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HABITAT SELECTION, SEASONAL POPULATION CHANGES, AND BEHAVIOUR OF THE AMSTERDAM ISLAND FUR SEAL *ARCTOCEPHALUS TROPICALIS* ON GOUGH ISLAND

by

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by

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ABSTRACT

The population size and seasonal cycle of the Amsterdam Island fur seal *(A. tropicalis)* at Gough Island (40°20′S, 9°54′W) were investigated in the summers of 1974/75 and 1975/76. Population size was determined by direct census of part of the coast, and by comparison with a reliable total census made in the summer of 1955/56. Correction factors for undercounting and seasonal cycle were applied. Population size is approximately 100 000 and is the largest known population of this species.

Seasonal cycle for various age and sex groups was determined by regular counting at four study beaches. A definite summer breeding peak and an autumn moulting peak exist in *A. tropicalis* at Gough Island. The peak in numbers ashore during the moult is an hitherto undescribed feature of the seasonal cycle of the Arctocephalinae.

Mainly nonbreeding seal colonies occur on the east coast while the breeding colonies are situated on the west coast. Their location is determined by topographical, oceanographic and climatological factors.

The diurnal haulout and activity patterns of *A. tropicalis* are described and environmental factors that modify it are discussed. High local ambient temperatures and solar radiation during the summer have a definite influence on the fur seals. Behavioural and postural adjustments are made use of to supplement physiological means of thermoregulation.

Postures and vocalizations as a means of communication in inter- and intrasexual encounters were investigated, and territorial male behaviour studied during the breeding season. Adult males show a seasonal change in territoriality and five territory types are distinguished, based on their location on the beach, time of formation, duration of maintenance, size, topographical definition, and their success in attracting females.

Interactions between territorial males involve little physical contact, with boundary displays to affirm territory boundaries and advertise territorial status, being more common. Fighting technique and boundary displays are described, as well as adult male involvement with adult females. The latter is mainly directed at the containment of females on a territory, assessment of their reproductive state and possibly also has a communicative value. Females' reactions towards the attention of adult males usually have elements of submission.

Mother-pup relations were investigated and an account is given of general intra- and interspecific behaviour.

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INTRODUCTION

MAMMAL RESEARCH ON GOUGH ISLAND

Since 1965 the South African Antarctic and Subantarctic research activities has been administered by the Department of Transport, on the advice of the South African Scientific Committee on Antarctic Research (SASCAR). The Mammal Research Institute of the University of Pretoria was made responsible for mammal research on the Prince Edward group of islands, Gough Island and in the South African sector of Antarctica. With permission from the British Government and the blessings of the British Antarctic Survey, the Mammal Research Institute commenced research on Gough Island, a British possession, during October 1974. Research efforts were directed at the two pinniped species breeding on the island i.e. the Amsterdam Island fur seal, *A. tropicalis*, and the Southern elephant seal, *Mirounga leonina.*

IDENTITY OF THE FUR SEAL ON GOUGH ISLAND

Based on cranial and dental characteristics King (1959a) separated the Amsterdam Island fur seal and the Kerguelen fur seal *A. gazella*, only at a subspecific level. as *A.g. elegans* and *A.g. gazella* respectively. Subsequently King (1959b) changed these names to *A. tropicalis tropicalis* and *A. t. gazella.* King (1959b) also noted that *A. t. tropicalis* inhabited islands north of the Antarctic Convergence while *A. t. gazella* occurred on islands south of the Antarctic Convergence. Previously these fur seals were considered conspecific and termed *A. gazella,* whilst Peters (1875) described the fur seals of Kerguelen as *Arctophoca gazella.* Swales (1956) termed the Gough Island fur seal *A. gazella* whilst Elliott (1953) thought them to be *A. pusillus.* However, Repenning, Peterson and Hubbs (1971) in a recent taxanomic review finally concluded that *A. t. tropicalis* and *A. t. gazella* were in fact two separate species and assigned the specific name of *A. tropicalis* (Gray, 1872) to the fur seal on Gough Island.

DISTRIBUTION AND NUMBERS OF *A. tropicalis*

A. tropicalis breed on Gough Island (Swales 1956), Nightingale and Inaccessible Island (Wace and Holdgate 1975), Amsterdam Island (Paulian 1964), Saint Paul (Segonzac 1972), Marion (Rand 1956) and Prince Edward Island (de Villiers and Ross 1974).

No breeding has been recorded on Tristan da Cunha (Elliott 1953; Wace and Holdgate 1975) although it may in fact occur*, whilst stragglers were reported from the Crozet Archipelago (Despin, Mougin and Segonzac 1972), the South African coast (Nel 1971) and South Georgia (Laws *in litt.*). A single specimen was reported from Maquarie Island (Csordas 1962).

Accounts of numbers of *A. tropicalis* on subantarctic islands show that Gough Island, even in the absence of accurate recent data, supports the largest population anywhere. Approximately 13 000 fur seals were counted during the period November 1955 to 1956 (Swales 1956). Segonzac (1972) counted 4 868 fur seals on Amsterdam Island during March 1970 and 353 fur seals on Saint Paul Island during February 1970. Swales (1956) estimated the population on Nightingale and Inaccessible Islands at approximately 600 animals. Condy *(pers. comm.)* estimated the Marion Island population at 8 000 seals with a further 2 500 on the neighbouring Prince Edward Island during 1974/75.

