that the Marion Island and South Georgia A. gazella samples differed significantly in only six of the 19 variables (Table 4). This is probably due to the presence of two small individuals in the Marion Island sample, as well as the small sample size. These two individuals, however, were both adults (OTU 16 suture index = 19; OTU 17 suture index = 20) and possibly represent the lower limit of the adult size range and were both retained and the two sample localities were combined for further analyses.

Table 2: Species variation in cranial morphology of *Arctocephalus tropicalis* (n=23), *A. gazella* (n=19) and their interspecific hybrids (n=5).

Variable and Species	Mean (mm)	S.E.	C V (%)	Range (mm)
Condylobasal length				
A.tropicalis	217,0	1,35	2,98	206,3 - 228,6
A.gazella	241,5	1,77	3,19	227,7 - 255,5
hybrid	231,5	4,51	4,36	221,3 - 247,4
Basilar length of Hensel				
A.tropicalis	194,8	1,21	2,97	185,3 - 204,0
A.gazella	217,7	1,57	3,14	207,3 - 230,9
hybrid	208,5	4,14	4,44	197,4 - 221,5
Palital length				
A.tropicalis	94,5	0,81	4,11	89,2 - 103,0
A.gazella	113,1	1,54	5,94	94,2 - 124,4
hybrid	103,4	2,70	5,84	93,8 - 109,2
Upper postcanine length				
A.tropicalis	57,6	0,58	4,83	51,6 - 62,6
A.gazella	64,8	0,78	5,23	57,9 - 70,4
hybrid	61,7	2,16	7,80	54,3 - 66,2
Optic foramen - condyl length				
A.tropicalis	98,4	0,67	3,26	93,1 - 105,1
A.gazella	108,3	0,99	3,99	102,8 - 119,6
hybrid	105,7	2,08	4,39	98,1 - 110,4
Palate width - molar 1				
A.tropicalis	22,3	0,35	7,55	19,2 - 25,5
A.gazella	28,7	0,50	7,62	23,7 - 33,4
hybrid	26,4	0,59	5,00	24,9 - 28,3
Palate width - molar 3				
A.tropicalis	23,4	0,42	8,59	20,5 - 27,8
A.gazella	31,3	0,46	6,46	27,8 - 36,7
hybrid	29,1	0,79	6,05	26,1 - 30,7
Palate width - molar 5				
A.tropicalis	28,2	0,55	9,26	23,6 - 33,5
A.gazella	40,9	0,80	8,50	35,3 - 51,1
hybrid	36,9	1,24	7,51	33,7 - 39,6
Zygomatic width				
A.tropicalis	133,0	1,15	4,13	122,3 - 142,8
A.gazella	147,5	1,92	5,67	132,2 - 167,3
hybrid	147,2	3,90	5,92	138,6 - 161,9

Table 2: (continued)

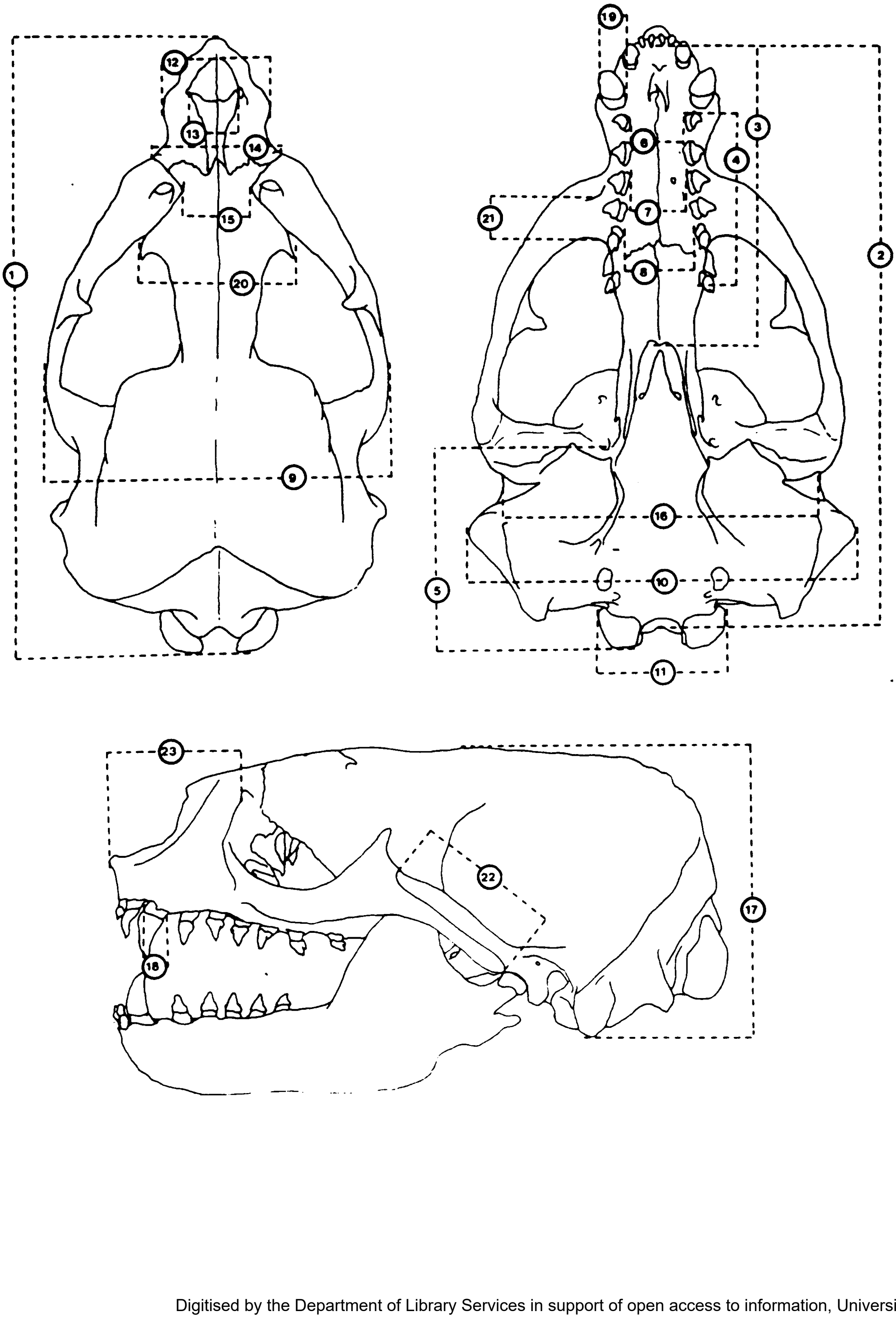
Variable and Species	Mean (mm)	S.E.	C V (%)	Range (mm)
Mastoid width				
A.tropicalis	123,5	1,10	4,28	115,9 - 135,3
A.gazella	138,1	2,52	7,97	112,9 - 164,6
hybrid	134,7	3,29	5,46	127,4 - 146,1
Occipital Condyl width				
A.tropicalis	48,3	0,43	4,23	44,5 - 51,8
A.gazella	54,2	0,75	5,99	47,6 - 59,8
hybrid	51,3	1,10	4,79	49,0 - 54,4
Rostral width				
A.tropicalis	43,6	0,61	6,70	38,1 - 49,5
A.gazella	56,9	1,02	7,78	49,7 - 65,3
hybrid	50,2	0,80	3,56	48,9 - 53,1
Max. nasal width				
A.tropicalis	26,3	0,46	8,29	22,7 - 29,9
A.gazella	33,1	0,45	5,96	29,3 - 36,5
hybrid	31,0	0,80	5,76	28,8 - 32,9
Preorbital process width				
A.tropicalis	50,4	0,67	6,40	45,2 - 56,6
A.gazella	65,5	0,76	5,09	57,4 - 74,1
hybrid	61,0	1,18	4,32	56,9 - 63,6
Interorbital process width (ant.)				
A.tropicalis	22,0	0,46	10,04	17,5 - 25,9
A.gazella	36,9	0,65	7,72	32,5 - 42,3
hybrid	32,7	1,58	10,81	27,5 - 35,9
Calvarial width				
A.tropicalis	106,6	0,87	3,92	98,6 - 113,1
A.gazella	117,4	1,44	5,36	107,9 - 135,4
hybrid	116,4	4,21	8,09	105,4 - 131,4
Skull height (at bulla)				
A.tropicalis	86,6	0,88	4,86	77,5 - 95,0
A.gazella	99,2	1,34	5,88	87,6 - 110,9
hybrid	95,5	1,46	3,42	91,8 - 99,5
Canine diameter (lengthwise)				
A.tropicalis	11,1	0,19	8,10	9,7 - 13,4
A.gazella	14,2	0,19	5,74	13,2 - 16,5
hybrid	12,2	0,69	12,60	10,1 - 14,1
Canine diameter (widthwise)				
A.tropicalis	9,3	0,17	8,82	7,7 - 11,0
A.gazella	12,1	0,22	8,00	10,9 - 14,8
hybrid	10,5	0,45	9,69	9,1 - 11,7

Table 3: Species variation in four cranial variables previously used to differentiate *Arctocephalus tropicalis* and *A. gazella* (King 1959a, Bonner 1968) but excluded from the present study.

Variable and Species	Mean (mm)	S.E.	C V (%)	Range (mm)
Supraorbital process width				
A.tropicalis	48,7	1,18	11,59	39,3 - 57,1
A.gazella	63,3	1,53	10,53	53,7 - 75,0
Zygomatic root width				
A.tropicalis	13,3	0,39	13,92	9,7 - 18,3
A.gazella	19,9	0,34	7,42	16,5 - 22,2
Squamosal-jugal suture length				
A.tropicalis	39,9	0,51	6,23	36,4 - 45,6
A.gazella	34,0	1,04	13,37	23,4 - 43,5
Gnathion to preorbital process length				
A.tropicalis	48,2	0,800	8,00	37,7 - 54,9
A.gazella	57,5	0,72	5,47	50,8 - 62,5

Figure 4: Diagramatic representation of the 19 variables utilized in the present study, as well as the four variables (20-23) previously used to differentiate between Arctocephalus tropicalis and A. gazella but excluded from the present study. 1 = condylobasal length; 2 = basilar length of Hensel; 3 = palital length; 4 = upper postcanine length; 5 = optic foramen-condyl length; 6 = palate width at molar 1; 7 = palate width at molar 3; 8 = palate width at molar 5; 9 = zygomatic width; 10 = mastoid width; 11 = occipital condyl width; 12 = rostral width; 13 = maximum nasal width; 14 = preorbital process width; 15 = interorbital process width (ant.); 16 = calvarial width; 17 = skull height (at tympanic bulla); 18 = canine diameter (lengthwise); 19 = canine diameter (widthwise); 20 = supraorbital process width; 21 = zygomatic root width; 22 = squamosal-jugal suture length; 23 = gnathion to preorbital process length.
See next page.

Figure 4: (continued)



Species delimitation

The values for A. gazella of all 19 variables were greater than those for A. tropicalis, with the interspecific hybrids having intermediate values (Table 2). Phenograms showing the interspecific relationships between the two species were computed from both the distance and correlation matrices.

The distance phenogram, with a cophenetic correlation coefficient of 0,782 clearly shows the separation of the two species (Fig. 5). Two major clusters are evident, A and B. Major cluster B, grouped relatively tightly, comprises all of the A. tropicalis specimens. Major cluster A comprises all of the A. gazella specimens as well as the interspecific hybrids and is further divided into subclusters C and D. The single A. gazella specimen forming subcluster D (OTU 10) is an extremely large specimen whose measurements formed the upper limit of the A. gazella range in 14 of the 19 variables (74%). Subcluster C subdivides into subdivisions E and F. Subdivision E comprises the larger A. gazella specimens (condylobasal lengths ⩾237,2mm, mean=242,3mm, n=16 range=237,2 - 253,4) as well as the largest hybrid (OTU 44, CBL=247,4mm). Subdivision F comprises the two small A. gazella specimens mentioned earlier (OTU 16, CBL=227,7mm and OTU 17, CBL=228,4mm) as well as the other four interspecific hybrids.

The correlation phenogram (Fig. 6) with a low cophenetic correlation coefficient of 0,534, did not separate the taxa, as no clear pattern was discernable in the placement of the OTU's in this phenogram.

The results of the principal component analysis are given in Table 5 as well as Figures 7 and 8. The first component accounts for 81,36% of the total variation and is an overall size component as suggested by the large and positive coefficients for all measurements (Table 5). The second component, which accounts for an additional 3,52% of the trace, is a shape component as the character loadings indicate that this component is influenced mostly by zygomatic width, mastoid width, maximum nasal width and calvarial width as well as the canine diameters (both lengthways and widthways) and the upper postcanine length. The third component which contributes an additional 3,10% to the total phenetic variation (total=87,99%), is influenced primarily by upper postcanine length, palate width at molar 3, and occipital condyl width.

Table 4: Geographic variation in cranial morphology of *Arctocephalus gazella* from Marion Island (MI, n=4) and South Georgia (SG, n=15). Underlined variables differ significantly (p ⩽ 0,05).

Variable and Locality	Mean (mm)	S.E.	C V (%)	Range (mm)	Probability
Condylobasal length					
MI	233,4	3,14	2,69	227,7-240,2	0,01
SG	243,7	1,71	2,72	234,9-255,5	
Basilar length of Hensel					
MI	211,6	2,42	2,28	207,3-218,4	0,04
SG	219,4	1,66	2,93	210,2-230,9	
Palital length					
MI	106,7	4,63	8,68	94,2-114,0	0,03
SG	114,9	1,28	4,33	105,5-124,4	
Upper postcanine length					
MI	63,4	1,36	4,29	60,2- 66,6	0,34
SG	65,2	0,91	5,40	57,9- 70,4	
Optic foramen - Condyl length					
MI	105,1	0,62	1,17	103,7-106,7	0,10
SG	109,1	1,15	4,10	102,8-119,6	
Palate width - molar 1					
MI	28,4	1,22	8.61	25,6- 31,3	0,77
SG	28,8	0,57	7,64	23,7- 33,4	
Palate width - molar 3					
MI	31,8	1,11	6,95	28,8- 34,0	0,61
SG	31,2	0,53	6,52	27,8- 36,7	
Palate width - molar 5					
MI	40,2	1,19	5,91	37,3- 42,6	0,64
SG	41,1	0,97	9,14	35,3- 51,1	
Zygomatic width					
MI	145,1	5,02	6,91	132,2-153,7	0,54
SG	148,2	2,10	5,50	135,3-167,3	

Table 4: (continued)

Variable and Locality	Mean (mm)	S.E.	C V (%)	Range (mm)	Probability
Mastoid width					
MI	128,7	6,04	9,39	112,9-138,8	0,05
SG	140,6	2,48	6,83	128,1-164,6	
Occipital Condyl width					
MI	53,1	0,84	3,16	51,0- 54,7	0,42
SG	54,6	0,91	6,47	47,6- 59,8	
Rostral width					
MI	56,7	3,35	11,83	49,7- 64,3	0,94
SG	56,9	1,02	6,93	52,6- 65,3	
Max. nasal width					
MI	31,1	0,83	5,31	29,3- 33,3	0,02
SG	33,6	0,45	5,17	31,0- 36,5	
Pre-orbital process width					
MI	61,6	1,70	5,52	57,4- 65,3	0,01
SG	66,5	0,66	3,83	64,0- 74,1	
Interorbital process width (ant.)					
MI	36,5	2,23	12,25	32,5- 40,8	0,74
SG	37,0	0,64	6,66	33,6- 42,3	
Calvarial width					
MI	112,4	2,28	4,06	107,9-117,7	0,07
SG	118,8	1,57	5,13	110,8-135,4	
Skull height (at bulla)					
MI	95,5	4,08	8,56	87,6-102,5	0,15
SG	100,2	1,27	4,92	92,7-110,9	
Canine Diameter (lengthwise)					
MI	14,3	0,47	6,61	13,2- 15,5	0,89
SG	14,2	0,21	5,74	13,5- 16,5	
Canine Diameter (widthwise)					
MI	12,7	0,83	13,06	11,0- 14,8	0,27
SG	12,0	0,19	6,14	10,9- 13,3	

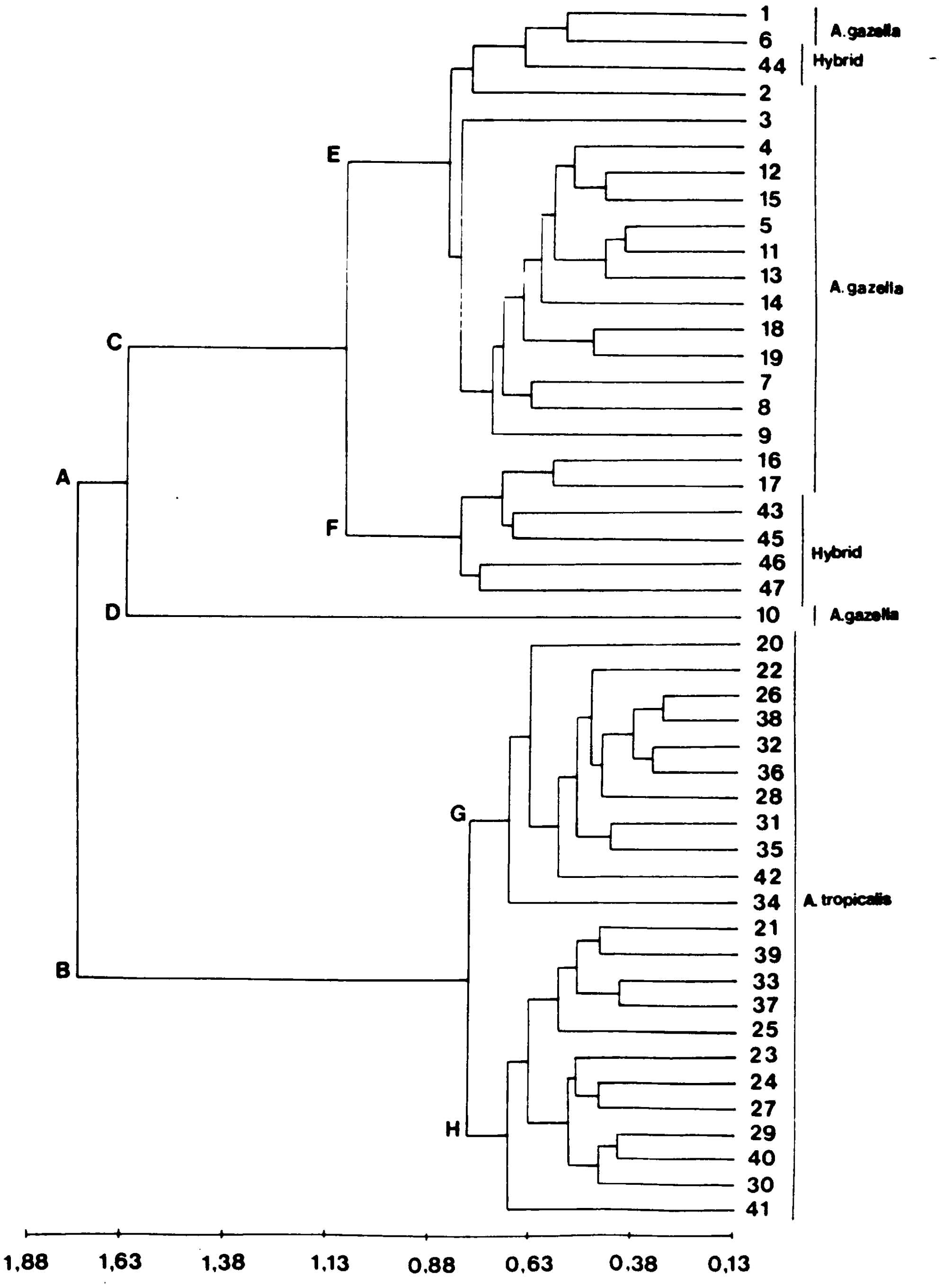


Figure 5: Distance phenogram of specimens of *Arctocephalus tropicalis*, *A. gazella* and their interspecific hybrids clustered by the unweighted pair-group method using arithmetic averages. Cophenetic correlation coefficient = 0,782.

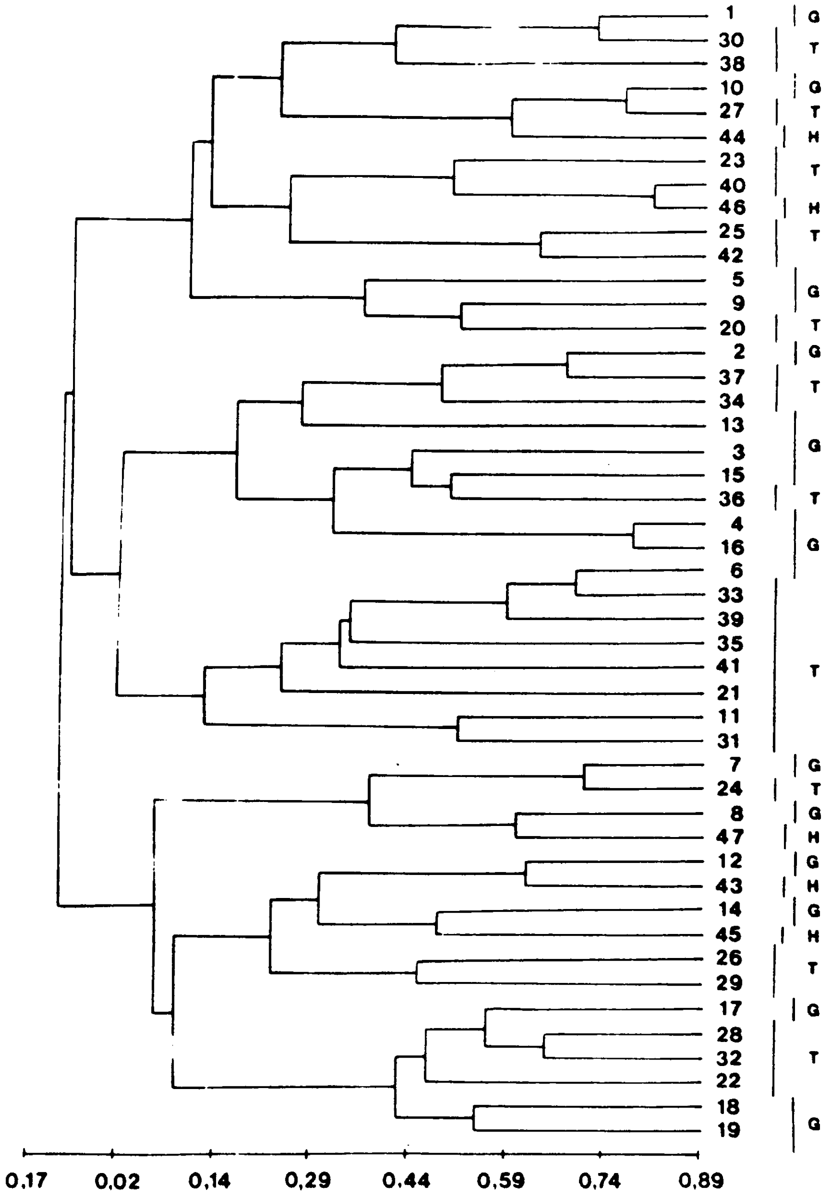


Figure 6: Correlation phenogram of specimens of <u>Arctocephalus tropicalis</u>, <u>A. gazella</u> and their interspecific hybrids clustered by the unweighted pair-group method using arithmetic averages. Cophenetic correlation coefficient = 0,534. Numbers refer to OTUs.

The ordination diagram illustrating the pairwise comparison of components I and II (Fig. 7) shows good separation between the *A. tropicalis* OTU's (20 - 42) and the *A. gazella* OTU's (1 -19) along component I with the *A. tropicalis* OTU's clustered on the left of the component scale while the *A. gazella* OTU's cluster towards the right of the component scale. The outlying *A. gazella* OTU (10) is the large specimen mentioned earlier. The interspecific hybrid OTU's (43 - 46) generally occupy an intermediate position between the two species with OTU 44 to the right of the component scale. The two species did not separate clearly along the second component as was to be expected by the small contribution by this component (3,52%) towards the total phenetic variation, although the *A. tropicalis* and interspecific hybrid OTU's did tend to cluster in the upper portion of that component when compared to the *A. gazella* OTU's.

In the ordination diagram illustrating the pairwise comparison of components I and II (Fig. 8) the separation of the *A.tropicalis* and *A. gazella* OTU's along component I is repeated. However, any further distinction was masked by the lack of separation along the third component as was to be expected from the low contribution of this component (3,10%) towards the total phenetic variation. The anomalous hybrid OTU (44) could represent a backcross with *A. gazella*.

The distinctiveness of the OTU's representing *A. tropicalis* and *A. gazella* are greatly enhanced by the addition of the minimum spanning tree (MST) connections to the principal component analyses ordination diagrams (Figs 7 & 8). All of the OTU's representing the two species have nearest relative connections with the exception of the two small Marion Island *A. gazella* OTU's (16 and 17) which are connected via an interspecific hybrid (OTU 43) to the other *A. gazella* OTU's. Revealingly, the MST connection between the two species is via an interspecific hybrid (OTU 47), emphasizing the intermediate nature of the interspecific hybrids.

Discriminant function analysis

The *A. tropicalis*, *A. gazella* and interspecific hybrids samples were compared pairwise in a two-group discriminant function analysis. The cranial variables selected by this procedure to maximize the separation between groups, and the corresponding standardized and unstandardized coefficients and the constants are presented in Table 6. The derived discriminant scores, plotted as frequency histograms (Fig. 9), clearly

Table 5: Factor matrix from the 19 variable principal component analysis of specimens of Arctocephalus gazella, A. tropicalis and their interspecific hybrids, showing the character loadings on the first three components.

Variable	Factor I	Factor II	Factor III
Condylobasal length	0,947	0,020	-0,176
Basilar length of Hensel	0,940	-0,004	-0,173
Palital length	0,924	-0,093	-0,078
Upper postcanine length	0,800	-0,132	-0,254
Optic foramen - condyl length	0,891	0,053	-0,165
Palate width - molar 1	0,946	0,094	0,167
Palate width - molar 3	0,918	-0,003	0,215
Palate width - molar 5	0,939	-0,029	0,182
Zygomatic width	0,886	0,353	0,134
Mastoid width	0,879	0,331	-0,078
Occipital Condyl width	0,806	-0,045	-0,440
Rostral width	0,957	-0,095	0,082
Maximum nasal width	0,881	-0,155	0,160
Pre-orbital process width	0,949	-0,021	0,177
Interorbital process width (ant.)	0,936	-0,119	0,179
Calvarial width	0,863	0,339	-0,067
Skull height (at Bulla)	0,930	0,126	0,008
Canine Diameter (lengthwise)	0,844	-0,393	-0,040
Canine Diameter (widthwise)	0,879	-0,246	0,068

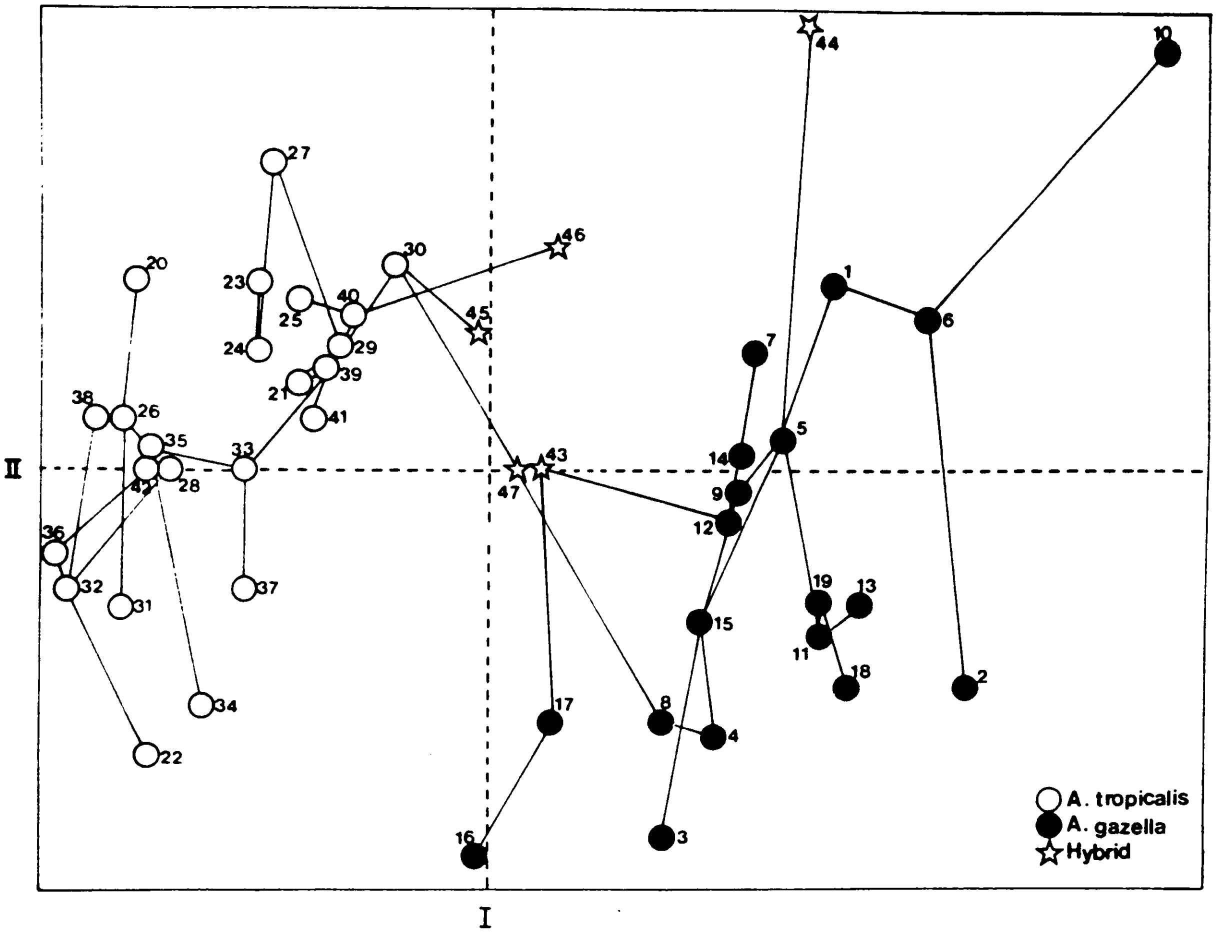


Figure 7: Pairwise comparison of factors I and II from the principal component analysis of the Arctocephalus specimens.

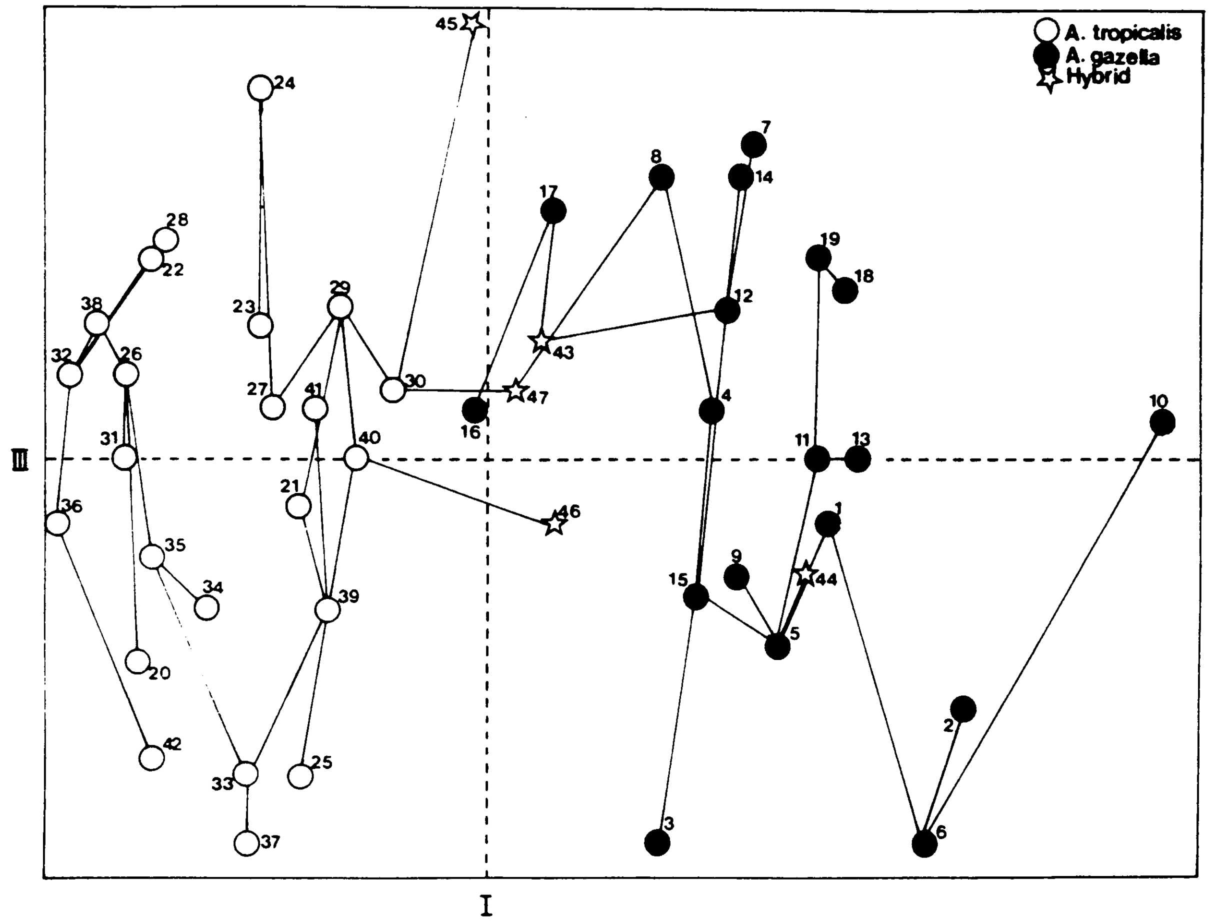


Figure 8: Pairwise comparison of factors I and III from the principal component analysis of the Arctocephalus specimens.

illustrate the separation between the two species and between the species and the hybrids. All OTU's were correctly classified *a posteriori*.

Discussion

The fur seals in this study exhibited relatively high variation (as expressed by the CV) for cranial measurements, especially when compared to skeletal measurements of bats (Swanepoel & Genoways 1978) and lagomorphs (Yates, Genoways & Jones 1979, Robinson & Dippenaar 1983). The CV's for skeletal measurements found here resemble those for the external morphological measurements in the aforementioned studies, external morphological measurements varying more than skeletal measurements (Swanepoel & Genoways 1978). This variability may be a feature of marine mammals (Repenning *et al*. 1971) and should be borne in mind when variables are selected for analyses.

The results of the multivariate analyses performed here are in agreement with earlier findings (Repenning *et al*. 1971) that *A*. *tropicalis* and *A*. *gazella* are phenotypically distinct species. The two species differ principally in the size of their skulls, with *A*. *gazella* being larger than *A*. *tropicalis*. Four measurements previously used to differentiate these two species, namely supraorbital process width, zygomatic root width, squamosal-jugal suture length and gnathion to preorbital process length (King 1959a, Bonner 1968) were found to be unsuitable for taxonomic purposes due to high intraspecific variation or interspecific overlap. The two species were most clearly separated in the phenogram generated from the distance matrix. The poor interspecific resolution obtained in the correlation phenogram was a result of the size negating effect of the correlation phenogram, which does not show clear differences between species of similar morphology. Similarly, the clearest differentiation between the two species was found along Component I (size) of the PCA ordination diagrams, with poor separation along the second and third components.

In addition to the above separation between these two species, the results of the discriminant function analyses provide a highly reliable means of distinguishing these two *Arctocephalus* species. Of the 19 variables used in this study, ten (Table 6(a)) provide maximum separation between adult male specimens of *A*. *tropicalis* and *A*. *gazella*. The measurements obtained for unknown specimens are multiplied by the measurements'

Table 6: Results of the two-group discriminant function analysis of (a) Arctocephalus tropicalis and A. gazella (b) A. tropicalis and the interspecific hybrids and (c) A. gazella and the interspecific hybrids.

Table 6(a)

Measurement	A.tropicalis $\bar{x}$(mm)	A.gazella $\bar{x}$(mm)	Unstandardised coefficients	Standardized coefficients
1. Basilar length of Hensel	194,8	217,7	-0,1058	-0,6638
2. Palate width at molar 1	22,3	28,7	0,2815	0,5423
3. Palate width at molar 3	23,4	31,3	-0,2027	-0,4086
4. Mastoid width	123,5	138,1	0,1503	1,2559
5. Preorbital process width	50,4	65,5	-0,1163	-0,3806
6. Interorbital process width (ant.)	22,0	36,9	-0,3724	-0,9358
7. Calvarial width	106,6	117,4	-0,1303	-0,6819
8. Skull height (at bulla)	86,6	99,2	0,1204	0,6024
9. Canine diameter (lengthwise)	11,1	14,2	-0,4916	-0,4239
10. Canine diameter (widthwise)	9,3	12,1	-0,4434	-0,3958

Constant 32,1282

Table 6(b)

Measurement	*A.tropicalis* $\bar{x}$(mm)	Hybrid $\bar{x}$(mm)	Unstandardised coefficients	Standardized coefficients
1. Palital length	94,5	103,4	-0,2483	-1,0639
2. Palate width at molar 1	22,3	26,4	0,4681	0,7650
3. Palate width at molar 3	23,4	29,1	-0,7595	-1,4986
4. Palate width at molar 5	28,2	36,9	-0,3032	0,8001
5. Mastoid width	123,5	134,7	0,1300	0,7350
6. Preorbital process width	50,4	61,0	0,7219	2,2678
7. Interorbital process width(ant.)	22,0	32,7	-0,9412	-2,3116
8. Canine diameter (lengthwise)	11,1	12,2	-0,5014	-0,5133

Constant 14,7029

Table 6(c)

Measurement	*A.gazella* $\bar{x}$(mm)	Hybrid $\bar{x}$(mm)	Unstandardised coefficients	Standardized coefficients
1. Upper postcanine length	64,8	61,7	0,4462	1,6466
2. Palate width at molar 1	28,7	26,4	1,3361	2,7459
3. Palate width at molar 5	40,9	36,9	-0,2565	-0,8622
4. Mastoid width	138,1	134,7	-0,2848	-2,9715
5. Occipital condyl width	54,2	51,3	0,4443	1,3862
6. Preorbital process width	65,5	61,0	1,1737	3,7747
7. Calvarial width	117,4	116,4	-0,2012	-1,4008
8. Skull height (at bulla)	99,2	95,5	-0,4715	-2,5717
9. Canine diameter (widthwise)	12,1	10,5	0,8168	0,8006

Constant -56,1406

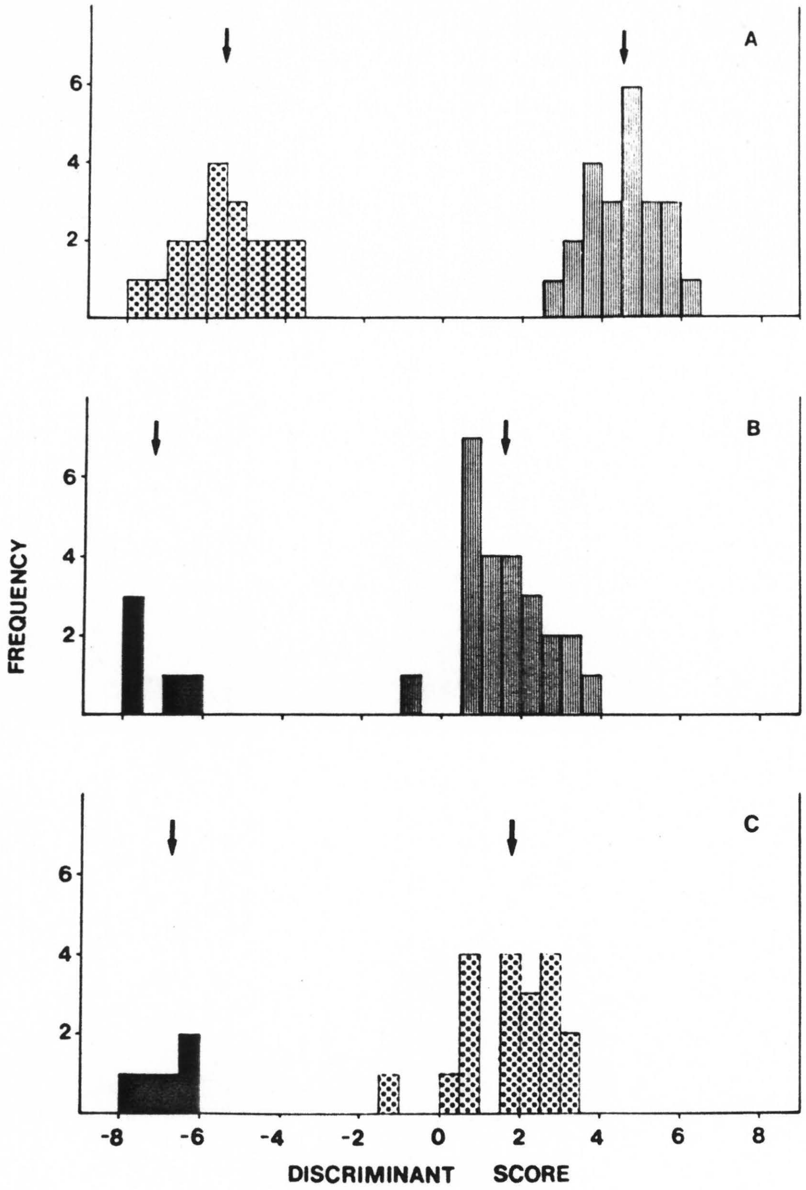


Figure 9: Histograms of discriminant scores from the two-group discriminant function analyses of (A) *A. tropicalis* (stripes) and *A. gazella* (dots) (B) *A. tropicalis* and the interspecific hybrids (solid) (C) *A. gazella* and the interspecific hybrids. Arrows indicate the positions of the mean discriminant scores.

corresponding unstandardized coefficients (Table 6(a)), summated and added to the appropriate constant. The resultant discriminant score can then be plotted in the histograms of discriminant scores (Fig. 9) and the unknown will group within the species with which it has the greatest affinity. This provides an accurate means of species identification between specimens of A. tropicalis and A. gazella, based entirely on cranial characters, and should prove of practical value in the identification of museum material of doubtful origin. At present the discriminant function analyses are limited to adult males of A. tropicalis, A. gazella and the interspecific hybrid. The benefits of including other age and sex classes as well as the remaining six arctocephaline species would be great, especially in the light of the increasing frequency of vagrant fur seals being recorded (Payne 1979a, Shaughnessy & Ross 1980, Kerley 1983).