MOTIVATION

The present study was undertaken to assess the numerical status of *A. tropicalis* on Gough Island. This would provide information on the historical trend in abundance of the Gough Island population, and an up to date figure for application in the stock assessment of the world population of *A. tropicalis.*

The seasonal and daily changes in the number of seals ashore were determined to contribute to the refinement of techniques to adjust counts to the time and circumstances of counting.

Furthermore, basic knowledge on the behaviour of *A. tropicalis* would contribute to the little information available on *A. tropicalis* in general and the Gough Island population in particular. This would provide a means by which *Arctocephalus* species can be compared and also aid in determining if discreet subpopulations of *A. tropicalis* exist within their breeding range.

*A single pup was found during 1975 (Van Ryssen 1976).

STUDY AREA

Gough Island (40° 20'S, 9° 54' W) lies well north of the Antarctic Convergence in the temperate zone of the South Atlantic ocean. The island covers approximately 83 km^2 with its longest and shortest axes being thirteen and seven kilometres respectively. It rears sharply out of the ocean to a centrally-situated plateau approximately 670 metres a.s.l., with four main peaks rising to a maximum altitude of 910 metres. This island has precipitous cliffs up to 457 metres high in places along the north-east and west coasts, descending to a minimum of 30 to 60 metres around the lowlands which are confined to the south and south-east sector of the island. Below about 300 metres a.s.l. an extremely dense vegetation occurs, consisting mainly of sedges, ferns (including the tree-fern *Blechnum palmiforme*) as well as the island tree, *Phylica arborea.* Walking is thus a strenuous and time consuming process. The coastal cliffs are covered by tussock-forming grasses *Poa flabellata* and *Spartina arundinacea* which often extend down gentler slopes to form vegetated areas of varying size with other species of grass at the back of beaches. Often, as a result of peat slips in the past, areas of turf are found even at the rear of beaches backed by steep bare cliffs.

Sites available to *A. tropicalis* vary from open flat boulder beaches and beaches composed of angular jumbled rock to rocky platforms, offshore rocks and ledges, the latter often being no more than narrow strips of negotiable areas at the foot of perpendicular cliffs and situated just above the waterline. Vegetated areas at the back of beaches are also occupied but inland areas are devoid of any seals since the steep cliffs form an effective barrier.

METHODS

The present investigation was undertaken during the austral summers of 1974/75 and 1975/76 and lasted from October to the end of February/beginning March on both occasions. During my first visit the two main study areas were Seal beach and Admiral beach on the south-east coast close to the South African meteorological station (Fig. 1). These two sites were selected on the strength of a biological reconnaissance during October 1973 (Shaughnessy 1975) undertaken to