From the PCA it is apparent that the hybrid specimens are intermediate in cranial morphology between the two parent species with some specimens tending towards one or the other parent species (eg. OTU 44). No information is available regarding the parentage of these hybrid individuals. The expected result of a diversity of generations (i.e. F1 and later hybrids, as well as hybrids backbred with the parent species) would be to produce a normal distribution of skull measurements as size is polygenic (Batt 1980).

The adult male hybrids can be phenotypically distinguished in the field on the basis of external appearance. This subjective definition of the hybrids is strongly supported by the present multivariate analyses, especially the PCA which has no a priori classification. These results tend to support the contention (Condy 1978) that these two species are hybridizing at the Prince Edward Islands. Furthermore, putative hybrids can be identified by means of the discriminant function results with a suite of eight cranial measurements providing maximum separation between A. tropicalis and the hybrids (Table 6(b), Fig. 9), or nine cranial measurements to separate A. gazella and the hybrids (Table 6(c), Fig. 9). Caution should however be exercised in the classification of putative hybrids which show affinities for the parent species in the discriminant function analysis. Multiple generation hybrids backbred predominantly with one of the parent species would be difficult to distinguish from that species. Further genetic information would be necessary for a decision in such a case.

CHAPTER 4

ELECTROPHORETICALLY DETERMINED TRANSFERRIN VARIATION

Introduction

The electrophoretic evaluation of biochemical genetic data has been used in studies of the taxonomy and population structure of a number of pinniped species including northern sea lions *Eumetopias jubatus* (Lidicker, Sage & Calkins 1981), grey seals *Halichoerus grypus* (McDermid & Bonner 1975, Heath 1978), harbour seals *Phoca vitulina* (McDermid & Bonner 1975), northern elephant seals *Mirounga angustirostris* (Bonnell & Selander 1974), southern elephant seals *M. leonina* (McDermid, Anathakrishnan & Agar 1972, Shaughnessy 1974) and southern fur seals *Arctocephalus* spp. (Shaughnessy 1970, 1976b). Shaughnessy (1970) described transferrin and haembinding protein variation in *A.p. doriferus* and *A. forsteri* and reviewed data on transferrins in other seal species.

As transferrin has been shown to exhibit polymorphisms in other *Arctocephalus* species (Shaughnessy 1970, 1976b) and is a fairly robust protein (Sutton & Karp 1965) able to withstand short periods of unfrozen storage, it was decided to investigate this protein to determine biochemical differences between *A. tropicalis* and *A. gazella* at Marion Island. It was not possible to investigate other protein systems due to the demands of other aspects of this project and limited time.

Methods

Blood was collected from live, forcibly restrained pups by cardiac puncture using a 1,20 x 38 mm (18-gauge by 1,5 in) needle, as well as from adult males killed for study material. Samples were kept cool until return to Base (4-24 h) where they were centrifuged and the serum separated and frozen. *A. tropicalis* samples were collected from two breeding colony sites, Mixed Pickle Cove and Cape Davis; *A. gazella* samples were collected from the Rook's Bay and Crawford Bay breeding colony sites. A single putative hybrid specimen was collected from Rook's Bay (Fig. 1).

Vertical polyacrilamide gel electrophoresis of serum was performed using water cooled buffer chambers with a constant voltage gradient of 8,0 V/cm for 40 min followed by 16 V/cm for 65 min. A modification of the technique of Maurer (1971), giving a small pore solution of 4%, was used. A 0,05% bromophenol blue marker indicated the extent of migration. After electrophoresis gels were fixed and stained for 2,5 h in Coomassie Brilliant Blue G (0,2 g/l in 25% trichloroacetic acid) and then destained and stored in 7% acetic acid.

Transferrin was isolated by protein precipitation with rivanol followed by rivanol-bound protein absorption onto potato starch (Sutton & Karp 1965). The resultant dilute transferrin solution was subjected to electrophoresis to locate the transferrin bands. Migration distances of transferrin bands were measured in relation to the origin and expressed as relative migration distances in relation to the distance moved by the albumin band.

Results

Two transferrin phenotypes were observed in the serum samples, namely T_fF and T_fS (Fig. 10). Transferrin F and S both possessed a major band surrounded by a hazy zone of stained protein. The strong band in each phenotype presumably represents an allele of the monomeric transferrin. These are preceded by a faint conformational band which probably comprizes proteins, denatured due to the unavoidable delay between collection and analysis, and in the T_fF phenotype there was a faint conformational band of similar mobility to the major band in the T_fS phenotype.

Population data for the transferrin phenotypes as well as the gene frequencies are presented in Table 7 (assuming Shaughnessy's (1970) inheritance pattern). These data do not permit determination of expected gene frequencies predicted by Hardy-Weinberg equilibrium. The two species appear fixed for alternative alleles; _A. tropicalis_ specimens are homozygous FF, while _A. gazella_, with one exception (a presumed rare variant) are homozygous for the slow allele. The single hybrid tested here proved to be homozygous for the slow allele.

Table 7: Population data for transferrin phenotypes and gene frequencies for *Arctocephalus* spp. on Marion Island.

Species	n	Transferrin Phenotypes T_fF	T_fS	Gene Frequencies F	S
A. gazella	28	27	1	0,96	0,04
A. tropicalis	104	-	104	-	1,00
Hybrids	1	-	1	-	1,00

Discussion

Shaughnessy (1970) postulated that the transferrin types of the southern fur seals (*Arctocephalus* spp.) are controlled by four alleles T_fA, T_fB, T_fC and T_fD at a single locus with no dominance and types A,B,C, and D representing homozygotes (T_fA/T_fA, etc.) and binary combinations of these representing heterozygotes AB, AC, AD, etc. (T_fA/T_fB, etc.). Shaughnessy (1970) recorded the phenotypes A, AC, C, AD, D and BD in the Australian fur seals *A. fosteri* and *A. pusillus doriferus* and on the basis of the above hypothesis, postulated the existence of the remaining phenotypes namely, B, AB, BC and CD. Shaughnessy (1976b) later recorded an additional transferrin type T_fP with a faster anodal migration rate than T_fA, in the Cape fur seal *A. p. pusillus* and found T_fA, T_fAC and T_fAP in this population.

Shaughnessy (1970) recorded a maximum of four bands in each phenotype with the homozygotes possessing a single major zone and the heterozygotes possessing two major zones, accompanied by two or three sub bands respectively. These sub bands may possibly be interpretated as conformational bands, produced through the denaturation of protein. The two homozygotes in the present study possessed a single major zone and and faint conformational bands. The differences in the resolution of the conformational bands between these two studies is possibly due to differences in technique (Shaughnessy 1974, Heath 1978).

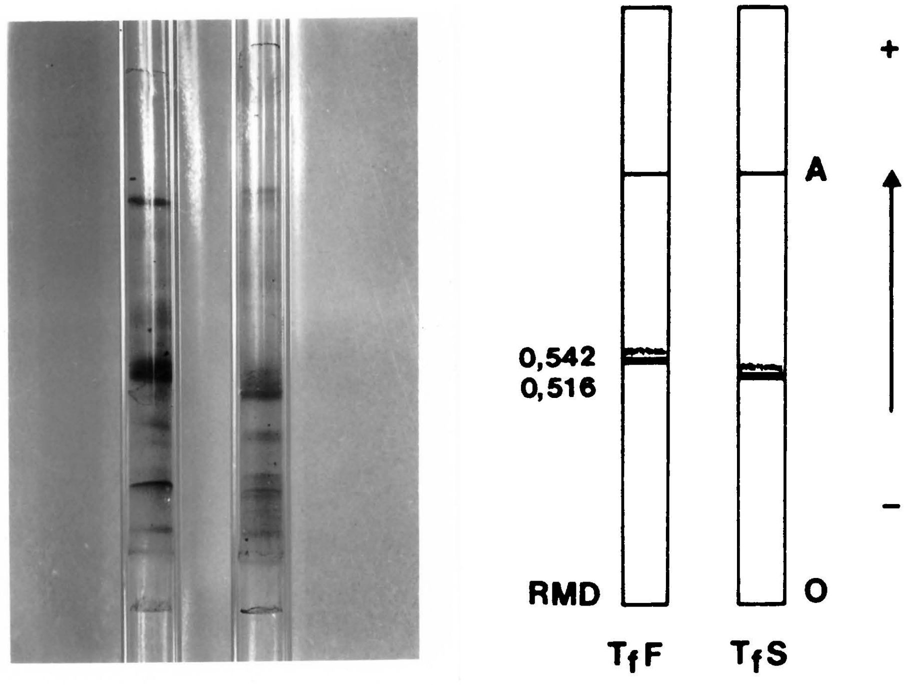


Figure 10: Electrophoretogram showing the transferrin phenotypes and relative migration rates (RMD). A = albumin, O = Origin, ↑ = direction of migration.

The two phenotypes observed here (F and S) represent homozygotes but cannot be identified in Shaughnessy's (1970) terminology, which would necessitate sampling these populations and applying comparable electrophoretic techniques. With no variation in *A. tropicalis*, and by virtue of the definition of a rare variant, probably no meaningful variation in *A. gazella*, both species sampled have a low genetic variability in terms of the transferrin locus. This could be due to the severe population bottleneck experienced by both species in the recent past due to the activities of sealers in the last century which resulted in their near extinction (Bonner 1981). These considerations, coupled wth the low genetic variability of marine mammals (Lidicker, Sage & Calkins 1981) could account for the observation of only two alleles in the present study. The variation that Shaughnessy (1970) found may be due to the fact that he sampled different populations.

The data presented here on transferrin phenotypes, although limited, are in agreement with Repenning *et al*'s (1971) conclusions based on skull morphology that *A. gazella* and *A. tropicalis* are genetically distinct species. These differences clearly provide evidence of the absence of gene flow and therefore show that these are two biologically distinct species.

The single S allele in the *A. gazella* sample could possibly represent an artifact. However this individual was a characteristic adult male, ruling out the possibility of species mis-identification; each sample was run until concurrent results were obtained, excluding the possibility of applying the wrong sample to a gel. The remaining possibility, of mislabelling a sample bottle, does exist but was guarded against in the collection procedure.

The low frequency of the S allele in the Marion Island *A. gazella* population could be an indication that this represents a rare mutant variant. The *A. gazella* population at South Georgia represents over 95% of the world stock of this species (Bonner 1981) and this population should be investigated for the presence of this allele.

A hybrid resulting from interbreeding of two species would be expected to be a biochemical intermediate (Sharp 1976). The expected transferrin phenotype of an *A. tropicalis*/*A. gazella* first generation hybrid would most likely be the FS heterozygote. The single hybrid specimen tested here, with intermediate body and skull morphology (Chapter 3, OTU 47) proved to be homozygous for the S allele and possibly represents a multiple generation back-cross hybrid. A larger sample of hybrids, preferably of known parentage, would possibly throw more light on this problem.

CHAPTER 5

POPULATION SIZES AND TRENDS, AND THE EXTENT OF HYBRIDIZATION

Introduction

In order to assess the extent of hybridization and possible interspecific competition, it was necessary to obtain an estimate of the population sizes of A. tropicalis, A. gazella and the interspecific hybrids on the Prince Edward Islands. This information, with the calculated population trends, is complementary to recent work on Gough Island (Bester 1980) and Amsterdam Island (Hes & Roux 1983).

Methods

The entire coastline of Marion Island, except for three small inaccessible coastal sections (Fig. 11), was censused by one observer on foot using direct methods from 26 January to 3 February 1981 when all pups had already been born. The accessible coastal sections of Prince Edward Island (Fig. 12) could not be counted during a single summer and the combined results (5 - 7 May 1981; 28 April and 12 - 13 May 1982) are used.

Beaches were systematically searched for fur seals and those in the inshore surf zone were included and offshore pods were ignored. All fur seals were classified according to their species, age and sex.

The following adjustments were made to the counts (vide Payne 1977, Condy 1978, Bester 1980, Laws 1980).

a. The corrections for undercounting of pups caused by the irregular terrain and the secretiveness of the pups were based on mark-recapture experiments at Sealer's and Cliff Beaches, Cape Davis, using Bailey's estimate (Caughley 1977). Pups were marked with enamel paint or monel-metal tags (Condy & Bester 1975). The mean correction factor of 16% (five trials) was expressed as a percentage of the estimated number of pups present.

b. A pup mortality figure prior to the data of the census was based on regular searches of the Cape Davis (*A. tropicalis*) and Rook's Bay (*A. gazella*) breeding colonies for dead pups. The pup counts were further adjusted by these figures to yield an estimate of the total number of births.

c. As the number of females counted was lower than the number of pups and each female normally bears only one pup (Payne 1977), the estimated number of births (adjustment b above) and the number of females were equated. The derived female numbers were further adjusted by assuming a pregnancy rate of 86%, found for *A. gazella* at South Georgia (Payne 1977), as applied to the Marion Island (Condy 1978) and Gough Island (Bester 1980) *A. tropicalis* populations.

d. The counts were not conducted during the peak haul-out of seals, therefore counts of adult males and immatures (older than one year) were adjusted by 83% and 29% respectively to compensate for known decreases at the date of the census (see Chapter 6).

e. Yearling seals were not present at the Islands during the censuses and were estimated from the previous year's pup production, using an estimated mortality to one year of age of 23,9% found for *A. gazella* at South Georgia (Payne 1977). The previous year's *A. gazella* pup production was estimated from the calculated rate of population increase (Bester 1980) determined in the present study (see Results). The previous year's *A. tropicalis* pup production was obtained from censuses during 1980/1981 (see results).

f. The counts at Prince Edward Island were carried out after the summer peak in *A. tropicalis* numbers, and the population was estimated from the pup : total number ratio determined for Marion Island.

g. More *A. gazella* pups and males were identified on Marion Island outside the census period than were counted during the census. Therefore the number of counted *A. gazella* was adjusted by the number of known individuals. Pups were marked with monel-metal tags and

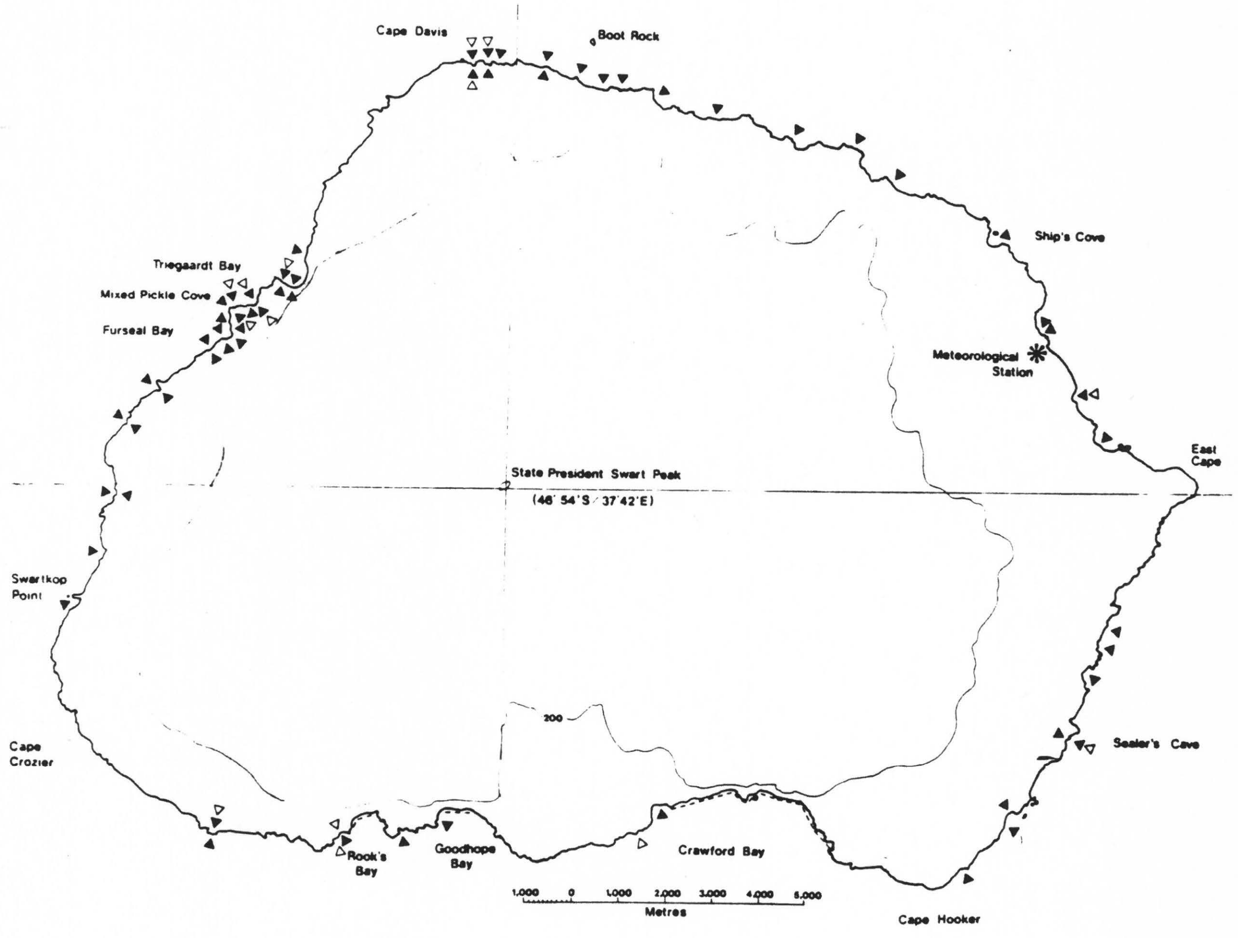


Figure 11: Marion Island, with the 200 m contour, showing localities where fur seals were recorded breeding in 1974/75 (Condy 1978, interior aspect) and 1980/81/82 (exterior aspect) (▶ = *A. tropicalis*, ▷ = *A. gazella*, ------ = inaccessible sections of the coast).