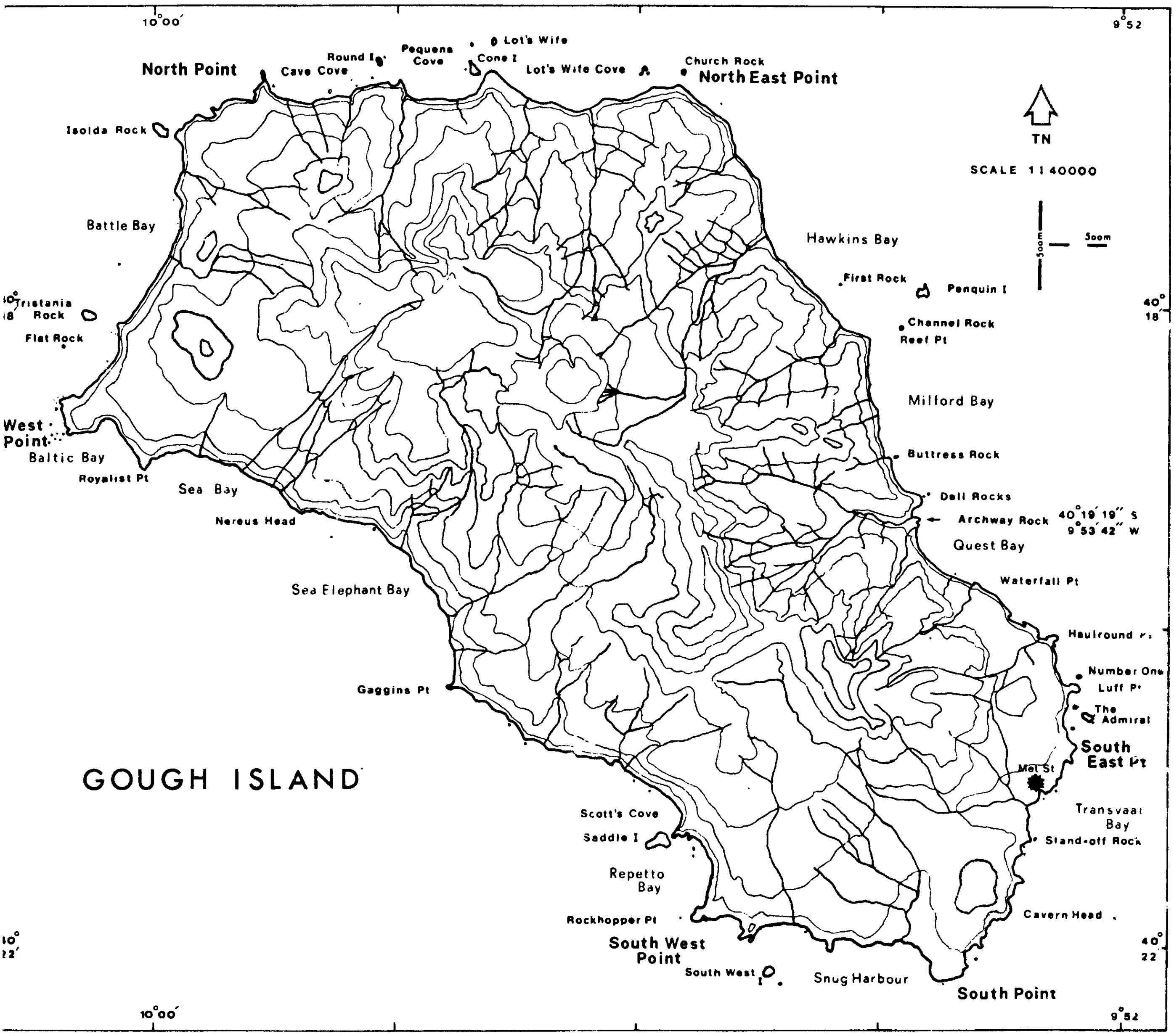

FIGURE 1 : Map of Gough Island

assess the possibilities for pinniped research. These sites, however, proved unsatisfactory for studies on breeding and reproductive behaviour since they were essentially hauling areas, and due to topographical obstacles no suitable vantage point could be found to observe the limited breeding without disturbing the animals. The nearest accessible major breeding sites were located on the south-west coast (Fig. 1) but due to logistic problems, mainly the lack of a full-time assistant, activities there during 1974/75 were restricted to a census of part of the coastline and a survey to select suitable study areas for a subsequent visit to the island. South Point beach and Waterfall Cove were selected and used as study areas during 1975/76 although they were not the best breeding colony sites. However they met a few essential requirements, these being:

(i) Within walking reach of the base considering time and effort.
(ii) Fresh water available.
(iii) Cliffs scaleable.
(iv) Within reach of a beach where a pontoon landing was possible so as to establish a food cache. This was done at South Point beach itself during the 1975 relief voyage of the M.V. "RSA" whilst a field camp was established on the cliff above Waterfall Cove.

Ancillary observations were made from Repetto Bay in the south-west, as well as from Haulround Point in the south-east, to South Point. Further data on the local distribution of *A. tropicalis* were collected during a circumnavigation of the island during the relief voyages of 1974 and 1975, and a cruise aboard the fishing vessel "Hilary" of the Tristan Investment Corporation. Pontoon landings were also made at various places along the east coast which are inaccessible overland.

All beaches visited during the study period were evaluated according to the size, shape and distribution of stones on them. A distinction was made between boulders, i.e. water-worn rounded stones, and rocks, i.e. rough angular stones, and their relative contribution to the general relief of a beach estimated. Stones of all sizes and types were measured (N=167) and arbitrarily grouped into size classes to provide points of reference in the description of the composition of beaches.

Study beaches were censused on a weekly basis using direct methods. Due to adverse weather conditions the interval between counts was not always the same, but these were carried out on the first acceptable day approaching, or subsequent to, the set interval of seven days. If a census was missed for a seven day period, the counts were done as soon as possible during the following seven day period and considered as if carried out during the missed census period. This was only done provided that the census did not extend more than two days into the next seven day period.

Since age and sex classifications were not always possible, many seals could not be positively allocated to a specific group. Only adult males (AM) and adult females (AF), larger subadults (SAM), yearlings (Y) and pups of the year were easy to identify. Sex identification in e.g. smaller subadults and yearlings was practically impossible without handling them individually. Suitable categories to accommodate seals not properly classified were created. The subadult class was therefore subdivided into four groups as follows:

(i) Easily identified subadult males of ± three years and older (SAM).

(ii) Unidentified subadults (SAU).

(iii) Small subadults of ± two years of age (SAs) which include both sexes.

(iv) Subadult females (SAF) which are similar in size to the small size category, but already showing some external characteristics of adult females. However some females classified as adults (since they have pups) and presumably primiparous approach the external characteristics of the subadult female class. Therefore the subadult female class are potential adult females, but when found on breeding colony sites without pups, and especially on nonbreeding colony sites, were regarded as belonging to the subadult group.

During the winters of 1975 and 1976 censuses were carried out for me by members of the South African meteorological team on the island. They were familiar with the research being carried out and could be trusted to supply reliable information on the sex and age group of easily identifiable individuals hauled out at the time of a census. Their counts were carried out on a fortnightly to monthly basis during my absence from the island.

Aspects of behaviour of *A. tropicalis* were studied at nonbreeding and breeding colony sites from vantage points, located on the slopes at the back of the beaches, which overlooked the colony sites. Observations were made with 7x35 wide angle binoculars especially suited for seal counts on a beach, but on occasions with binoculars with a larger magnification. Aspects of behaviour were usually recorded during set observation periods, but also on a more casual basis, usually prior to and during census periods.

Activity patterns and time budgets of *A. tropicalis* age and sex categories were carried out by means of scan sampling (Altmann 1974) as well as by focal animal sampling using a stopwatch. During scan sampling groups of seals were scanned at set time intervals and the categories of behaviour exhibited by each individual scored on data sheets (weather permitting) or recorded on a Sony portable tape recorder. Depending on the number of animals under observation, scans were carried out every five, 10 or 15 minutes, the time lapse used being constant for a whole set observation period. Larger groups of seals were scanned at longer intervals so as to be able to complete a scan before the commencement of the next scheduled scan.

Details of social behaviour were recorded on a portable tape recorder and transcribed afterwards. Tape recordings of vocalizations were made on Scotch magnetic tape using a Uher 4400 Report tape recorder and a M517 microphone but sound spectographs could not be obtained in time for inclusion in this report.

RESULTS AND DISCUSSION

GROUP CLASSIFICATION AND CHARACTERISTICS

For the purpose of the present study the fur seal population has been categorized into different age and sex groups. In the field seals could not be accurately aged by visual means alone but the general groupings used sufficed for the intended study. These groupings follow Rand (1956a) for the Cape fur seal, *A. p. pusillus,* Bonner (1968) for *A. gazella* and Stirling (1971a) and Miller (1975a) for *A. forsteri.* Coat colour, the presence and prominence of a crest, development and appearance of the mystacial vibrissae, body size, and behaviour were characteristics used to allocate animals to different age and sex groups.

Clark (1875), Rand (1956b), Swales (1956) and Paulian (1964) described the external characters of *A. tropicalis* occuring on islands north of the Antarctic Convergence. However since no seals could be culled for closer inspection and thus no cured pelts prepared, the present description of the colouration reflects their appearance in the field and may not entirely represent the situation in study skins as coat colour could be influenced by staining, dampness of the coat, as well as the different angles from which it was viewed.

The groupings used here are as follows:

ADULT MALES

Adult *A. tropicalis* males (Rand 1956b; Paulian 1964) are much larger than adult females (Fig. 2) and this disparity in size holds true for fur seals in general especially at the onset of the breeding season, e.g. *Callorhinus ursinus* (Scheffer and Wilke 1953), *A. p. pusillus* (Rand 1956a) and *A. gazella* (Bonner 1968).

A conspicuous feature of this age class in *A. tropicalis* is the presence of a very distinct tuft of longer guard hairs forming a crest of varying prominence on the head. Although some subadult males also possess prominent crests they usually lack the combination of features characterizing adult males. The dorsum of the adult male varies from almost black to grey with a very conspicuous cream to yellow chest and throat. The latter area is in distinct contrast to the darker dorsum which can be strongly grizzled, and extends up on the level of the ear pinnae, around the eyes, and across the bridge of the nose, with the resultant effect that the dark colouration of the head and crest comes to a clearly marked point between the eyes. The extent to which the light colour of the chest extends ventrally may vary, but can reach the level of the anterior insertion of the foreflippers. Around the ventral side of the foreflippers' insertion a brown to dark chocolate area is present, which may extend as a continuous broad band across the ventral side between the foreflippers. The belly appears from light brown to dark chocolate and is in some cases indistinguishable from the aforementioned dark brown area. The fur on the flippers varies from dark chocolate to fawn and in many instances the dorsum and flipper fur differ entirely in colour, e.g. a dark grey dorsum and fawn flipper fur.

Older males tend to have an overall brown ginger hue in the coat and the chest fur can become russet, probably due to staining. The top of the crest also becomes lighter in colour. Very old males have a uniformly yellow-white to grey-white chest, throat, face and dorsum, including the crest, and the only darker areas present are around the flippers and on the head. Flipper fur is buff and belly dark brown.

Occasionally very dark specimens are seen. They are almost black overall with the normal lighter colour of the chest, interspersed with darker guard hairs, limited to the muzzle and throat.

In all adult males mystacial vibrissae are well-developed with the longer ones normally reaching to a level well below the ears, and in extreme cases to approximately halfway down the chest. However in some older animals the whiskers only reach to the corners of the mouth due to wear.

ADULT FEMALES

In general, female colouration is in softer tones than that of adult males, with the dorsum usually dark to grey and the chest and throat cream to conspicuously yellow, this shade extending up behind the eyes in a crescent shape (Fig. 2). It rarely extends over the eyes to blend with the similarly light-coloured face. Especially in what I consider to be primiparous females the darker colour of the dorsum invades the lighter colour of the throat at a point below the ears to form a diffuse darker band, or an incomplete ring around the throat. The belly is usually brown to fawn with occasionally a narrow lighter area extending on either side from the insertion of the foreflippers backwards to form a lighter zone between the belly and dorsum similar to *A gazella* females (Bonner 1968), but this feature is usually absent. Similar to adult males, ventral to the inside of the

FIGURE 2 : Adult male and female *A. tropicalis* showing their disparity in size as well as their external characteristics

FIGURE 3 : Adult female and pup. Note the white vibrissae of the adult female which distinguish her from subadult females and subadult males

FIGURE 4 : A subadult male showing the small topnotch of guard hairs on the head and the dark vibrissae

insertion of the front flippers a darker area forms an incomplete band between the flippers. This however does not simulate the distinct circular dark patch extending right round the base of the front flippers found in *A. gazella* females (Bonner 1969). Flipper fur is predominantly brown to fawn. Older adult females have completely white vibrissae (Fig. 3) whilst in younger females the white can be limited to one or two vibrissae on each side of the muzzle, or else sparsely patched with white especially at the roots. Females of all age classes lack crests although one adult female showed a small but definite topnotch of guard hairs on the head. This however can be considered the exception.