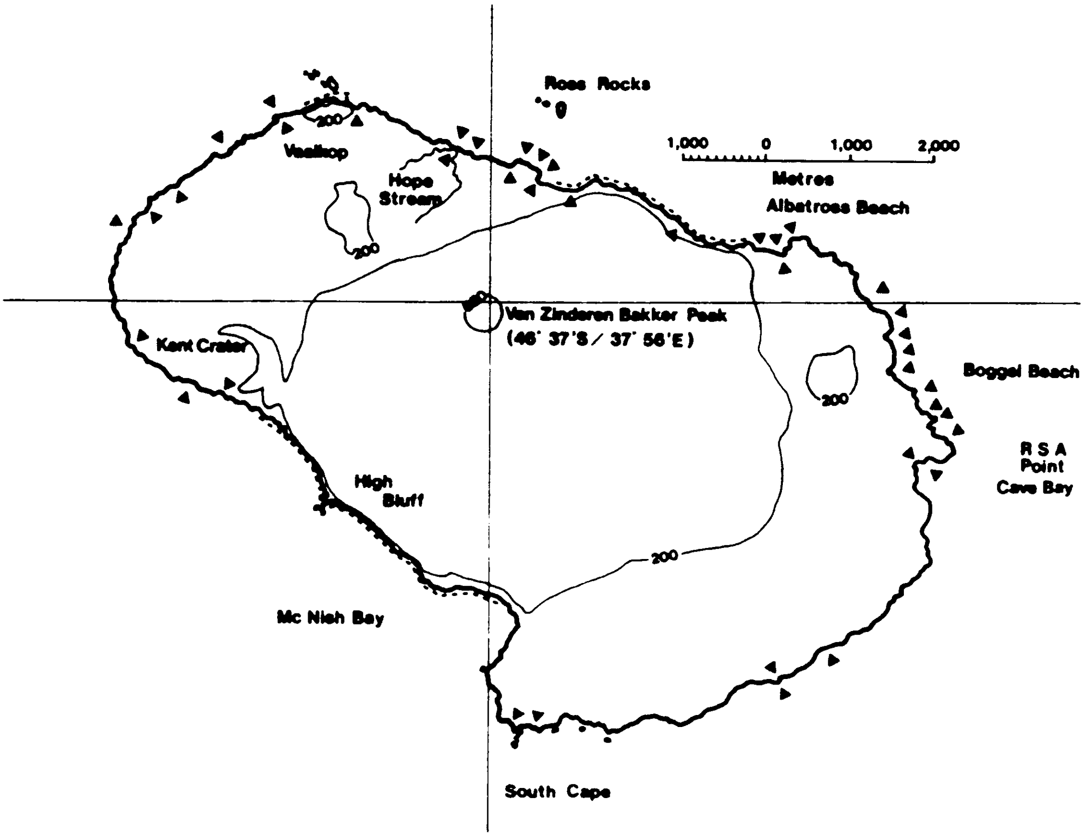


Figure 12: Prince Edward Island, with the 200 m contour, showing localities where A. tropicalis were recorded breeding in 1974/75 (Condy 1978, interior aspect) and 1980/81/82 (exterior aspect)(▶ = A. tropicalis, ----- = inaccessible sections of the coast).

individual adult A. gazella males were recognised by distinctive scars, wounds and colouration.

h. Only adult male hybrids could be identified in the field (Condy 1978), therefore the population size of hybrids was estimated from the proportion of males to the total numbers calculated for A. tropicalis on Marion Island.

The annual exponential rates of population increase (r) were calculated using data in Rand (1956a), Condy (1978), and the present results and the exponential function

$$N_t = N_o e^{rt}$$

(Caughley 1977) where

N_o = population numbers at the start of observations,
N_t = population numbers after time t,
e = base of natural logarithms.

Results

Numbers of A. tropicalis

Numbers of A. tropicalis counted on Marion Island are presented in Table 8. These figures were adjusted (a-e in Methods). The 1981/82 numbers of live pups is 3813 (a) with 4101 births (7,0% mortality, see (b)) to yield an estimate of 4768 adult females (c). The estimates of adult males and immatures are 5244 and 3554 respectively (d). The 1980/81 pup production (2535 pups counted, adjusted by (a) and 7,0% mortality for (b)) was 3256 births, with 2478 yearlings surviving to 1981/82 (e). The total A. tropicalis population on Marion Island is thus estimated to be 19857 seals.

Numbers of A. tropicalis counted on Prince Edward Island are presented in Table 9. The 2300 pups counted were adjusted for undercounting (a) and the higher mortality figure (9,4% (b)) to the later census date to yield an estimate of 3030 births. The total population of A. tropicalis on Prince Edward of 14761 is calculated from the ratio of births : total numbers (1 : 4,8) found on Marion Island.

Table 8: Numbers of A. tropicalis counted on Marion Island from 26/1/82 to 2/2/82 with adjusted totals.

LOCALITY	ADULT MALES	ADULT FEMALES	PUPS	SUB-ADULTS
Cliff Beach, Cape Davis	9	66	52	18
Sealer's Beach, Cape Davis	88	122	114	343
Cape Davis to Triegaardt Bay	42	64	6	36
Triegaardt Bay, South Section	63	247	397	187
Mixed Pickle Cove	62	147	292	205
Fur Seal Peninsula	292	1281	1984	490
Fur Seal Bay	62	210	238	73
Fur Seal Bay to Swartkop Point	51	95	22	199
Swartkop Point Beach	37	48	1	103
Swartkop Point to Rook's Bay West	54	17	8	161
Rook's Bay West	11	2	8	89
Rook's Bay to Sealer's Cave	37	9	4	210
Sealer's Cave	2	11	18	15
Sealer's Cave to Ship's Cove	17	16	21	173
Ship's Cove to Cape Davis	38	49	28	214
UNADJUSTED TOTALS	865	2384	3193	2516
ADJUSTED TOTALS	5244*	4768**	3813***	3554*

* adjustment d   ** adjustment b & c   *** adjustment a.

(See text for legends)

The total population of A. *tropicalis* on Marion and Prince Edward Islands was therefore estimated at 34528 seals.

Numbers of A. *gazella*

A total of 43 pups and 20 A. *gazella* adult males were individually identified, in addition to 14 immatures counted on Marion Island (Table 10). The pup numbers yield an estimate of 55 adult females (8,7% (b) and (c)) and 30 yearlings (e), and a total population estimate of 162 A. *gazella* on Marion Island.

The censuses of Prince Edward Island were conducted after the postweaning dispersal of A. *gazella* pups (see Chapter 6). These counts can therefore not be used to estimate the Prince Edward Island population, although the 61 A. *gazella* counted on Prince Edward Island (Table 10: combined counts for 1980/81 and 1981/82) indicate that there are approximately as many A. *gazella* on Prince Edward Island as there are on Marion Island. The total population of A. *gazella* on both Islands is thought to be in the order of 300 - 400 seals.

Numbers of Hybrids

During the 1980/81 austral summer 11 assumed hybrid adult males of which five were culled, and during 1981/82 four assumed hybrid males, were identified on both islands. Assuming that the ratio of adult males : total population is the same as for A. *tropicalis* on Marion Island (1 : 3,8) then the 1980/81 total number of hybrids is estimated at 37 seals.

Population trends

Comparable counts for 1974/75 (Condy 1978) and 1981/82 (Table 11) for Marion Island (N_o = 1115, N_t = 3193, t = 7 years) indicate a mean exponential rate of increase for unadjusted A. *tropicalis* pup numbers of 15,0% per year on Marion Island and the increase in pup numbers at the major breeding colonies is shown in Table 11. The total estimated A. *tropicalis* populations' annual rate of increase was 14,9% (N_o = 7000, N_t = 19857) over the same period, and 11,9% from 1951/52 (N_o = 500 ; Rand 1956a) to 1981/82 (t = 31 years). The mean rate of increase in A.

Table 9: Numbers of A. tropicalis counted on Prince Edward Island during 1981 and 1982.

DATE	LOCALITY	ADULT MALES	ADULT FEMALES	PUPS	SUB-ADULTS
28/4/82	Vaalkoppie West to Kent Crater Bay	22	5	5	40
12/5/82	McNish Bay to Cave Bay	21	2	2	57
6/5/81	Cave Bay	7	9	7	113
13/5/82	RSA Point to Boggel Beach	7	32	90	11
13/5/82	Boggel Beaches	20	113	561	81
13/5/82	Boggel Beach to Albatross Beach	31	213	559	71
13/5/82	Albatross Beach	7	27	125	17
7/5/81	Ross Rocks Beach	31	158	412	115
7/5/81	Ross Rocks to Hope Stream	11	39	36	9
7/5/81	Hope Stream Beach	46	144	503	338
	UNADJUSTED TOTALS	203	742	2300	852

(see text for legends and adjusted totals)

Table 10: Numbers of A. gazella counted on the Prince Edward Islands during the census periods and the numbers of recognized individuals on Marion Island.

LOCALITY	ADULT MALES	ADULT FEMALES	PUPS	SUB-ADULTS
Marion Island unadjusted counts	4	23	33	14
Marion Island recognized individuals	20	-	43	-
Prince Edward Island unadjusted counts	6	21	8	26

(See text for legends and dates of the censuses) gazella pup number on Marion Island from 1974/75 (N_o = 15 ; Condy 1978) to 1981/82 (N_t = 43, t = 7 years) was 15,1% per year.

Extension of breeding sites

Localities where A. tropicalis and A. gazella were recorded breeding on Marion Island during the 1974/75 (Condy 1978) and 1980/81 and 1981/82 austral summers are presented in Figure 11. The number of breeding localities utilised has increased. The increase of A. tropicalis pup numbers has resulted in an increase in the number of pups born within established breeding colonies (Table 11) on the west coast and an increase in the number of breeding localities on the east coast. The increase in the number of A. gazella pups is reflected in the establishment of five new breeding localities, including a relatively large colony at Crawford Bay, as well as the tenfold increase in A. gazella pups at Rook's Bay since 1974/75. There are no comparable data for Prince Edward Island before 1980/81 although an increase in the number of A. tropicalis breeding localities has occurred (Fig. 12), and the position of A. gazella breeding localities is uncertain as the censuses were carried out after post-weaning dispersal of the pups had occurred.

Discussion

Circumstances prevented carrying out sequential counts over a period of time or multiple counts in a near-instantaneous time frame which would have allowed the calculation of confidence limits around the population estimates.

The estimates of the Arctocephalus populations presented here are considered to be accurate as the censusing techniques and adjustments to the counts are valid. The application of pregnancy and mortality rates from the South Georgia A. gazella population to these populations is thought to be justified as these populations have similar histories and growth rates, and the population growth rate is a function of fecundity and mortality. Although parts of Marion Island were inaccessible, this does not detract from the accuracy of the census, as during April 1982 these sections were searched from the air by helicopter. No seals were

Table 11: Unadjusted *A. tropicalis* pup numbers, mean annual percentage increase (r x 100), proportion of pups and change in the proportion of pups on the main breeding beaches on Marion Island for the period 1974/75 to 1981/82.

LOCALITY	UNADJUSTED** PUP NUMBERS 1974/75	UNADJUSTED PUP NUMBERS 1981/82	r x 100	PROPORTION OF PUPS 1974/75	PROPORTION OF PUPS 1981/1982	CHANGES IN THE PROPORTION OF PUPS 1974/75 - 1981/82
Cliff Beach, Cape Davis	12	52	20,95	1,08	1,63	+0,55
Sealer's Beach, Cape Davis*	52	114	11,21	4,66	3,57	-1,09
Triegaardt Bay	59	397	27,23	5,29	12,43	+7,14
Mixed Pickle Cove*	118	292	12,94	10,58	9,15	-1,43
Fur Seal Peninsula*	720	1984	14,48	64,57	62,14	-2,43
Fur Seal Bay*	125	238	9,20	11,21	7,45	-3,76
Remainder of Island	25	116	21,92	2,24	3,63	+1,39
Total Marion Island	1115	3193	15,03	100	100	

* Historically recorded fur seal beaches (Rand 1956a). ** Data from Condy (1978).

observed and these exposed narrow beaches did not appear to be suitable for fur seals. Similarly, the inability to count the inaccessible sections on Prince Edward Island which appeared to have similar topography, does not affect the accuracy of the Prince Edward Island census.

Although 1500 A. tropicalis pups were tagged on Marion Island (representing 39,3% of the pups), no tagged pups were found on Prince Edward Island during April/May 1982. A significant inter-island movement of pups, which would decrease the accuracy of the Prince Edward Island census was therefore unlikely prior to the date of census. The census of Prince Edward Island was carried out during post-weaning dispersal of A. gazella, illustrating the importance of complimentary studies on the seasonal cycle of censused seal populations (Laws 1980), as a count of pups during the post-weaning dispersal would yield a serious underestimate.

The pup undercount correction factor obtained here (16%) is lower than correction factors of 34% estimated for A. tropicalis on Marion Island (Condy 1978), 33% for A. tropicalis on Gough Island (Bester 1980) and 54% for A. gazella on South Georgia (Payne 1977). Although this factor is dependant on censusing techniques, population density and topography (Payne 1977), the seal numbers extrapolated from pup counts should be considered a minumum.

The A. gazella pup numbers were not adjusted for undercounting as this figure is from individually identified pups. This figure is possibly an underestimate due to the difficulties of identifying isolated A. gazella pups in the crowded A. tropicalis colonies, but is considered a better estimate of A. gazella pup numbers than the census data.

The rates of A. tropicalis increase for the period 1974/75 to 1981/82 are higher than the 11% per year previously recorded for the period 1951/52 to 1974/75 on Marion Island (Condy 1978). The present growth rate of 14,9% per year is similar to rates found in other Arctocephalus populations after the initial slow recovery from sealing operations. On South Georgia, Payne (1977) recorded the A. gazella population to be increasing at an annual rate of 16,8% for the period 1958/59 to 1972/73, based on adjusted counts. On Gough Island unadjusted A. tropicalis pup numbers showed a 15,9% annual increase between 1955/56 and 1977/78, while the total estimated population increased by 13,9% per year over the same period (Bester 1980). On Amsterdam Island the *A. tropicalis* population showed similar trends, increasing at 7,8% and 16,5% annually from 1955/56 to 1970/71 and 1970/71 to 1981/82 respectively (Hes & Roux 1983).

It would appear that all of the abovementioned fur seal populations have been following the classic sigmoid growth pattern since the cessation of indiscriminate sealing of the last century. The Marion Island *A. tropicalis* population has completed the initial slow establishment phase, characterized by slow growth and entered the period of rapid population growth characterized by a high annual rate of increase (Bester 1980, Hes & Roux 1983). This high rate of population increase will continue until density dependent factors such as breeding space and food resources (specifically the availability of food to lactating cows) become limiting. The recovery of the Prince Edward Islands fur seal population to this phase of rapid population increase in the 60 years since the last recorded sealing (Anon. 1921) has been considerably faster than the time necessary (100 years) to reach this phase estimated by Hes & Roux (1983).

As on Gough Island (Bester 1980) and Amsterdam Island (Hes & Roux 1983) the increase in the Marion Island *A. tropicalis* population has resulted in an increase in pup numbers within established breeding colonies as well as an increase in the number of breeding localities (Fig. 11, Table 11). The annual rates of increase on beaches historically recorded as centres of fur seal activity on Marion Island (Rand 1956a) are below the average rate of increase for the whole island. These beaches have presumably acted as foci for the recolonization of Marion Island, and as on Amsterdam Island (Hes & Roux 1983), have become overcrowded with a resultant decrease in the rates of increase, probably through emigration of seals to neighbouring less crowded beaches. This is also reflected in the decrease in the proportions of pups found on these beaches in relation to the total pup population of Marion Island (Table 11). Conversely, the more recently colonized beaches have above average rates of increase and the proportion of pups on these beaches in relation to the total Marion Island pup population has increased (Table 11). The high rate of increase found for the Triegaardt Bay colonies (27,2%) is similar to that found for recently colonized sections of Amsterdam Island (Hes & Roux 1983), indicating that breeding space at these localities is as yet not limiting.

The high rate of increase in A. gazella pup numbers (15,1% per year) since 1974/75 is similar to that for the Marion Island A. tropicalis population and indicates that this population has completed the unstable colonizing phase (MacArthur & Wilson 1967). This would have relied on immigration from other populations, possibly South Georgia, which is the location of over 95% of the world population of A. gazella (Bonner 1981). However, this rate of increase is higher than would be expected at the present low population levels with the population in the establishment phase characterized by slow growth rates (Odum 1971, Hes & Roux 1983). This indicates that immigration of A. gazella is still occurring at Marion Island, in addition to the population growth through endogenous pup production.

The estimate of the number of hybrids presented here is the first quantitative assessment of the extent of hybridization between A. tropicalis and A. gazella. The method used to estimate the number of hybrids indicates the order of magnitude of the hybrid population. However should the hybrids be subject to either negative or positive heterosis, this estimate would be an over- or underestimate respectively. In terms of population sizes the hybrids represent 9,3% of the A. gazella population and 0,1% of the A. tropicalis population. It would appear that hybridization is limited and the species integrity of A. gazella and A. tropicalis is being largely maintained through behavioural, ecological or genetical processes (Condy 1978), although the possible role of A. gazella immigration is uncertain. With no previous data on the extent of hybridization it is not possible to predict any trends for the continued interbreeding of these two species.

CHAPTER 6

COMPARISON OF SEASONAL HAUL-OUT PATTERNS

Introduction

Pinnipeds exhibit seasonal patterns of presence and absence from land as a function of their nutritional and reproductive requirements (King 1983). Condy (1978) suggested that temporal differences in these seasonal haul-out patterns may be limiting the hybridization between A. tropicalis and A. gazella at the Prince Edward Islands. As slight shifts in the timing of reproductive events may be sufficient to limit or prevent hybridization between sympatric species (cf. Wood & Guttman 1982), the seasonal haul-out patterns of these two fur seal species at the Prince Edward Islands were compared. This information is also complementary to recent work on A. tropicalis at Gough Island (Bester 1981a) and Amsterdam Island (Roux & Hes in press).

Methods

A. tropicalis numbers were counted weekly by one observer at Sealer's Beach (breeding colony) and Cliff Beach (established breeding colony) at Cape Davis as well as Trypot Beach (idle colony) (Fig. 1) from September 1980 to April 1981 with additional observations at Rook's Bay (nonbreeding colony) from October 1981 to April 1982. The A. gazella seasonal haul-out was determined by irregular censuses at Rook's Bay (breeding colony) from October 1981 to April 1982. The counts of A. gazella were smoothed using a weighted mean,

$$\bar{N}_x = \frac{2N_x + N_{x+1} + N_{x-1}}{4}$$

to remove the effects of incidental fluctuations owing to low numbers of seals in this breeding colony.

All colonies were counted in the mid-afternoon peak haul-out (Bester 1977) and seals classified according to sex and age. Median birth and weaning/departure dates were calculated indirectly using a simplified probit analysis (Caughley 1977). Fur seals were considered to be moulting when they were visibly shedding fur or had accumulations of fur under their hindflipper nails.

Results

A. tropicalis seasonal haul-out

Adult males

Adult males were rarely recorded on the island during winter (M.N. Bester pers. comm.) with lowest numbers during August, September and October and increasing rapidly thereafter at all colony sites during November and December to reach a peak from mid-December to early January (Figs 13-15). Numbers declined during January to a low at the end of January/beginning February, followed by another increase to a second higher peak in early March. Numbers decreased subsequently towards winter. Some adult males commenced moulting in early January and most were moulting during the March peak, as were a few in July.

Adult females

After weaning their pups of the previous pupping season in late October, adult female numbers ashore were low in early November. Pregnant females returned towards the end of November to give birth, with numbers ashore increasing rapidly in early December to reach a maximum on 23 and 24 December for the established breeding (Fig. 14) and breeding (Fig. 13) colony sites respectively, about seven days after the peak of births. Female numbers ashore were in excess of the final pup yields for these colony sites, although some post-parturient females had already departed on feeding excursions. A small number of females also hauled out at non-breeding colony sites to give birth and some hauled out occasionally, during this period, at idle colony sites where no breeding was witnessed. After the onset of pupping females presumably entered a post-parturient oestrus and copulations were frequently recorded during the December peak in female numbers. A single attempted copulation was recorded on 14 February 1981.