SUBADULTS

Subadult males (Fig. 4) are similar in coat colouration to adult males but no clear demarcation between the dark dorsum and light-coloured face, throat and chest is normally found. In all but subadults approaching adult status the dorsal colouration also extends fully or partially around the throat below the level of the ears, as is the case in all subadult females and some adult females as described previously. Subadult males only occasionally have predominantly white mystacial vibrissae and in both younger subadult males and females the vibrissae are wholly black or sparsely patched with white. Subadults of both sexes just above the yearling class are usually silver-grey dorsally with cream to almost white chests and throats, and this colouration also extends in a crescent shape up behind the eyes. Here the distinction between sexes is usually impossible but the "whickering" of males, a vocalization almost exclusive to this sex group, as well as the presence or absence of a penial opening can serve to sex an animal. Only in older subadult males does the presence of a crest become evident.

YEARLINGS

In the literature this age group is not always clearly defined and the demarcation of this group tends to vary. Rand (1956a) considered them to be seals in their first year of life, but after they had lost their black natal coat and before their next moult, at approximately fifteen months of age. This definition was also apparently followed by Bonner (1968), Stirling (1971a) and Miller (1975a), and was followed in the present study.

Yearlings are characterized by their small size, and flippers which look disproportionately small in comparison with the plump body, the latter mainly due to the fluffed appearance of their coats. The chest and throat already have a lighter cream to yellowish colour in contrast with the darker silver-grey dorsum and brownish belly. Sexing yearlings is impossible unless they are individually inspected and often this age class, especially when hauled out after the breeding season at approximately fifteen months of age for their moult, are indistinguishable from young subadults when judged on external characteristics alone.

PUPS

Pups are covered with black woolly fur (Fig. 3) and the guard hairs can be white-tipped and rooted, giving it a grizzled appearance but never as conspicuously as in *A. gazella* pups which are distinctly "white-faced" from about three weeks of age (Bonner 1968). The belly is brownish and tends to become darker (brown) with age and the vibrissae are short and curved with a black to greyish colour. Pups moult their natal coat at approximately four months of age at the completion of which they attain yearling status.

LOCAL DISTRIBUTION

Logistics, topography of the island and the inaccessibility of beaches put a limitation on the collection of detailed information on the local distribution of *A. tropicalis* for Gough Island as a whole. Counts from the bridge of the M.V. "RSA" were unsatisfactory and the success of it varied with distance from the shore, visibility and the degree of concealment available to seals according to the topography of the beaches. Pontoon landings provided ground counts but since these were carried out early in the season with the main body of fur seals yet to arrive, conclusions on the strength of these counts could be made by inference only.

Previous reports on *A. tropicalis* at Gough Island (Elliott 1953; Swales 1956; Holdgate 1958) indicated that the island as a whole was inhabited by this seal during the summer season only. For example, Swales (1956) found beaches around the island to be colonized by fur seals during a census between November 1955 and May 1956. His counts also included pups of the season. Most seals were encountered on the west coast as is evident from a breakdown of his census (Swales 1956). Elliott (1953) found fur seals to be numerous on all suitable sites during February although the south-west shore was not included in his count, this area being scarcely visited.

In the present study the popularity of sites varied with their general topography, physiognomical characteristics and prevailing environmental conditions, but none were found to be entirely vacant. In fact, almost every beach available was packed with seals especially during times of their maximum haulout. However, the coastline from Repetto Bay in the south-west to South Point was found to support predominantly breeding colonies, while the south-east coast from Haulround Point to South Point was mainly occupied by nonbreeders (Fig. 5). The latter situation is most probably also true for the east coast north of Haulround Point. Although the latter part of the coastline was inspected early in the season, and before pupping commenced, only few yearlings were encountered at the various localities subjected to a ground count during October 1975 (Table 1). The presence of yearlings at Reef Point, Hawkins Bay and Dell Rocks does not necessarily mean that they had been born there since at this time a concentration of 28 yearlings was present on Seal Beach (20 October 1975) although only one pup was born there during the 1974/75 pupping season. However, the presence of adult females at Reef Point and Hawkins Bay, at least one with a yearling in attendance, as well as the discovery of a prematurely stillborn pup at Reef Point, shows that at least isolated births do occur but not in sufficient numbers to consider the east coast a successful pupping location. Moreover, The Glen was visited during the height of the pupping season (15 December 1975) and provided the approximate count of a thousand fur seals of which, however, only three were pups of the season. An offshore cruise (14 March 1975) aboard the M.V. "Hilary" revealed the presence of a large number of seals from The Glen to North-east Point, but no pups were detected although some may have been present. The available evidence therefore indicates that the east coast in general is frequented predominantly by nonbreeding *A. tropicalis.*