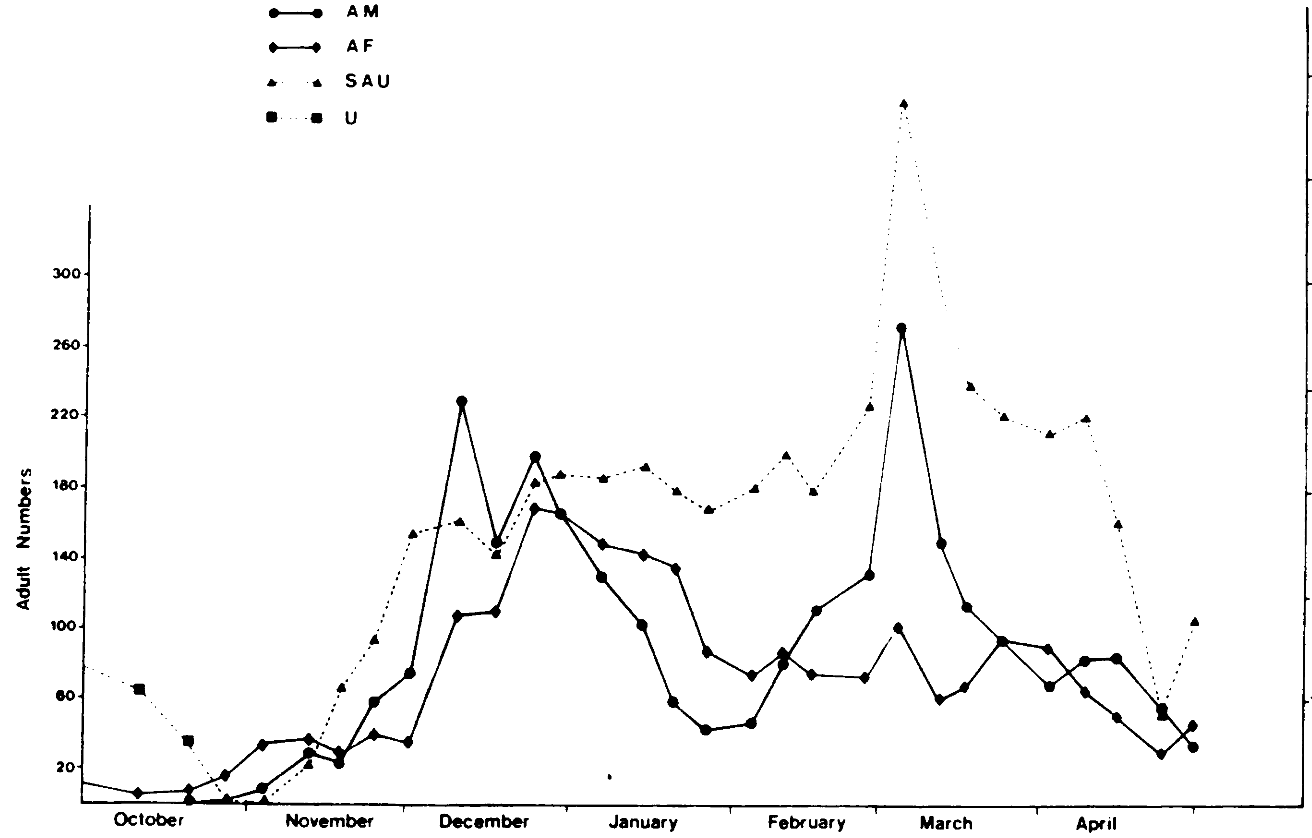


Figure 13: Changes in _A_. _tropicalis_ numbers of different age and sex classes during the austral summer of 1980/81 at a breeding colony site, Sealers' Beach, Cape Davis (for legends see text).

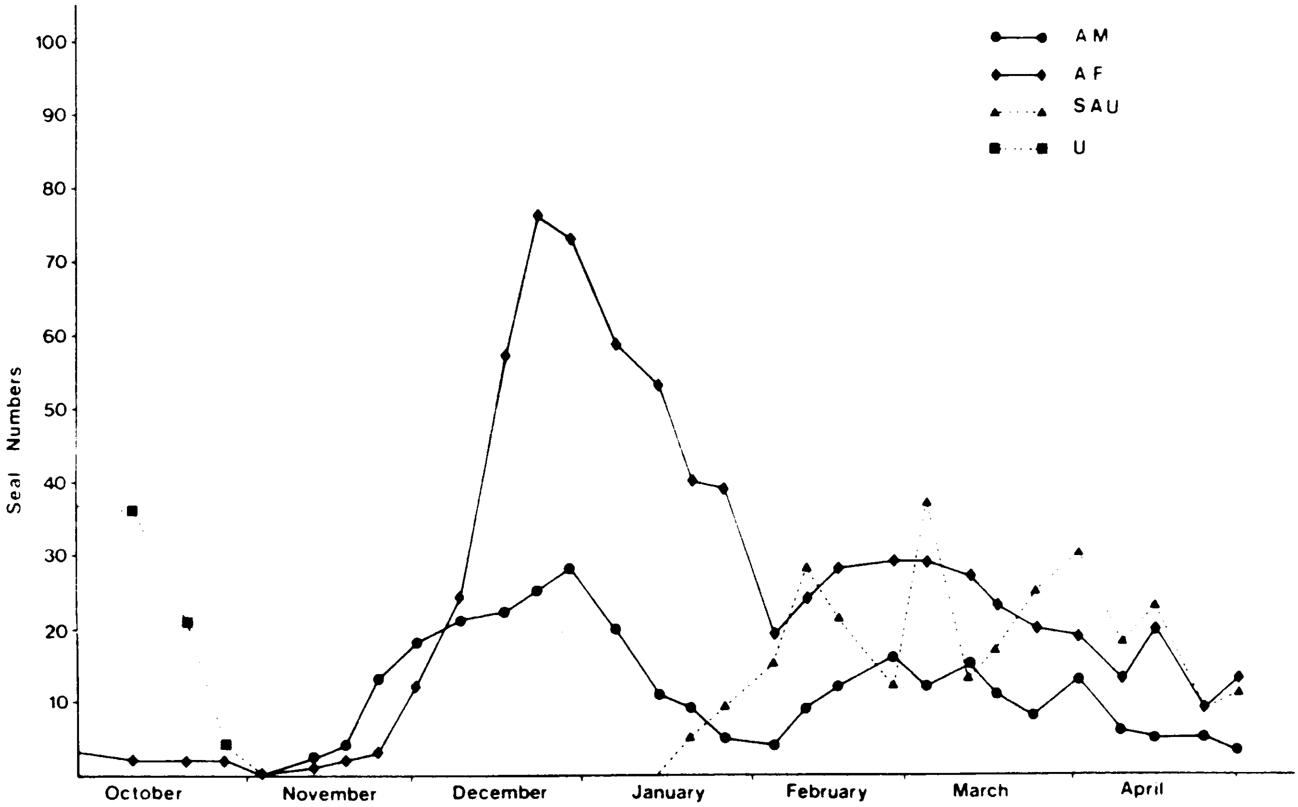


Figure 14: Changes in A. tropicalis numbers of different age and sex classes during the austral summer of 1980/81 at an established breeding colony site, Cliff Beach, Cape Davis (for legends see text).

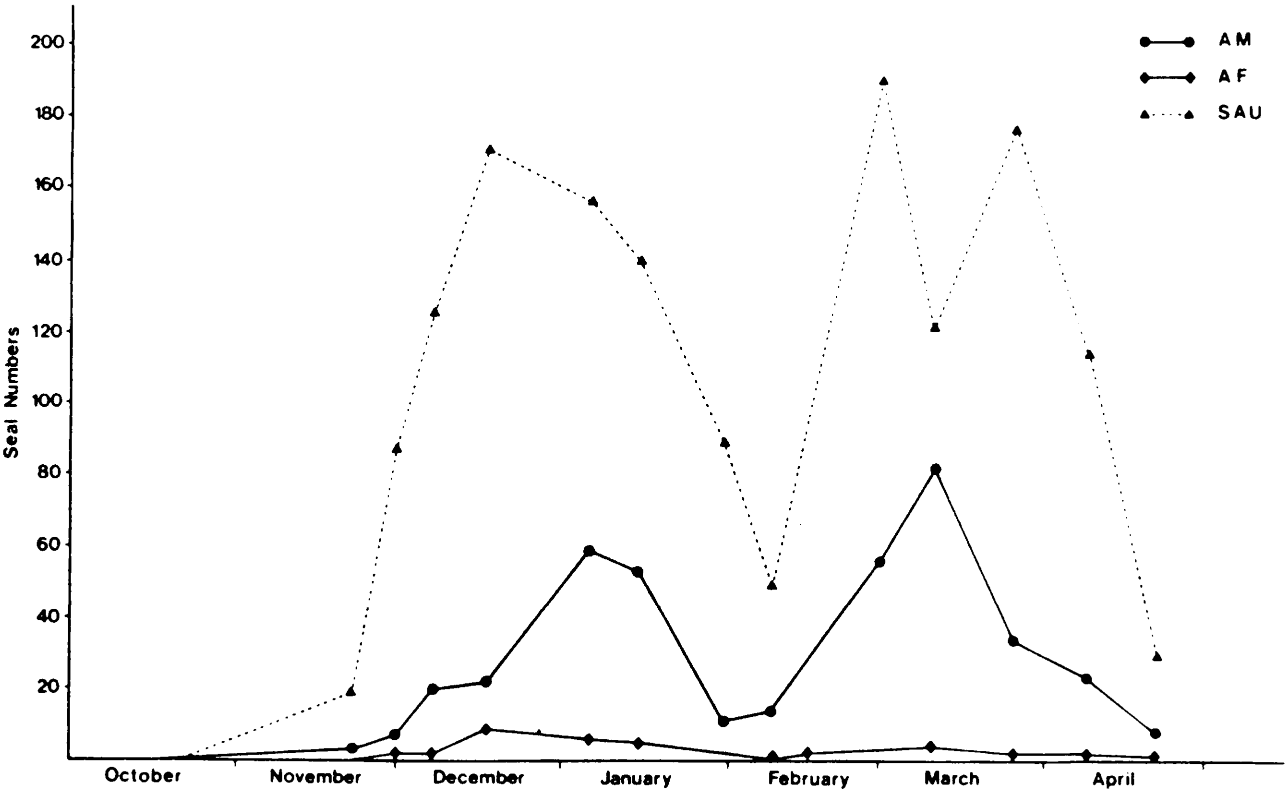


Figure 15: Changes in _A._ _tropicalis_ numbers of different age and sex classes during the austral summer of 1981/82 at a non-breeding colony site, Rook's Bay (for legends see text).

Adult female numbers declined to a low by the beginning of February, increasing again at the established breeding and breeding colony sites at the beginning of March. Lactating females returned to feed their pups throughout winter although their numbers were always lower than the number of under-yearlings present and declined towards the end of October as the under-yearlings were weaned. The timing of the adult female moult was generally the same as for the adult males.

Subadults

Subadults were present at the Island in low numbers throughout the winter, hauling-out at the breeding, non-breeding (Figs 13-15) and idle (Trypot Beach - not graphically displayed) colony sites in late November/early December. On the established breeding colony site (Fig. 14) where territorial adult males occupied most of the available beach area, subadults were absent during the December breeding peak. They started to haul-out at this locality in mid-January when the adult male numbers were declining and then fluctuated inversely in relation to the number of adult males hauled out (Fig. 14), decreasing again towards the end of April. At breeding, non-breeding (Figs 13 & 15) and idle (Trypot Beach) colony sites subadult numbers increased during December, followed by a decline in January to reach a minimum in late January/early February, especially at the non-breeding colony site (Fig. 15). Subadult numbers increased in February to a maximum for the year in early March at all colony sites (Figs 13 - 15). At the non-breeding colony site subadult numbers then decreased as adult male numbers increased, followed by another increase in subadult numbers as male numbers decreased again (Fig. 15). At all colony sites subadult numbers decreased during April to the low numbers of winter. The timing of the subadult moult was generally the same as for the adult males.

Pups and under-yearlings

Pups were born from the beginning of December to the second week in January, excluding a few premature and late births. The median date of birth at the Sealer's Beach, Cape Davis breeding colony site was 17 December 1980 with a standard deviation for the season of births of 19,1 days (Fig. 16). Pups started to moult their black natal coats in early March. On 4 March 1982 no pups inspected (n = 43) were visibly moulting, on 23 March 1982 89,2% of pups (n = 37) were moulting and by 5 April 5,3% of pups (n = 38) had completed their moult. A few stunted pups had not started to moult by May, when most pups had completed the moult to become silver-coloured under-yearlings.

By the end of January pups were entering the surf zone and rock pools, as well as the inland vegetated areas, especially when associated with freshwater streams and pools. Although some movement of pups may have occurred between neighbouring beaches, no movement to the proximate Prince Edward Island (22 km NNE) by tagged pups (n = 1400) had occurred by mid-May. Under-yearlings continued to be fed by their mothers until weaning started towards the end of September. During early October the number of under-yearlings decreased rapidly (Figs 13 & 14) and the latest observed suckling was on 27 October 1980. By early November all the under-yearlings had departed from the Island, indicating weaning at 10 - 11 months of age. Under-yearlings were absent from the Island during the breeding season, with some yearlings hauling-out to moult in April.

Total numbers

Figure 17 shows that established breeding, breeding and non-breeding colony sites have similar haul-out patterns for total numbers of seals. The low numbers during winter reached a minimum in October followed by a breeding season peak in December and a moulting season peak in March. On the established breeding colony site maximum numbers occurred during the December breeding peak (Fig. 17) while on the breeding and non-breeding colony sites, maximum numbers occurred during the autumn moulting peak.

_A_. _gazella_ seasonal haul-out

The seasonal haul-out pattern of _A_. _gazella_ at Rook's Bay for the 1981/82 austral summer is presented in Figure 18. The haul-out pattern of _A_. _gazella_ adult males was similar to that of _A_. _tropicalis_ adult males with minimum numbers in late October and late January, but the December breeding peak and autumn moulting peak were earlier and later respectively in _A_. _gazella_ than in _A_. _tropicalis_ adult males (Figs 14 & 18).

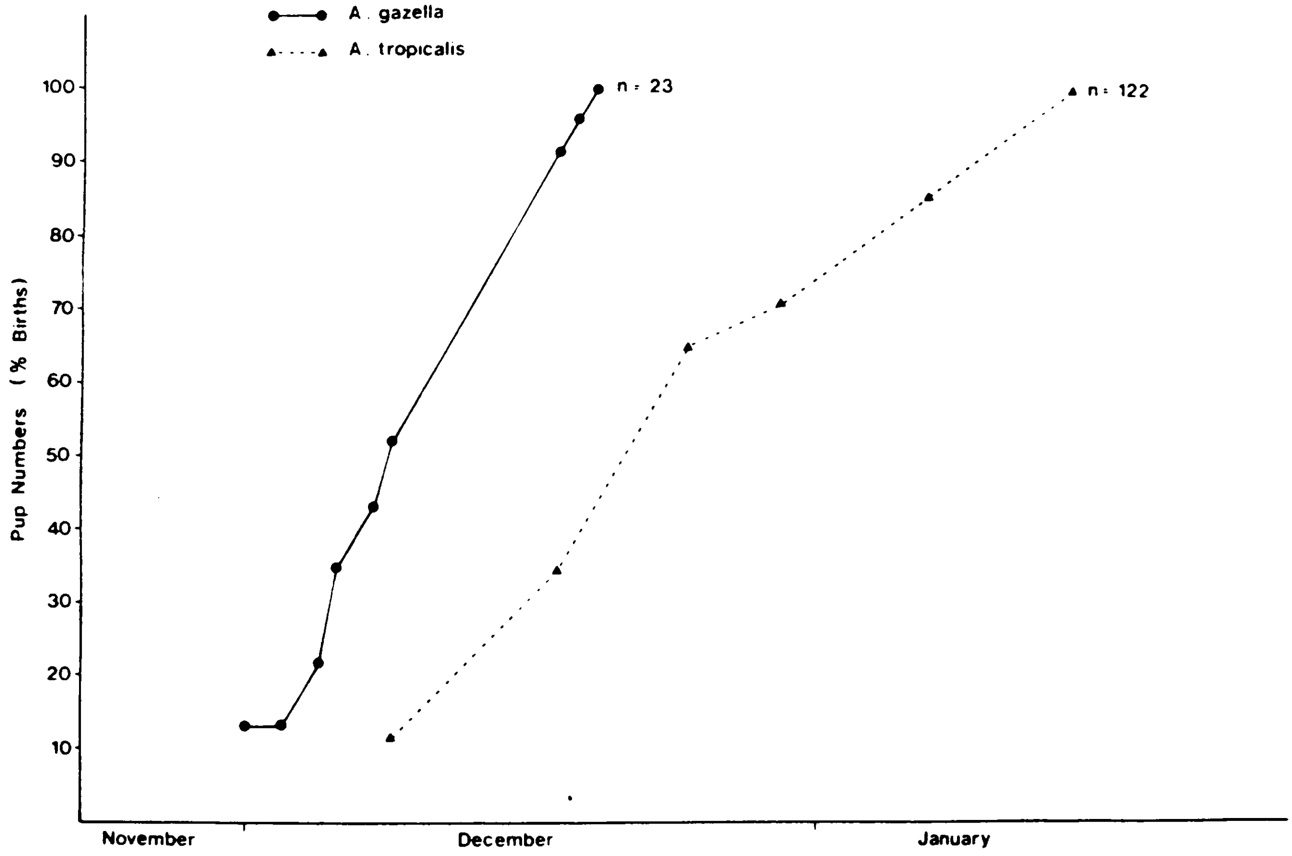


Figure 16: Season of births for A. tropicalis (Sealers' Beach, Cape Davis, 1980/81, median date of birth = 17/12) and A. gazella (Rook's Bay, 1981/82, median date of birth = 6/12) plotted as a percentage of births to date.

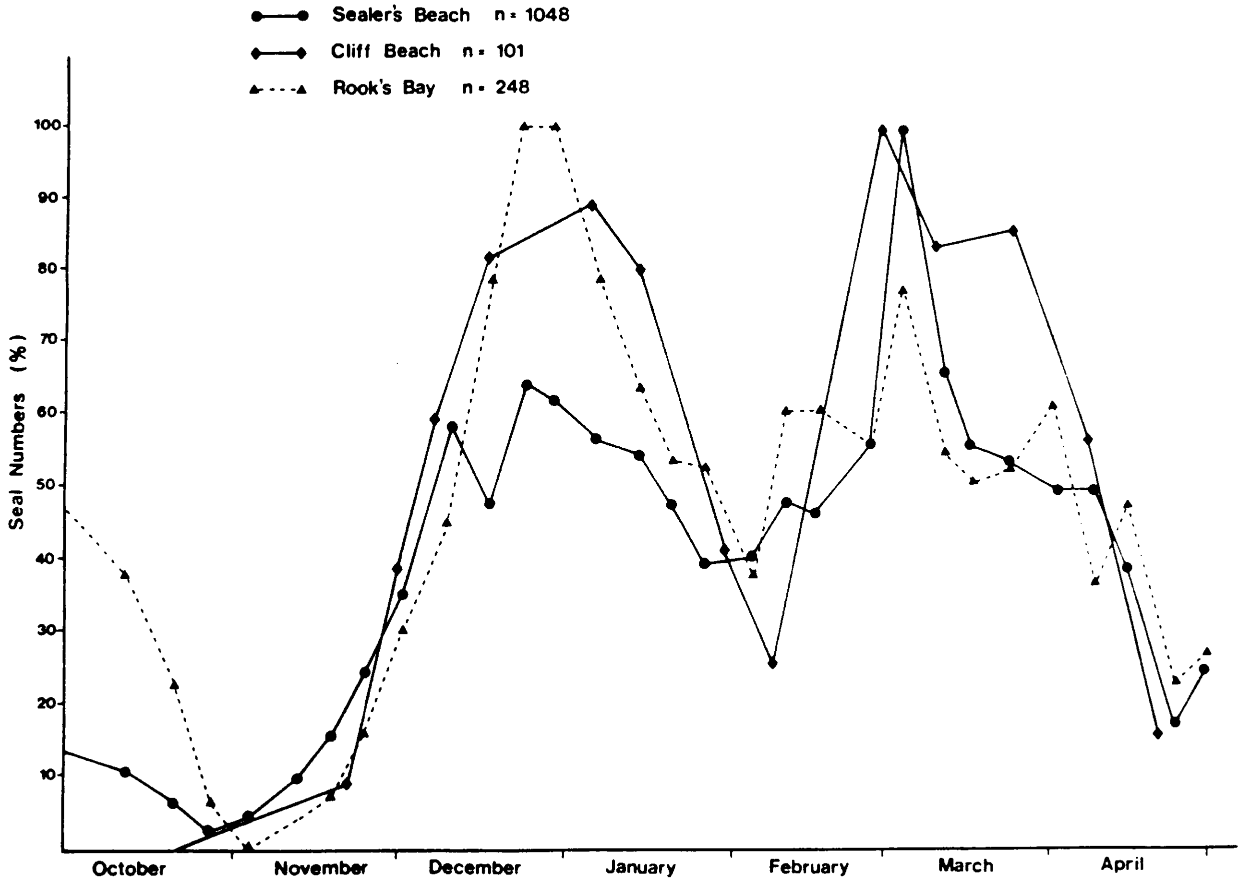


Figure 17: Changes in A. tropicalis numbers (excluding pups) at three different seal colony types, expressed as a percentage of the maximum numbers hauled out. Sealers' Beach, Cape Davis = breeding colony, Cliff Beach, Cape Davis = established breeding colony, Rook's Bay = nonbreeding colony.