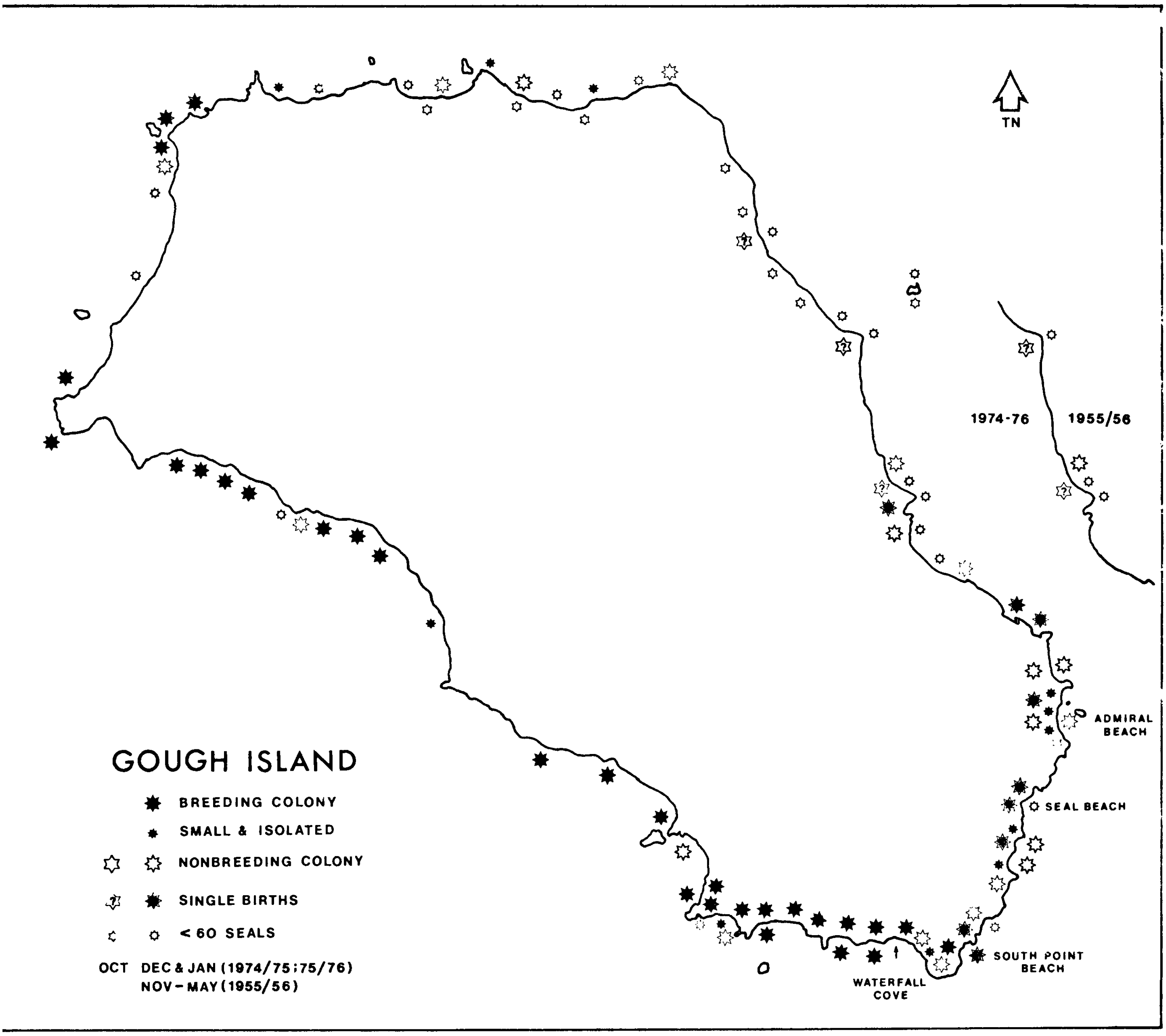

FIGURE 5 : Past and present distribution of *A. tropicalis* at Gough Island. The main study beaches are indicated

TABLE 1: *A. tropicalis* **numbers on east coast sites north of Haulround Point, Gough Island, during October 1975**

Locality	Date	Adults		Subadults			Year-lings	Pups
		AM	AF	SAM	SAU	SAF		
Reef Point	13/10/75	1		1	1		3	1*
Reef Point	29/10/75	1	1	6	8	2		
Hawkins Bay	13/10/75	7	1	7	9	1	1	
	29/10/75	2	2	6	50	2		
The Glen	26/10/75	1		2	40	1		
Dell Rocks	26/10/75	1		3	65	4	4	

*Prematurely stillborn

The status of *A. tropicalis* on the north coast is not clear but from the topography and physiognomical characteristics of the beaches it probably does not support large breeding colonies. A visit to these sites during the pupping season should resolve the problem. The west coast, on the other hand, already in 1955/56 (Swales 1956) supported approximately 75 percent of the total Gough Island fur seal population, and extensive breeding colonies occurred (Fig. 5).