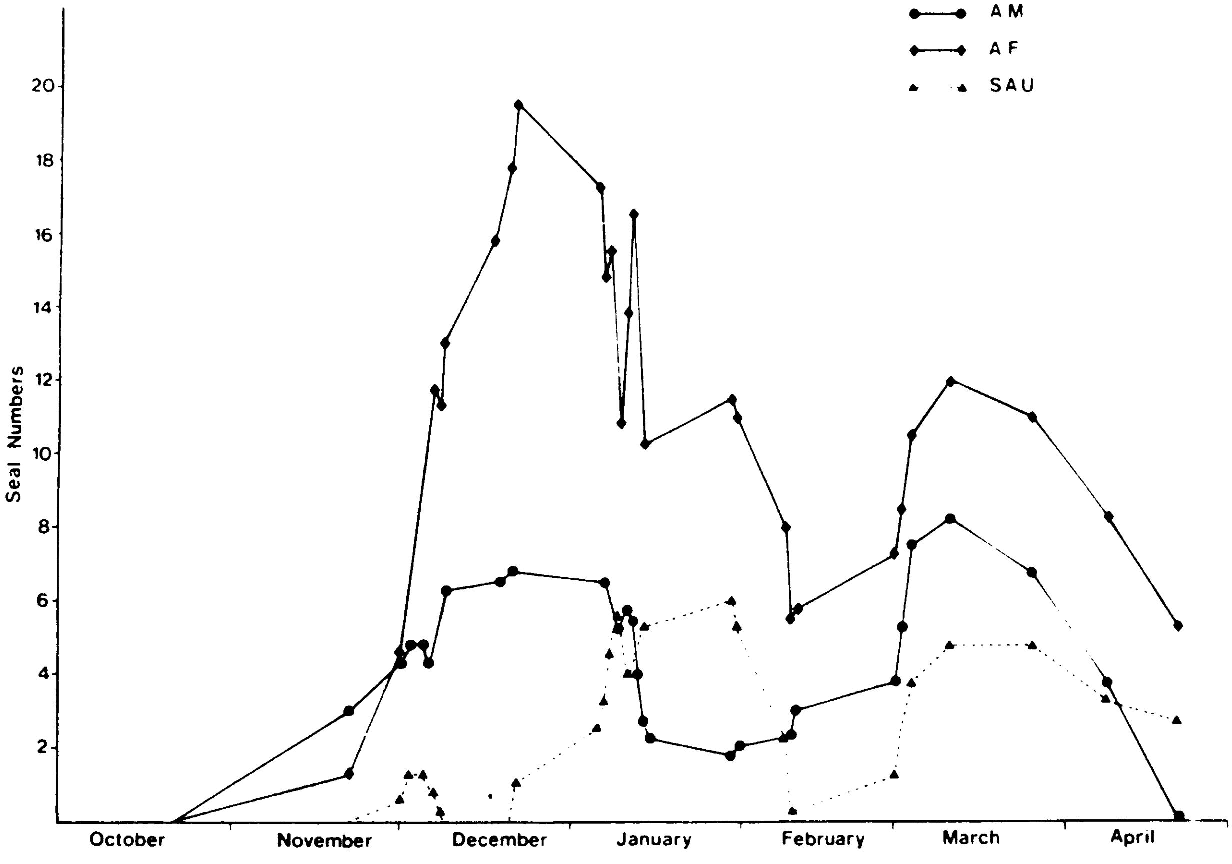


Figure 18: Changes in A. gazella numbers of different age and sex classes during the austral summer of 1981/82 at a breeding colony site, Rook's Bay. Curves smoothed by weighted mean (for legends see text).

The seasonal haul-out of adult females for *A. gazella* was similar to that of *A. tropicalis* between October and April. However,no *A. gazella* adult females were recorded on the Island during winter, from June to October (M.N. Bester pers. comm.). As in the adult males the December breeding and autumn moulting peaks were respectively earlier and later for *A. gazella* than for *A. tropicalis* adult females (Figs 14 & 18). *A. gazella* adult female numbers decreased in March/April when they started to wean their pups. The oestrus was presumably the same as in *A. tropicalis* and copulations were recorded in mid-December.

A. gazella subadult numbers were low during the December breeding peak (Fig. 18) which was similar to the situation for *A. tropicalis* subadults at the established breeding colony site (Fig. 14). This was followed by an increase as adult male numbers declined, to a peak in late January. The February low of *A. gazella* subadult numbers was similar to that of *A. tropicalis* (Figs 15 & 18) but the autumn moulting peak was later for *A. gazella* than for *A. tropicalis* subadults. *A. gazella* subadults were rarely recorded on the Island during winter, although this may be a result of the low numbers of this species on the Island.

Pups and under-yearlings

Pups were born from the end of November to mid-December (Fig. 16). The median date of birth was 6 December in 1981 with a standard deviation for the season of births of 8,3 days, indicating an earlier and shorter birth season than for *A. tropicalis*. By the end (29/30th) of January 44,4% of the pups inspected (n = 36) were moulting. On 11 February 95,8% (n = 24) of the pups were moulting and by 10 March 94,4% (n = 18) of the pups were fully moulted, indicating an earlier pup moult for *A. gazella* than for *A. tropicalis*.

By late December, as the harems began to break up, the pups started to move inland, frequently spending much of the time in freshwater pools and streams, but they did not appear to enter the sea. At least some movement to sea occurred in early February as on 10 February 55,5% (n = 18) of the pups were absent from the beach during the day, but eight of these (tagged individuals) returned during that night and the following day.

Weaning commenced in late March when under-yearlings started to depart and the median date of weaning/departure was 28 March 1982, indicating a weaning age of 112 days, markedly shorter than for A. tropicalis.

Discussion

The seasonal haul-out pattern presented here is more comprehensive than previously determined for A. tropicalis on Marion Island by Condy (1978) who presented monthly counts and did not identify the double peaked nature of the summer haul-out. This illustrates the importance of relatively frequent counts to determine the seasonal haul-out patterns of pinnipeds.

The pattern described here for A. tropicalis on Marion Island agrees well with that for the same species on Gough Island (Bester 1981a) and Amsterdam Island (Roux & Hes in press) with small temporal shifts, possibly artificially produced, owing to differences in census dates or environmental factors. Bester (1981a) and Roux & Hes (in press) observed that small temporal changes in numbers of seals ashore do occur between different years and colony sites. Features such as the median birth date would be less likely to be influenced by short-term changes in the number of seals hauled out, as numbers of seals ashore fluctuate in response to physical environmental variations (high temperatures and solar radiation - Bester 1977). It is clear that at both Marion Island (this study) and Gough Island (Bester 1981a) the different classes (AM, AF, and SAU) all show a double peaked haul-out. However on Amsterdam Island (Roux & Hes in press) and the Crozet Islands (Jouventin et al. 1982) the autumn moulting peak of A. tropicalis numbers was apparent only for adult males, possibly due to the small colonies and low representation of subadults in these studies. Also on the Crozet Islands counts were carried out on a sporadic opportunistic basis over five years, which with a rapidly increasing population (Jouventin et al. 1982) makes the interpretation difficult (see Table 2 and Fig. 3 in Jouventin et al. 1982).

The inverse relationship between adult male and subadult numbers, also recorded on Gough Island, is due to the territorial behaviour of the adult males excluding subadults from breeding colony areas (Bester

1981a). The birth season and suckling period found here for *A. tropicalis* agree well with those for other *A. tropicalis* populations (Bester 1981a; Roux & Hes in press).

The pattern described for *A. gazella* on Marion Island is similar to that for *A. gazella* on South Georgia where Payne (1979b) found a median date of birth of 4 December (6 December - this study) and an estimated weaning age of 110 - 115 days (112 days - this study).

The seasonal haul-out pattern of these two species differs in three respects. First, in the earlier, shorter pupping season and secondly the younger weaning age (112 days compared to ± 300 days with a concomitant higher growth rate) of *A. gazella* pups. Thirdly, *A. gazella* adult females and under-yearlings are absent from the Island during winter. Furthermore, the later autumn peak of *A. gazella* may be an indication that adult males, females and subadults of *A. gazella* moult later that those of *A. tropicalis*. In their absence from land during winter *A. gazella* differ from the other species of *Arctocephalus* (Rand 1959, Bonner 1981, Stirling 1971a,b).

The intraspecific synchrony and interspecific asynchronous haul-out patterns of these two species throughout their ranges suggest that genetic factors influence the timing of haul-out (see also Ling 1969, Bartholomew 1970, Miller 1975). The function of this synchrony is to ensure that the dispersed members of the species aggregate for the purpose of breeding, and that pups are produced and weaned at a time when environmental conditions are most favourable (Ling 1969). It would appear that *A. gazella* has adopted the strategy of an earlier, shorter pupping season and younger weaning age to exploit the brief summer season of the high latitudes which are *A. gazella*'s normal breeding range. At South Georgia lactating *A. gazella* females are able to exploit the summer concentrations of krill *Euphausia superba* (Bonner 1968). The short lactation period would be advantageous in that females would not have to suffer the energetically expensive costs of being pregnant and lactating during the winter when environmental conditions and food resources are presumably less favourable in the vicinity of the island breeding localities. On the other hand *A. tropicalis* is adapted to the less rigorous lower latitudes and can apparently afford to be both pregnant (implantation in April - M.N. Bester pers. comm.) and lactating during the winter.

Although there is temporal separation between the seasonal haul-out patterns of *A. tropicalis* and *A. gazella* on Marion Island, there is also extensive overlap. Adult males of both species are ashore and maintaining territories during the period when females of both species are in oestrus. Thus temporal differences in the annual cycle would not function to prevent hybridization.

CHAPTER 7

COMPARISON OF PUP GROWTH

Introduction

In an attempt to find a mechanism for the observed differences in the suckling periods of A. gazella and A. tropicalis at Marion Island, pup growth of these two species was investigated. Pup growth was also investigated in order to determine whether pup growth could indicate that A. gazella were utilising a suboptimal habitat on Marion Island with poor pup growth compared to that at South Georgia. The arctocephaline breeding strategies are compared.

Methods

Pups born during the 1981/82 austral summer were weighed using a 20 kg, 25 kg (to the nearest 100 g) or 100 kg (to the nearest 500 g) spring scale. All A. gazella pups present at the Rook's Bay breeding colony site at each weighing session (n = 13 - 21) were weighed fortnightly until their departure at the end of March. A sample of 30 - 40 A. tropicalis pups, selected at random, at the Sealer's Beach, Cape Davis breeding colony was weighed fortnightly until April and monthly thereafter until the end of September. Sex was determined and the results for males and females were analysed separately. Weight at birth was obtained from individuals less than 18 h old and pooled for the sexes to increase the sample size, as there is no significant difference in weight at birth in fur seals (Rand 1956b, Payne 1979b, Mattlin 1981).

Pups were tagged in February (Condy & Bester 1975) and the possible effect of tagging on growth was investigated by weighing tagged (n = 75) and untagged (n = 78) A. tropicalis pups on 17 May 1982. Median dates of birth of 6 December and 17 December for A. gazella and A. tropicalis respectively, were calculated indirectly using a simplified probit

Table 12: Absolute, relative and daily growth rates for male (M) and female (F) *A. tropicalis* and *A. gazella* pups on Marion Island. Mo = mass at start of period, Mt = mass at end of period.

A. tropicalis

Period Days	Sex	Mo kg	Mt kg	Absolute Increase g	Relative Increase %	Rate g/day
0-30	M	4,2	7,9	3 720	88,6	124,0
	F	4,2	7,0	2 800	66,6	93,0
30-60	M	7,9	9,9	2 030	25,6	67,7
	F	7,0	8,2	1 200	17,1	40,0
60-96	M	9,9	12,4	2 450	24,6	68,1
	F	8,2	11,1	2 900	35,4	80,5
96-109	M	12,4	14,3	1 900	15,3	146,2
	F	11,1	11,7	600	5,4	46,2
109-140	M	14,3	16,2	1 900	13,3	61,3
	F	11,7	13,2	1 500	12,8	48,4
140-287	M	16,2	16,4	200	1,2	1,4x10^{-2}
	F	13,2	13,5	300	2,3	2,0x10^{-2}
0-60	M	4,2	9,9	5 750	136,9	95,8
	F	4,2	8,2	4 000	95,2	66,7
0-109	M	4,2	14,3	10 000	240,5	92,7
	F	4,2	11,7	7 500	178,6	68,8
** 0-203	M	4,2	17,0	12 800	304,8	63,1
	F	4,2	16,1	11 900	283,3	58,6
* 0-287	M	4,2	16,4	12 200	290,5	42,5
	F	4,2	13,5	9 300	221,4	32,5

A. gazella

Period Days	Sex	Mo kg	Mt kg	Absolute Increase g	Relative Increase %	Rate g/day
0-32	M	4,2	10,0	5 760	137,1	180,0
	F	4,2	8,8	4 550	108,3	142,2
32-66	M	9,9	12,9	2 890	29,0	85,0
	F	8,8	10,9	2 190	25,0	64,4
66-97	M	12,9	16,0	3 190	24,8	102,9
	F	10,9	13,0	1 191	10,9	38,4
97-111	M	16,0	18,4	2 320	14,5	165,7
	F	13,0	13,6	560	4,3	40,0
0-55	M	4,2	11,4	7 160	170,5	130,2
	F	4,2	10,0	5 760	137,1	104,7
***0-111	M	4,2	18,4	14 160	337,1	127,6
	F	4,2	13,6	9 390	223,6	84,6

* Birth to weaning ** Birth to maximum weight

Table 13: Comparable calculated pup weights (kg) and growth rates (g/day) of male (M) and female (F) fur seals at Marion Island.

Species	Sex	Birth weight kg	Weaning weight kg	Weight gain kg	Growth rate g/day
*A. gazella**	M	5,5	17,8	12,3	110,5
	F	5,8	14,2	8,4	74,4
	M + F	5,7	15,7	10,0	89,0
*A. tropicalis***	M	5,4	-	-	77,8
	F	5,0	-	-	61,0
	M + F	5,0	-	-	71,5

* Calculated from birth to weaning.

** Calculated from birth to 120 days.

Table 14: Comparable information on weaning and growth of *Arctocephalus* spp.

Species	*A. gazella*	*A. forsteri*	*A.p.pusillus*	*A. tropicalis*
Locality	South Georgia	New Zealand (Open Bay Islands)	South Africa	Amsterdam Island
Weaning age (days)	110 - 115	± 300	± 330	± 300
Birth weight (kg ± SD)	5,9 ± 0,54 5,4 ± 0,33	3,9 3,3	6,0* 5,5	4,7 ± 0,89
Weaning weight (kg ± SD)	17,0 ± 2,60 13,5 ± 2,05	14,1 ± 0,37 12,6 ± 0,35	29,8* 23,4	18,0 14,4
Growth to ± 60 days (g/day)		60 54	85* 78	118,3* 74,0
Growth to ± 110 days (g/day)	98 84		85* 48	81,8* 76,9
Growth to ± 300 days (g/day)		37,6* 30,7	72* 54	44,3* 32,3
Reference	Payne (1979b)	Mattlin (1981)**	Rand (1956b)	Tollu (1974)

* Values calculated from data presented.

** Data for the good growth year 1975/1976.

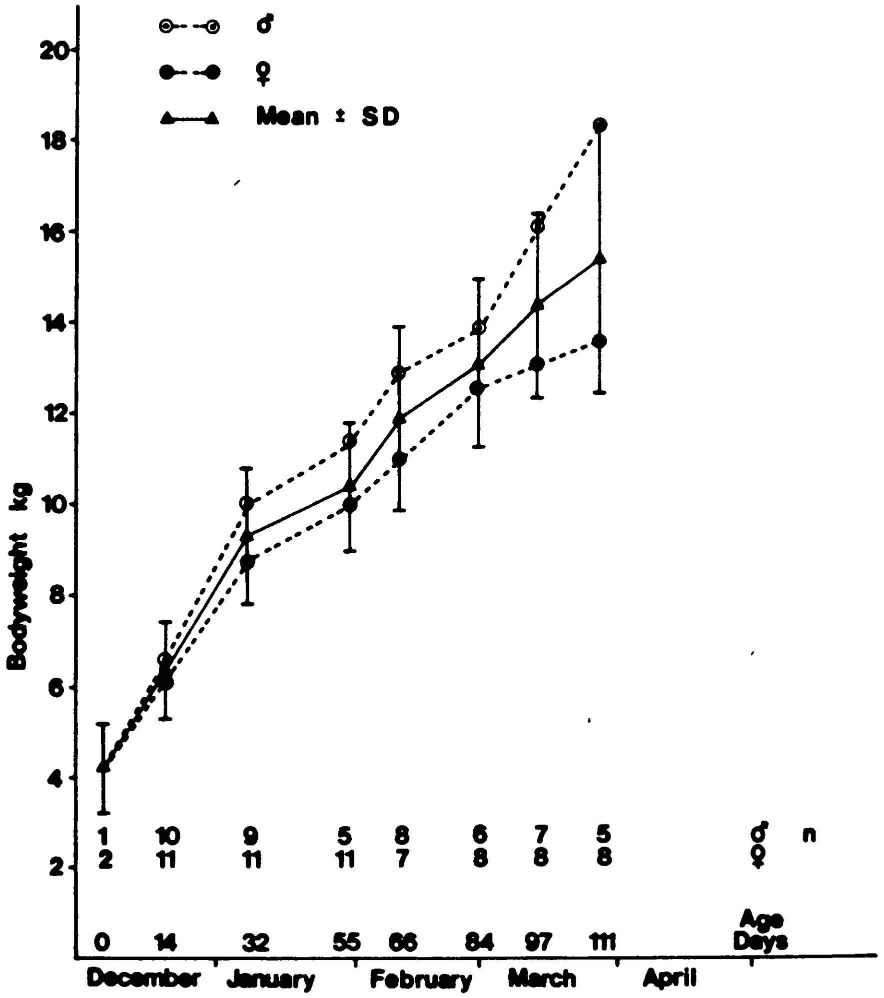


Figure 19: Weight increase up to weaning of _A_. _gazella_ pups at Marion Island.

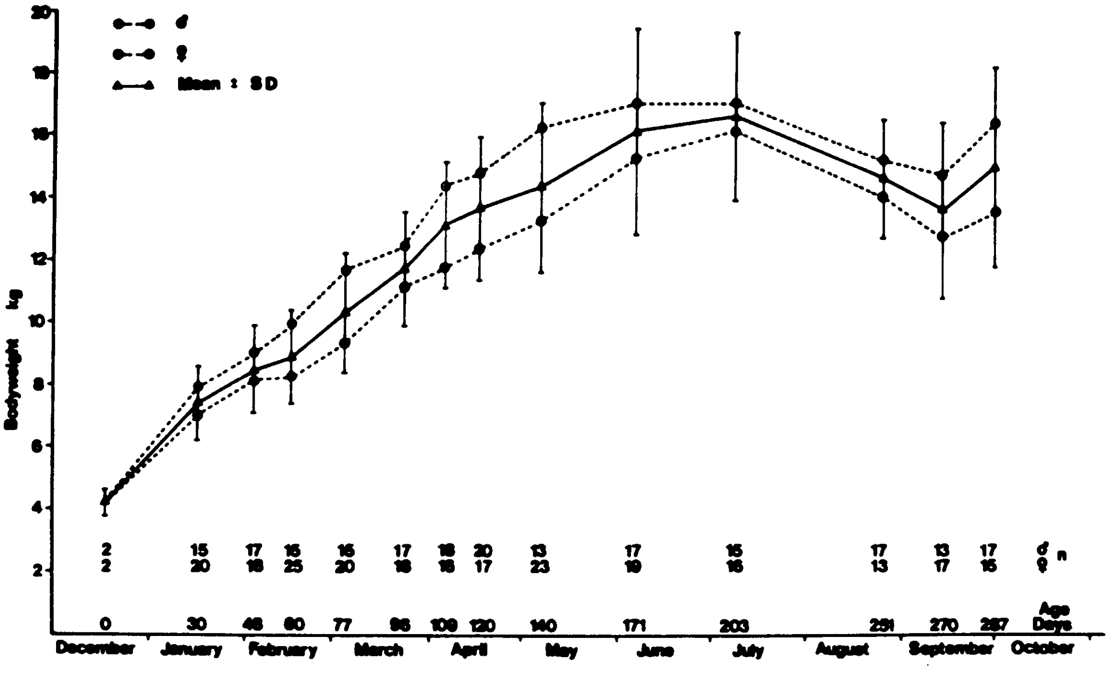


Figure 20: Weight increase up to weaning of *A. tropicalis* pups at Marion Island.

analysis, as was the median weaning/departure date of 28 March for A. gazella (Chapter 7). All ages were calculated from the appropriate median date of birth, this being valid owing to the synchrony of fur seal births.