Observations during 1974/75 and 1975/76, as well as previous records mentioned above, clearly indicate that all available sites are occupied by *A. tropicalis* during the summer haulout (Fig. 5). This situation is parallelled on the Bird and Willis Islands of the South Georgia group where all the beaches are occupied by *A. gazella* (Bonner 1968), but contrasts markedly with the situation on other antarctic and subantarctic islands where fur seals do not occupy all the beaches available to them and are limited to parts of the coastline. For example, at Marion and Amsterdam Islands (Rand 1956b, Paulian 1964) fur seals were limited to the north-western sides only, whilst at Macquarie, Kerguelen, Heard and McDonald Islands (Csordas and Ingham 1965; Lesél 1968,. *In:* Budd and Downes 1969; Budd and Downes 1969; Budd 1972), fur seals were chiefly encountered on sheltered beaches in the eastern sector. All islands just mentioned, except McDonald Island, have available beaches on the remaining parts of their coastlines. The present localized distribution of fur seals on these islands indicates a paucity in numbers rather than specific habitat preference since, although it is safe to accept that fur seals recolonizing an island or in phase of expansion would first occupy preferred sites, the fur seals at Marion Island (Condy *pers. comm.*) and Macquarie Island (Csordas and Ingham 1965) have appeared at previously unoccupied beaches with the increase in their numbers during the past twenty years.

The present study shows that although all beaches on Gough Island are occupied by fur seals during the austral summer there is however a dinstinct preference for certain localities to be used as breeding sites. This would suggest that the total breeding population has not yet reached its maximum size as regards beach space since at Bird Island, for example, some breeding seals are found on all beaches (Bonner 1968). However, direct comparison between islands is difficult as the restricting factors governing breeding site selection are obviously not the same on each. For example thermoregulatory needs, which hardly come into play in colder latitudes but may have a considerable influence on island seal populations which lie in lower latitudes, being a major difference.

THE ECOLOGY OF THE FUR SEAL AT GOUGH ISLAND

Habitat types available

The habitat available to fur seals at Gough Island is primarily rocky beaches, there being no sandy beaches with the exception of Capsize Sands on the east coast which, however, was found to be devoid of sand during Shaughnessy's (1973) visit. The island has a very rugged and broken coastline indented by coves and bays separated from one another by headlands of varying size. The latter vary from perpendicular coastal cliffs plunging into the sea to broad rocky platforms and extremely rocky sections jutting out to sea. Many offshore rocks e.g. Stand-Off Rock and the Midshipman, as well as towering islets, lie just offshore and are used as hauling-out sites. The precipitous character of the islets, however, usually limits hauling-out space e.g. the Admiral and the Commodore, while Penquin Island on the other hand has a much gentler and scaleable southern slope which affords resting place for numbers of seals.

Beaches vary a lot in size, the size, shape and arrangement of the rocks on them, as well as the slope which in turn may be affected by the amount of stacking of rocks that occurs. Beaches also differ in the degree of access afforded to higher ground and the degree of protection from high seas offered by offshore rocks and adjacent headlands. Most beaches which were closely inspected had areas of peaty mud and/or vegetated areas at the rear and all shared the common feature that they were backed by steep cliffs or tussock-clad slopes which effectively isolated them from inland areas.

To determine the factors governing breeding-site selection, and aided by the preference of certain age and sex groups of the fur seal for certain sites according to their topography and structure, haulout areas were categorized into different types. This classification cannot be considered rigid since different sites have their own peculiarities which could influence their attractiveness, and within its confines can have areas which simulate another type. However, on the basis of rock (boulder) size, their distribution over the beach and their relative contribution to the general relief of the site, areas available for the haulout of seals can be allocated to one of six different types.

TYPE 1 : OPEN BOULDER BEACH (FIG. 6)

This beach type is normally very flat and exposed with a gentle slope towards the sea. It is composed of boulders of varying size (0,01 – 0,4 m^3), often interspersed with occasional angular rocks but, however, never to such an extent as to change its essentially overall open character. Little stacking of boulders occurs and where the backing cliff is well set back, areas of peaty mud and/or vegetated areas are usually present which can be indicative of the upper limit to where the sea can reach during storms. This feature is usually lacking on narrow beaches of this type, especially if they are exposed to the incoming swell.

TYPE 2 : JUMBLED ROCKY BEACH (FIG. 7)

This type is represented by beaches with irregular contours formed by large angular rocks (0,4 – 7 m^3) interspersed with large boulders (0,07 – 0,4 m^3).

FIGURE 6 : The example shown here is an open boulder beach (Type 1). Note the open character of the beach and the even distribution of idle males occupying it

FIGURE 7 : Jumbled rocky beach (Type 2). This beach shows the irregular profile of this beach type with the ample sheltered spaces inbetween and underneath the angular rocks

Stacking at these sites predominates with a concomittant abundance of sheltered areas inbetween and under rocks. Frequently large rocks (> 7 m^3) are found mingled with the rest or situated on the seaward fringe. Depending on the width of the beach, peaty areas are present or absent with the latter situation a rule on narrow beaches backed by a cliff. Often this beach type is fronted by narrow rock platforms jutting out from beneath it, and according to the arrangement of the different sized rocks and boulders on it, has a slope that varies from moderate to steep.