Results

At five months of age A. tropicalis pups tagged three months previously had the same weight as untagged pups ($t = 1,25$; $p > 0,1$; $df = 181$).

The mean birth weight of both species was the same, calculated from two male and two female A. tropicalis ($x \pm S.D. = 4,2 \pm 0,4$ kg) and one male and two female A. gazella ($x \pm S.D. = 4,2 \pm 1,0$ kg). Both species showed dimorphic growth and males grew faster than females (Figs 19 & 20), although the few recorded birth weights did not differ. The A. gazella males were consistently heavier than females and were significantly heavier at weaning ($t = 4,71$; $p < 0,01$; $df = 11$). Similarly A. tropicalis males were significantly heavier than females for all months except in June/July when maximum preweaning weight was attained by both sexes.

The A. gazella pups of both sexes exhibited an extremely high growth rate in the first month, more than doubling their birth weight (Table 12). Up to weaning, mean A. gazella growth was described by the linear function ($r = 0,9936$; $p < 0,001$):

$$\text{Mass (kg)} = 5,56 + 0,089 \text{ Age (days)}. \qquad \text{Equation 1}$$

Although slower than A. gazella, A. tropicalis growth was also fastest in the first month (Table 12) and weight gain was linear up to 120 days, and is described by the function ($r = 0,9943$; $p < 0,001$):

$$\text{Mass (kg)} = 4,99 + 0,072 \text{ Age (days)}. \qquad \text{Equation 2}$$

and they doubled their birth weight by 48 days (calculated from Equation 2). After 120 days A. tropicalis growth slowed slightly until the pups peaked in weight in July at the age of 203 days (Table 12, Fig. 20), thereafter losing weight, recovering perceptibly at the end of September when they were weaned. Pup weight and growth rates calculated from the regression equations of weight on age (Equations 1 & 2 for the sexes combined) are presented in Table 13.

A. tropicalis pup growth rates for Marion Island were similar to those for the same species on Amsterdam Island (Tollu 1974) while those for A. gazella were higher than at South Georgia (Payne 1979b) (Table 14).

Discussion

Linear measurements such as standard or curvilinear lengths (American Society of Mammalogists 1967) are difficult to take accurately from live pups as they resist handling vigorously and this problem increases as the pups become larger (Tollu 1974, Mattlin 1981). On the other hand, seal pups can be weighed quickly and efficiently with the minimum of disturbance. Body weight is however not an ideal criterion for monitoring growth in fur seals as stomach contents vary and lactating females do not tend their pups constantly but depart to sea on feeding trips (mean absence in A. forsteri is 5,0 ± 2,1 days - Stirling 1971b) during which time pups fast and lose weight (Rand 1956b, Bonner 1968). Pups suckle intensively when their mothers are present, and 3,15 l of milk was found in the stomach of an A. tropicalis pup weighing 12,0 kg excluding stomach contents (Bester & Kerley 1983), representing approximately 20% of bodyweight. Consequently any sample would include both heavy, suckled pups as well as lighter, fasted pups. As feasted or fasted pups in any random sample should balance, and to allow comparison with other studies, body weight was used as the growth criterion in the present study. The birth weights calculated from the regressions of weight on age are overestimated as they are calculated from a sample that includes heavier, suckled animals. This in turn leads to an underestimation of the weight gained and therefore causes an underestimation of growth rates as seen here, and would account for the lower growth rates found for A. gazella at South Georgia by Doidge, Croxall & Rickets (1984).

Tagging has been suggested as contributing towards fur seal pup mortality (Chapman & Johnson 1968, Mattlin 1978a, Payne 1979b) and tagged pups presumably grow less well than pups that have not been tagged (Payne 1979b). However, Mattlin (1981), although discontinuing the use of tags because of doubts as to their effect on pup survival, found no apparent effect of tagging on growth. Similarly in the present study, tagging was found to have no effect on pup growth. Payne (1979b) suggested that tagging may have the greatest effect on pups under a month of age. In the present study and Mattlin's (1978a, 1981) study, pups were tagged at an approximate age of two months, possibly thereby minimizing the effect of tagging on growth.

Faster growth in males than females has been recorded in other arctocephaline species (Scheffer & Wilke 1953, Rand 1956b, Crawley & Brown 1971, Tollu 1974, Payne 1979b, Mattlin 1981). Payne (1979b) found that in *A. gazella* at South Georgia this intersexual difference in growth is maintained until female growth slowed at five years while the males continued to grow until approximately 10 years of age. Case (1978) demonstrated a linear relationship between adult body weight and growth rates in fissipeds and rodents on an interspecific comparative basis. Therefore these intersexual differences in the fur seals' postnatal growth are part of the differential growth patterns which lead to the pronounced sexual dimorphism in the fur seals where the adult males are commonly more than twice the size of the adult females. Male body size is maximized because of the ultimate advantage large body size confers on the breeding success of harem males in polygynous species (Le Boeuf & Briggs 1977, McCann 1981). With both sexes existing in the same environment and exploiting the same food resource (milk), presumably equally available, the mechanism of this differentiation in growth rates in pups must be genetic. Genetic controls influencing rapid growth rates cause more efficient utilisation of food and promote feeding rates via increased growth hormone efficiency of the anterior pituitary (Case 1978), coupled wth the protein-anabolic effects of androgens in the males (Gorbman & Bern 1962). Kolesnik & Timofeeva (1980) found that in the northern fur seal *Callorhinus ursinus* male pups have a higher efficiency of food assimilation than females. Furthermore, pup growth in *A. forsteri* differed between two successive years, possibly due to unfavourable environmental and feeding conditions, with similar pup growth for males and females in the first two months of the poor growth year while males grew faster than females for the same period in the good growth year (Mattlin 1981). It would therefore appear that in *A. forsteri*, male pups can exploit good conditions more effectively and grow faster than female pups.

The *A. gazella* birth weights at Marion Island are lower than those at South Georgia, possibly due to the small sample size in the present study. Female *A. gazella* growth to weaning and weaning weights at Marion Island (Table 12), are similar to those on South Georgia (Table 14), while these are higher for the males at Marion Island. Although the *A. gazella* sample size is small in the present study these trends do indicate that the *A. gazella* growth rates at Marion Island are higher than at South Georgia. As pup growth is probably limited by the periods that the female has to spend at sea feeding and these absences are related to food availability, it is possible that there is more food available *per capita* in the vicinity of Marion Island than South Georgia. The fur seal population at the Prince Edwards Islands is much smaller (see Chapter 5) than at South Georgia (554 000 in 1978 and increasing - Bonner 1981) suggesting less competition for the available food at the Prince Edward Islands. Competition for food at the Prince Edward Islands may be further reduced by differences in prey preferences between *A. tropicalis* and *A. gazella*. Little is known about the diets of fur seals at Marion Island although Condy (1981) estimated that *A. gazella* preyed more on krill (*Euphausia* spp.) than *A. tropicalis* which preferred fish and squid. The small difference in growth between female *A. gazella* pups at Marion Island and South Georgia could indicate that they are already growing at or near their physiological maxima (Case 1978) at South Georgia. However the males have the physiological capability to grow faster and are limited at South Georgia, agreeing with the above-mentioned strategy of males to maximise their growth. It is apparent that although Marion Island is the most northerly extension of the *A. gazella* breeding range, conditions at Marion Island are at present not marginal or limiting for pup growth.

The *A. tropicalis* birth weights, weaning weights and growth to weaning at Marion Island are similar to those determined for this species at Amsterdam Island by Tollu (1974), who found a similar growth curve with maximum weights in July followed by a decline and then slight recovery before weaning (Fig. 20). The observed decrease in body weight of *A. tropicalis* pups during July/August may result from a scarcity of food in winter, forcing the adult females to spend more time at sea and less time ashore feeding their pups. Alternatively weaning could be initiated at this time, forcing the pups to seek their own food, which would account for the increase in pup weights in September. Some of the older, larger pups could be weaned and have departed by late August, leaving the younger, smaller pups at the colony site, which would depress the mean weight obtained. This would be plausible if pups born in late November were weaned at nine months of age, within the range of weaning ages determined for *A. tropicalis* (Bester 1981a, Chapter 6).

Although some species have been poorly studied, there appear to be two widely differing breeding strategies which include differences in the suckling period and pup growth in the fur seals. The first is a short suckling period with a high pup growth rate and weaning occurring before implantation of the blastocyst, as found in *A. gazella* (Bonner 1981, present study) and *C. ursinus* (Scheffer & Wilke 1953, Gentry 1981). Both these species inhabit polar waters and are predominantly pelagic over winter. By comparison the species inhabiting more temperate latitudes, including *A. tropicalis*, *A. forsteri* and *A. p. pusillus*, have relatively long suckling periods, and slower pup growth and with weaning occurring shortly before the birth of the next pup (Table 14). The anomalously high pup growth of *A. p. pusillus* (Table 14) can be related to the larger body size of this species. These species are generally less pelagic over winter, with a proportion of the population (pups and nursing adult females) present at the breeding colony sites throughout the winter. The remaining fur seal species, *A. australis*, *A.galapagoensis*, *A. philippii* (Bonner 1981) and *A. townsendi* (Pierson 1978) appear to follow the second strategy, and the low latitude *A. galapagoensis* has a protracted lactation period (Trillmich in press).

The short lactation period of *A. gazella* and *C. ursinus* is probably an adaptation to the rigorous environment of the high latitudes where optimal seasonal conditions are usually of short duration. As a result of the short lactation periods, lactation and pregnancy, both energetically expensive, are temporally separated in these two species. Moreover, this allows the females to disperse from the breeding localities during the winter when food sources may be suboptimal to seek better food sources. The fur seal species having longer lactation periods, are adapted to the less rigorous lower latitudes and are probably not severely limited by food resources over winter, enabling the breeding females to be both pregnant (implantation in April in *A. tropicalis* - M.N. Bester, pers. comm.) and lactating over winter.

These observed differences in suckling periods and pup growth rates between *A. tropicalis* and *A. gazella* have interesting implications with regard to the observed hybridization between them, possibly acting to limit viable hybridization through pup mortality. A hybrid pup born to an *A. tropicalis* adult female would benefit from the longer suckling period, and winter pup survival could therefore be enhanced. However, a hybrid pup born to an *A. gazella* adult female, possibly possessing genes for the slower growth characteristic of *A. tropicalis*, maybe weaned prematurely and thereby limit hybridization between these species.

CHAPTER 8

COMPARISON OF BREEDING HABITAT SELECTION

Introduction

Condy (1978) suggested that differences in preferred breeding habitats of *A.tropicalis* and *A. gazella* may exist and could be functioning to reduce hybridization between these two species at the Prince Edward Islands. As habitat selection has been shown to be a viable mechanism in the prevention or limitation of hybridization (Cory & Manion 1955, Hinde 1959), the breeding habitat selection of these two fur seal species at the Prince Edward Islands was investigated.

Methods

Seal colonies were classified according to the age and sex composition during the December breeding peak, as either nonbreeding or breeding colonies. Due to the low numbers of *A. gazella* present at the Prince Edward Islands (Chapter 5), colony types of this species could not be distinguished. The occurrence of *A. gazella* pups, pure breeding aggregations, territorial adult males and nonbreeding individuals was recorded in relation to their habitat.

Habitats

As the beach topography at the Prince Edward Islands is similar to that on Gough Island, the fur seal habitat classification formulated by Bester (1982) for Gough Island was used. This is briefly as follows:

Type 1. Open boulder beach: Essentially open in character, exposed, with a gentle gradient.

Type 2. Jumbled rocky beach: Relatively steep beach with stacking of large angular rocks.

Type 3. Intermediate beach: A combination of Type 1 and Type 2 with an irregular profile and limited stacking.

Type 4. Extremely rocky beach: Massive angular talus with numerous large interstices and an irregular profile.

Type 5. Rocky platform: A relatively smooth, raised wave-cut platform.

Type 6. Offshore rocks and islets: Usually not available to fur seals due to their precipitous nature.

A detailed classification of beach topography is given by Bester (1977, 1982). Beaches intergrade between all five beach types and the classification of a single beach or section of beach was made according to the predominant physiognomic features. The above beach classification was extended by the inclusion of an accessibility index for the inland vegetated areas.

A : Inland vegetated areas easily accessible to all classes of fur seals.

B : Inland vegetated areas inaccessible to fur seal pups and under-yearlings and access is limited to the larger size classes.

C : Inland vegetated areas inaccessible to all fur seals.

Results

Habitats Available

See Figures 1 and 2 for localities mentioned here. Offshore rocks and islets are rare at Marion Island. Boot Rock is the only islet which is accessible around its base but does not appear to be extensively utilised. Fur seals occasionally haul-out on small tidal rocks. At Prince Edward Island a rocky platform at the base of Ship Rock appeared to support a small number of non-breeding _A. tropicalis_.

Open boulder beaches are common on the southeast, northeast and east coasts of Marion Island and infrequent on the west coast. The west coast is dominated by the more rugged Types 2, 3 and 4 beaches which are found scattered along the remainder of the coast. There are few Type 5 beaches on Marion Island. The vegetation in the inland vegetated areas generally belonged to the _Crassula moschata_ or _Callitriche antarctica-Poa cookii_ complexes (Gremmen 1981).

A prominant feature of the coastline of Prince Edward Island are the precipitous cliffs of the west coast which result in exposed narrow beaches which are not utilised by fur seals (Chapter 5). The north-east, southeast and east coasts of Prince Edward Island are similar to those of Marion Island with rugged Types 2, 3 and 4 beaches interspersed with more open Type 1 beaches. Although Prince Edward Island was visited after the summer breeding peak in numbers ashore of A. tropicalis, the observed distribution of breeding localities probably remained unchanged, as the under-yearlings and adult females A. tropicalis were still associated with the breeding localities on Marion Island at this time. The distribution of breeding localities for A. gazella on Prince Edward Island could not be determined as the under-yearlings had already dispersed after weaning (Chapter 6).

Habitat Selection

The distribution of fur seals at the Prince Edward Islands has been presented in Chapter 5 (Figs 11 & 12). Fur seals haul-out on and utilise all accessible habitats except for sandy beaches and flat cobble beaches which are extensively utilised by southern elephant seals M. leonina and king penguins Aptenodytes patagonicus. Fur seals do haul-out on the more rugged flanks of these beaches. At Swartkop Point on the West coast, fur seals are excluded from the rear of the large Type 2 beach by the presence of a breeding colony of Macaroni penguins Eudyptes chrysolophus.

A. tropicalis

Breeding of A. tropicalis occurred on beaches that were relatively easily accessible from the sea and provided refuge from high seas either by the availability of higher ground or the presence of a moderating factor such as a fringe of rocks to seaward or a headland acting as a breakwater. Breeding colonies occurred on the more rugged Types 2, 3 and 4 beaches (Fig. 21), with two exceptions. In Triegaardt Bay a breeding colony was located on an open boulder beach, as well as at Fur Seal Peninsula, which is a broad, rocky platform (Type 5) backed by a wide strip of talus with clusters of rocks on the platform (Fig. 22). On the latter the breeding aggregations were limited to the more rugged areas. Breeding fur seals tended to be associated with the more rugged portions of beaches that intergraded between the Types 1 and 4.

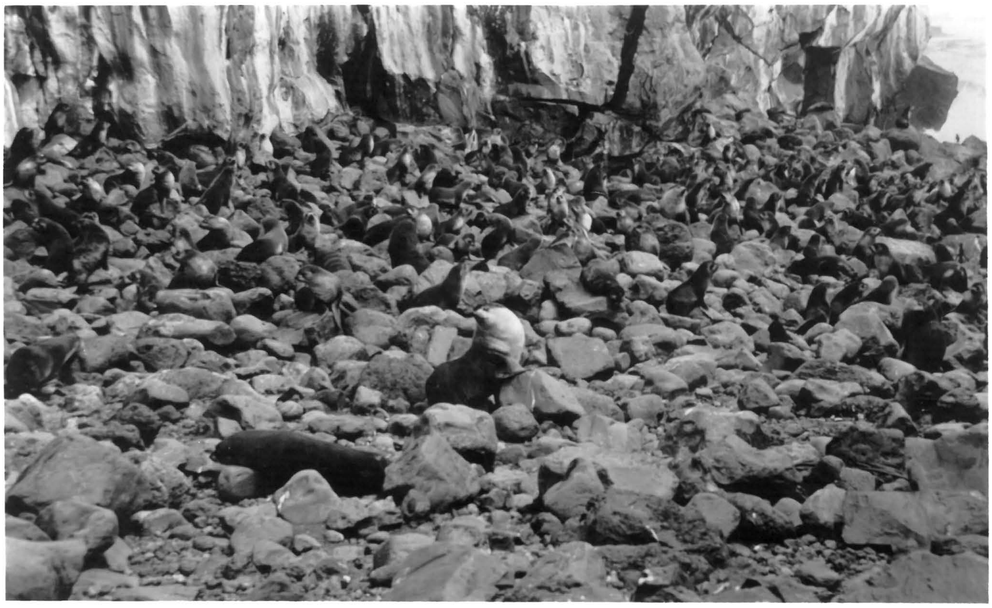


Figure 21: Mixed Pickle Cove on the west coast of Marion Island represents a type 3A beach and supports an established breeding colony of A. tropicalis.

Figure 22: A section of Fur Seal Peninsula on the west coast of Marion Island. The landward strip of talus (type 2) can be seen in the foreground with the rocky platform (type 5) in the background.

Breeding seals favoured the foreshore. Despite the accessibility of inland vegetated areas no breeding aggregations of A. tropicalis were observed on this habitat type during the December breeding season peak. After the breakup of the aggregations in January (Chapter 6) pups moved inland to the vegetated areas, especially when these areas were associated with freshwater streams and pools which the pups utilised extensively. Adult females were also frequently found in these areas, nursing their pups. The most extreme example of this inland movement was found at Ross Rocks beach on Prince Edward Island where pups were found up to 800 m inland and 50 m above sea level, on a steep grassy slope.

Nonbreeding colonies occurred on the less rugged, more open beach types and on accessible inland areas. Nonbreeding adult males and subadults were found on the vegetated areas inland of the areas used by breeding colonies, as well as the more open portions of beaches utilized by breeding colonies.

A. gazella

On Marion Island, breeding of A. gazella occurred on open Type 1 beaches or inland vegetated areas (Fig. 23). During the 1981/82 austral summer, 71% (n = 7) of the pure A. gazella aggregations were located on vegetated areas (Fig. 24) and the remaining 29% were on open Type 1A beaches. Similarly 77% of A. gazella cows (n = 39), not all within pure A. gazella aggregations, gave birth on vegetated areas, differing markedly from the preferred A. tropicalis birthsites of rocky areas. Those A. gazella cows that gave birth on rocky beaches later moved inland to suckle their pups where access to inland areas was possible. Of 34 sightings of individually identified adult males (excluding harem males), 76% were on vegetated areas, 15% on open rocky areas and 6% on jumbled rocky areas. Subadult A. gazella were most frequently encountered on vegetated areas and were never seen on rugged types 2, 3 or 4 beaches.

Figure 23: The western end of Rook's Bay on the southwest coast of Marion Island, showing a type 3A beach occupied by breeding *A. tropicalis*, a type 1A beach occupied by breeding *A. gazella* and the inland vegetated areas occupied by breeding *A. gazella* and non-breeding *A. tropicalis*.

Figure 24: An *A. gazella* harem on the vegetated area of Rook's Bay.

Discussion

The populations of fur seal at the Prince Edward Islands are increasing exponentially (Chapter 5) and do not appear to be limited by a resource such as breeding space. Therefore, although the present observations do indicate the preferred habitat types of these fur seals, the range of habitat types utilised would presumably increase under greater population pressure, with fur seals forced to use suboptimal habitats (cf. Rand 1956a, p. 76).

Distribution

The distribution of fur seals around Marion Island is similar to that on Gough Island (Bester 1982) and Amsterdam Island (Hes & Roux 1983) with the majority of breeding occurring on the west coast (Fig. 11). It would appear that the mid-latitude fur seals prefer the exposed, windward west coast of their breeding localities. A variety of reasons have been suggested for this observed distribution including: (1) the thermoregulatory benefit derived from living on the cooler, windward coasts (2) as a result of former hunting pressure, with those colonies located on the less accessible west coasts surviving and forming foci for recolonization (3) the exposed west coasts may provide the best habitat types due to the erosive action of the sea (Paulian 1964, Wilson 1974, Mattlin 1978b, Bester 1981b, 1982).

Wilson (1974) suggested that if the habitat used has significance as an aid in thermoregulation then differences in habitat selection would be expected at different latitudes of the species range. He also demonstrated some differences in habitat selection in the New Zealand fur seal *A. forsteri*. This would appear to be the case for both fur seal species at the Prince Edward Islands. The Prince Edward Islands represent the most southerly, coolest limit of *A. tropicalis*' breeding range and at the more northerly, warmer Gough (Bester 1981a) and Amsterdam Islands (Paulian 1964), *A. tropicalis* showed a relatively rigid selection for the exposed west coast for breeding colony sites. However, at the Prince Edward Islands this selection of the west coast for breeding does not appear to be as obligatory, as on Prince Edward Island, over 95% of the breeding occurs on the leeward east coast (Fig. 11, Table 10), the west coast being largely innaccessible. Similarly the Prince Edward Islands represent the most northerly, warmest breeding locality of A. gazella, which at its more southerly, cooler breeding localities chooses the protected leeward east coasts (Bonner 1968, Budd 1970, 1972, Bester 1981c). However, on Marion Island A. gazella breeds mainly on the exposed southwest coast and not on the lee coast as found further south. Therefore it is apparent that habitat selection of the fur seals on the Prince Edward Islands is a function of changing thermoregulatory requirements with changing latitude and it would appear that fur seals at the warmest or coolest extremes of their ranges select the windward or leeward coasts respectively, as a thermoregulatory aid, although accessibility, protection from high seas, etc. will all play a role.

The selection of the less accessible (for man) coasts to avoid exploitation does not explain the observed distribution of fur seals on the Prince Edward Islands. The largest concentrations of fur seals are relatively easily accessible to man and generally have associated with them signs of former sealer activities (Rand 1956a, pers. obs.).

Although the rugged Types 2, 3 and 4 habitats are more abundant on the west coast of Marion Island, possibly due to the erosive action of the sea, these habitat types are found on the remainder of the coast but are more intensively utilised by A. tropicalis on the west coast.

A. tropicalis

Similarly to Gough (Bester 1982), Amsterdam (Paulian 1964), and Possession Islands (Jouventin et al. 1982), A. tropicalis on the Prince Edward Islands prefers to breed on rocky, rugged beaches. The choice of irregular terrain may provide protection from weather extremes, with shelter from direct solar radiation (Bester 1982) as well as shelter from wind, rain and snow (Rand 1956a). Adult females do not obligatorily pup in caves or crevasses as suggested by Condy (1978), as A. tropicalis are not confined to rugged beaches but may also breed on open boulder beaches.

The availability and use of inland vegetated areas on the Prince Edward Islands leads to aggregations of fur seals utilizing an area containing markedly different habitat types. The age and sex composition of fur seals utilising an area varies with the habitat type. The mechanism of separation of the different age/sex groups into the different habitat types is probably through the aggressive behaviour of adult males holding territories in the preferred rugged breeding habitat. The nonbreeding adult males and subadults are thereby excluded from this habitat and occupy the less preferred open rocky and vegetated areas. Similarly, the movements of pups and adult females into the inland vegetated areas is possibly to avoid adult males which aggressively occupy territories after the aggregations have broken up in January.

A. gazella

Inland vegetated areas and open rocky beaches are the preferred breeding habitat of *A. gazella* on Marion Island. This does not appear to be a result of the exclusion of *A. gazella* from the more rugged habitat types by *A. tropicalis* as this species also uses the vegetated and open rocky areas. At South Georgia *A. gazella* utilises open shingle beaches and access to and utilisation of vegetated areas is a common feature of their breeding localities, although rugged rocky areas are extensively utilised (Bonner 1968). On McDonald Island *A. gazella* were found breeding on a sandy beach with non-breeders on an adjacent boulder beach (Budd 1972). On the Crozet Islands Jouventin *et al*. (1982) found that *A. gazella* preferred vegetated or open rocky areas.

Speciation of the Southern fur seals is thought to have occurred allopatrically (Davis 1958) with recent contact between *A. gazella* and *A. tropicalis* (Jouventin *et al*. 1982, Condy 1978). In instances of recent species contact, species separating ethology, which would prevent hybridization and limit competition, has frequently not had sufficient time to develop (Gill 1980), although differences in habitat preferences may be important in this regard (Hinde 1959). Pinnipeds cannot develop exclusive breeding habitat preferences as they are limited to the fringes of their terrestrial breeding localities, and sympatric pinnipeds will have some overlap in their habitat requirements. However, as demonstrated with southern elephant seals *M. leonina* and fur seals *A. tropicalis*, interspecific competition for breeding areas is limited by differences in habitat selection (Condy 1978, Bester 1982). Similarly it would appear that competition between *A. gazella* and *A. tropicalis* at Marion Island may be reduced by the observed differences in their breeding habitat preferences.

The ecological separation between *A. tropicalis* and *A. gazella* on Marion Island during their terrestrial phase, through observed differences in preferred breeding habitat types, is in agreement with Condy's (1978) suggestion. However, these differences in habitat selection do not appear to be sufficient to prevent hybridization as breeding localities of both species overlap on open rocky beaches. In addition, sexually mature, non-aggregation *A. tropicalis* adult males (idle bulls) are found on the preferred *A. gazella* breeding localities, and the subadults of both species associate with each other at non-breeding localities.

An important feature of the overlap in breeding habitats of these two closely related species is that the proximity of their breeding localities may allow opportunities for potential heterospecific imprinting (Manning 1979, Martin 1982). Similarly, a consequence of the subadults of both species associating with each other on the vegetated areas may be a failure to fully develop interspecific discriminating behaviour which would prevent hybridization.

CHAPTER 9

CONCLUSIONS

The results of this investigation support the recognition of *A. tropicalis* and *A. gazella* as valid species. Besides external appearances these two species may be separated using both morphometric and electrophoretic techniques. *A. tropicalis* and *A. gazella* have similar skull morphology and the delimitation of adult males of these two species is largely dependent on the overall size differences of their skulls, *A. gazella* having larger skulls than *A. tropicalis*. The inclusion of other age and sex classes into the multivariate analyses would be of use in the identification of these species. Electrophoretically *A. gazella* exhibited a greater transferrin mobility than *A. tropicalis* with no apparent gene flow between these two species, as indicated by the analysis of this single locus. Greater protein polymorphism is expected if more loci are examined, contributing significantly towards a better understanding of the interrelationships between these two species.

Despite the aforementioned validity of these two species status, it would appear that they are hybridizing at the Prince Edward Islands, in agreement with Condy's (1978) suggestion. The hybrids can be phenotypically distinguished in terms of their external appearance in the field, as well as in terms of their cranial morphology, the last mentioned criteria being an objective method.

The extent of hybridization between *A. tropicalis* and *A. gazella* at the Prince Edward Islands is however limited to only 0,1% of the total estimated fur seal population at the Prince Edward Islands of approximately 35000 seals. Furthermore when this is compared to the total world population of these two species (c. $1,6 \times 10^6$ seals - Bester 1980, McCann & Doidge in press) the extent of hybridization is at present insignificant and does not invalidate the recognition of these two species.

At the Prince Edward Islands a greater proportion of the smaller A. gazella population will suffer the risk of hybridization, than the more numerous A. tropicalis (Anderson 1977, Alatalo, Gustafsson & Lundberg 1982), with the hybrid numbers representing approximately 10% of this population. Conversely, the low numbers of A. gazella at the Prince Edward Islands are probably acting to limit the extent of hybridization, by reducing the number of interspecific contacts that can be made. Similarly, hybridization, whether successful or not, would limit the endogenous increase of the A. gazella population at the Prince Edward Islands, as hybridization would make use of A. gazella reproductive potential. The A. gazella population at the Prince Edward Islands appears to be partially maintained by immigration of A. gazella from other localities. The most likely source of these seals would be South Georgia where the 1984 population was estimated to be c. 1,2 million seals, and increasing (McCann & Doidge in press). The number of interspecific contacts that can be made at the Prince Edward Islands therefore appears to be a function of the immigration of A. gazella from South Georgia, which is in turn probably related to the fur seal population expansion at that locality.

Observed differences in seasonal haul-out patterns of A. tropicalis and A. gazella do not appear sufficient to prevent hybridization as suggested by Condy (1978), as their breeding periods overlap and A. tropicalis adult males are already hauled out by the time that A. gazella adult females come ashore to give birth before the onset of a post-partum oestrus. Concomitant with their earlier weaning, A. gazella pups grow faster than A. tropicalis pups. These differences in suckling periods and pup growth rates between the two species may act as a mechanism to limit hybridization through pup mortality, as a hybrid pup born to an A. gazella adult female may be weaned prematurely. Similarly to the differences in seasonal haul-out patterns, the observed differences in breeding habit preferences of these two species are insufficient to prevent hybridization as breeding localities of both species overlap on open rocky beaches and sexually mature A. tropicalis adult males are found on inland vegetated areas which are the preferred breeding habitat of A. gazella.

The limited extent of hybridization and the high percentage of A. gazella births within pure A. gazella harems (82%) indicates that some degree of species recognition does occur. The mechanisms of this species recognition are probably behavioural. The vocalizations of two species do differ markedly (unpubl. data) and other behavioural differences, beyond the scope of this project, probably occur.

It is not known whether the hybrids are reproductively viable and none of the identified hybrid adult males were observed in a harem situation. Should the hybrids prove to be reproductively nonviable, then the present situation would represent a waste of reproductive effort by the parents of such hybrids (Alatalo et al. 1982). In order to investigate this aspect of these species interrelationships it would be necessary to set up a long term experiment in captivity where family relationships can be manipulated to produce interspecific hybrids which could be used to test reproductive viability as well as supply material for further genetic analyses.

SUMMARY

The present study was initiated to investigate the interrelationships between the two species of fur seals, A. tropicalis and A. gazella which are sympatric and appeared to be hybridizing on the Prince Edward Islands. A description of the study area, the history of taxonomic confusion of these two species and their worldwide distribution are presented by way of introduction.

The skull morphology of a sample of adult male subantarctic fur seals A. tropicalis (from Marion Island) and Antarctic fur seals A. gazella (from Marion Island and South Georgia) as well as their interspecific hybrids (from Marion Island) were compared. Individual variation was found to be high and 19 variables were included in the multivariate analyses. Phenograms were generated based on both the distance and correlation matrices, and showed good separation between the two species. In the principal component analyses, the first component (size) accounted for 81,36% of the variation, while the second component (shape) contributed a further 3,52% of the variation. The two species separated well on the two dimensional projection of the first two components, with the putative hybrids plotting between the two species clusters. Species integrity was tested using an a priori discriminant function analysis which confirmed all classifications as correct. These results support the contention that these two species are hybridizing at the Prince Edward Islands and allows positive identification of adult males of both species and the interspecific hybrids.

An electrophoretic investigation of transferrin polymorphisms was performed to determine whether there were any biochemical differences between these two fur seal species. Two transferrin phenotypes were observed, with A. gazella showing a higher transferrin mobility than A. tropicalis, with no apparent gene flow between the two species. The results for the single hybrid specimen were ambiguous.

Fur seals were counted at the Prince Edward Islands during the 1981/82 austral summer. Classified counts, adjusted for pup undercounting and mortality, pregnancy rates and seasonal haul-out patterns, provided population estimates of 34528 A. tropicalis, between 300-400 A. gazella and 37 interspecific hybrids. Both species showed a population growth

rate of 15,0% annually and have expanded their breeding distribution on the Islands. At present the extent of hybridization appears limited.

The seasonal haul-out patterns of A. tropicalis and A. gazella were determined by regular counts of seals at seal colonies on Marion Island during the 1980/81 and 1981/82 austral summers. Both species showed similar patterns with summer (breeding) and autumn (moulting) peaks in numbers ashore in December and March respectively. The A. gazella haul-out was before that of A. tropicalis with an earlier calculated median date of birth. A. gazella pups were weaned earlier than A. tropicalis pups. The differences in the seasonal cycle between the two species are not sufficient to prevent hybridization as their breeding periods overlap and A. tropicalis males were already hauled out by the time that A. gazella females came ashore to give birth before going into a post-partum oestrus.

Fur seal pups at Marion Island were weighed frequently until weaning (112 days in A. gazella and ± 300 days in A. tropicalis) and the mean birthweight of both species was the same (4,2 kg). Males grew faster than females as part of the differential growth patterns which lead to adult sexual dimorphism. A. gazella growth was linear to weaning and faster than A. tropicalis growth which was linear to 120 days of age, slowing until 203 days of age and thereafter losing weight but recovering perceptibly prior to weaning. A. gazella pup growth at Marion Island is faster than at South Georgia, indicating that conditions at this, their most northerly breeding locality are not limiting for pup growth. The decrease in A. tropicalis pup bodyweight in July/August may result from either a scarcity of food in winter or weaning having been initiated. The two groups (polar and non-polar) of fur seals exhibit two strategies which include differences in pup growth and suckling period, the polar species having a short suckling period and rapid pup growth and are predominantly pelagic over winter, while the more temperate species have a longer suckling period and slower pup growth and are less pelagic over winter. These differences in suckling periods and pup growth rates between the two species may act as a mechanism to limit hybridization through pup mortality, as a hybrid pup born to an A. gazella female may be weaned prematurely.

The breeding habitat preferences of these two species at the Prince Edward Islands were investigated. The preferred breeding habitats of A.

gazella are inland vegetated areas or open rocky beaches, while *A. tropicalis* prefers to breed on rugged, rocky beaches but will also breed on open rocky beaches. Therefore, although there are some differences in breeding habitat preferences, these are not sufficient to prevent hybridization as breeding localities of both species overlap on open rocky beaches and sexually mature *A. tropicalis* adult males are found on inland vegetated areas.

In conclusion it would appear that although *A. tropicalis* and *A. gazella* are phenotypically valid species, they are hybridizing at the Prince Edward Islands. The extent of hybridization appears to be limited principally by the low *A. gazella* numbers reducing interspecific contact. Further phenetic, electrophoretic and captive interbreeding investigations are desirable.

OPSOMMING

Die huidige studie is aangepak om die onderlinge verwantskappe tussen die twee spesies pelsrobbe, A. tropicalis en A. gazella, wat simpatries is en skynbaar op die Prins Edwardeilande kruisteel, te ondersoek. 'n Beskrywing van die studie area, die geskiedenis van die taksonomiese verwarring tussen hierdie twee spesies en hul wêreldwye verspreiding word ter inleiding aangebied.

Die skedelmorfologie van 'n monster volwasse subantarktiese pelsrobmannetjies, A. tropicalis, (vanaf Marioneiland) en Antarktiese pelsrobmannetjies, A. gazella (vanaf Marioneiland en South Georgia) sowel as hul interspesifiese hibriede (vanaf Marioneiland) is vergelyk. Daar is bevind dat individuele variasie hoog is en 19 veranderlikes is in die veelvoudig-veranderlike ontledings ingesluit. Fenogramme, gebaseer op beide die afstand - en korrelasiematrikse, is gemaak en het 'n duidelike skeiding tussen die twee spesies aangedui. In die hoofkomponentontleding was die bydrae van die eerste komponent (grootte) verantwoordelik vir 81,36% van die variansie, terwyl die tweede komponent (vorm) 'n verdere 3,52% tot die variansie bygedra het. Die twee spesies het goed geskei op die tweedimensionele projeksie van die eerste twee komponente, en die veronderstelde hibriede was tussen die twee spesiesgroepe geleë. Die geldigheid van die spesies is getoets deur 'n a priori diskriminantfunksieontleding te gebruik wat al die klassifikasies bevestig het. Hierdie resultate ondersteun die standpunt dat die twee spesies op die Prins Edwardeilande kruisteel en dit laat positiewe uitkenning van volwasse mannetjies van beide spesies, sowel as die interspesifiese hibriede toe.

'n Elektroforetiese ondersoek van transferrien-polimorfismes is uitgevoer om vas te stel of daar enige biochemiese verskille tussen die twee spesies pelsrobbe bestaan. Twee transferrien fenotipes is waargeneem, met A. gazella wat 'n hoër beweeglikheid van transferrien getoon het as A. tropicalis, met geen opsigtelike genevloei tussen die twee spesies nie. Die resultate vir die enkele hibried was dubbelsinnig.

Pelsrobbe is gedurende die 1981/82 suidelike somer by die Prins Edwardeilande getel. Geklassifiseerde tellings, aangepas vir ondertellings van welpies en sterftesyfer, dragtigheidstempo en

seisoenale aankomspatrone, het bevolkingsskattings van 34528 *A. tropicalis*, tussen 300-400 *A. gazella*, en 37 interspesifieke hibriede gelewer. Beide spesies het 'n jaarlikse bevolkingsgroei van 15% getoon en het hul teelkolonies se verspreiding op die eilande uitgebrei. Skynbaar is kruisteling teenswoordig beperk.

Die seisoenale aankomspatrone van *A. tropicalis* en *A. gazella* is deur gereelde tellings van robbe in robkolonies te Marioneiland gedurende die 1980/81 en 1981/82 suidelike somers vasgestel. Beide spesies toon soortgelyke patrone met somer (teling) en herfs (verharing) pieke in getalle opland. (respektiewelik Desember en Maart). Die *A. gazella* aankoms was voor die van *A. tropicalis* met 'n vroeër berekende mediaan van geboortedatums. *A. gazella* welpies was vroeër as *A. tropicalis* gespeen. Die verskille in die seisoenale siklus tussen die twee spesies is nie genoegsaam om kruisteling te verhoed nie aangesien hul teeltydperke oorvleuel en *A. tropicalis* mannetjies alreeds aan wal was teen die tyd dat *A. gazella* wyfies aan wal gekom het om geboorte te gee, alvorens die *post partum* estrus.

Pelsrobwelpies te Marioneiland is herhaaldelik tot en met spening (112 dae in *A. gazella* en ± 300 dae in *A. tropicalis*) geweeg, en die gemiddelde geboortegewig van beide spesies was dieselfde (4,2 kg). Mannetjies het vinniger as wyfies gegroei wat deel vorm van die differensiele groeipatrone wat tot volwasse geslagsdimorfisme lei. *A. gazella* se groei was reglynig tot en met spening en vinniger as *A. tropicalis* se groei, wat reglynig was tot 'n ouderdom van 120 dae, vertraag het tot op 203 dae, en daarna 'n gewigsverlies getoon het met 'n merkbare herstelling voor spening. Die groei van *A. gazella* welpies te Marioneiland is vinniger as te South Georgia, wat aandui dat omstandighede hier, hul mees noordelike teel-lokaliteit, nie beperkend vir die groei van welpies is nie. Die afname in die liggaamsgewig van *A. tropicalis* welpies in Julie/Augustus mag voortspruit uit of 'n skaarste aan voedsel in die winter, of deurdat spening 'n aanvang geneem het. Die twee groepe (polêr en nie-polêr) pelsrobbe toon twee strategieë wat verskille in die groei van welpies en die sogingstydperk insluit; die polêre spesies met 'n kort soogtydperk en snelle groei van welpies wat oorwegend pelagies gedurende die winter is, terwyl die meer gematigde spesies 'n langer soogtydperk en langsamer groei van welpies toon en in 'n mindere mate pelagies gedurende die winter is. Hierdie verskille in sogingstydperke en welpie groeitempo's tussen die twee spesies mag as 'n meganisme dien om kruisteling deur welpie-mortaliteit te beperk, aangesien 'n hibried-welpie wat uit 'n *A. gazella* wyfie gebore is, te gou gespeen mag word.

Die habitatsvoorkeur vir teling by die twee spesies op die Prins Edwardeilande is ondersoek. Die voorkeurhabitat vir teling van *A. gazella* is binnelandse plantbegroeide gebiede of oop klipstrande, terwyl *A. tropicalis* voorkeur aan gebroke klipstrande gee, maar ook op oop klipstrande teel. Dus, alhoewel daar sekere verskille in die habitatsvoorkeur vir teling is, is dit nie voldoende om kruisteling te verhoed nie aangesien teelkolonies van beide spesies op oop klipstrande oorvleuel en volwasse, geslagsrype *A. tropicalis* mannetjies op binnelandse plantbegroeide gebiede aangetref word.

Ter afsluiting wil dit voorkom dat, alhoewel *A. tropicalis* en *A. gazella* fenotipiesgesproke geldige spesies is, hul wel op die Prins Edwardeilande kruisteel. Dit wil voorkom asof die mate van kruisteling hoofsaaklik deur die lae *A. gazella* getalle, wat interspesifiese kontak verminder, beperk word. Verdere fenetiese, elekroforetiese en in gevangenskap kruisteling ondersoeke is wenslik.

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