TYPE 3 : INTERMEDIATE TYPE (FIG. 8)

On these beaches there is a preponderance of boulders (0,01 – 0,4 m^3) but a considerable number of single or clumped large rocks (0,4 – 7+ m^3) is also present, to give it an irregular profile. Stacking is however limited and this beach type resembles more closely a Type 1 rather than a Type 2 beach.

TYPE 4 : EXTREMELY ROCKY BEACH (FIG. 9)

This type of beach shows a preponderance of extremely large rocks (> 7 m^3) which often attain heights of eight metres and vary between 7 – 308 m^3 in volume. It ranges from jumbled talus blocks to a moderately sloped beach which terminates rather abruptly at its seaward edge, unless the seaward approach is tempered by e.g. the presence of smaller angular rocks and/or boulders occurring on a rocky ledge which just clears the sea. Owing to the stacking of the rocks these beaches, especially in extreme cases, are honeycomed by hollows and crevasses up to four metres high.

TYPE 5 : ROCKY PLATFORMS (FIG. 10)

Rocky platforms usually extend from the base of a cliff or slope, a metre or more above sea level, and provide an open expanse of relatively smooth rock surface which can, however, be studded with large loose rocks. Usually a strip of jumbled rock or talus is found at its junction with the coastal cliff. This is especially the case when such a platform acts as a headland separating beaches of different types. Platforms can also be encountered as the seaward extensions of

FIGURE 8 : Intermediate beach type (Type 3). Note the clumped distribution of large rocks on this essentially open beach

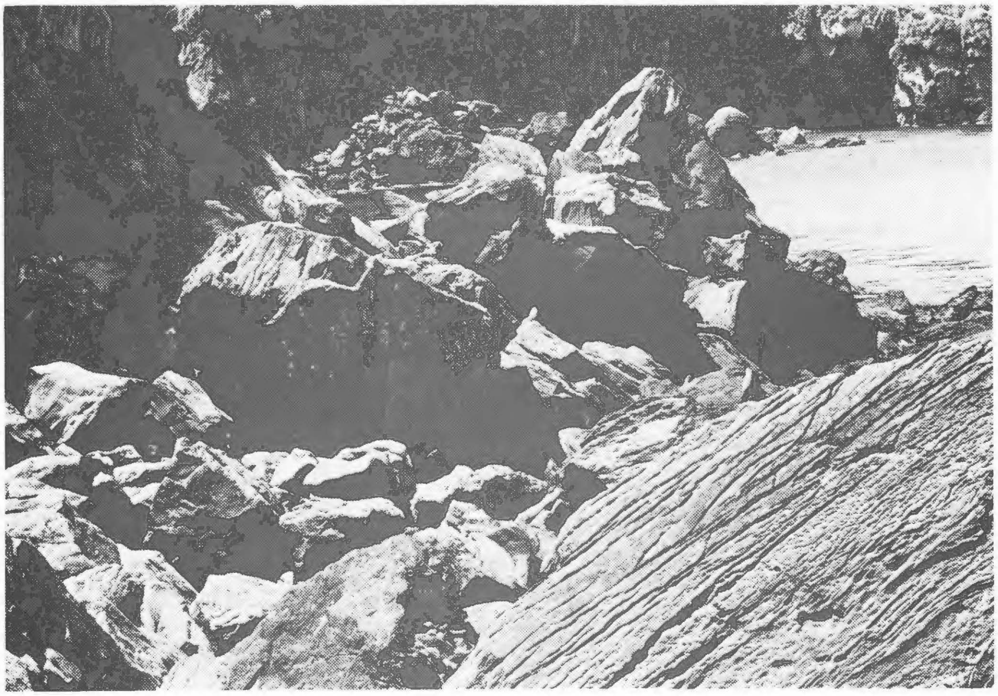

FIGURE 9 : Extremely rocky beach (Type 4). This beach shows the irregular profile of this beach type with stacked talus blocks which raise the general surface of the beach considerably higher than sea level

beaches (Types 2 and 4) in the form of small peninsulas with gullies making inroads on the sides, providing easy access to the beaches from which they originate. Rock pools, frequently with a considerable surface area and depth are sometimes found on rocky platforms, especially where depressions or fissures are close to the edge of the platform and within reach of the breakers that crash against it.

TYPE 6 : OFFSHORE ROCKS AND ISLETS (FIG. 11)

The precipitous character of the islets usually precludes their availability to fur seals. However, offshore rocks can be utilized and the numbers of seals present are determined chiefly by the height above sea level and prevailing sea condition. A further important contribution of offshore rocks and islets is that they break the impact of very heavy seas on the immediate adjacent coastline. Offshore rocks and islets allocated to this category are those which are exposed under prevailing tide conditions.

Open boulder beaches are common on the whole north coast with headlands composed of angular rock separating them. Large expanses of open boulder beaches are also present from North-east Point to Quest Bay (Fig. 1). However, from Waterfall Point southward Type 2 and Type 4 beaches as well as rocky platforms (Type 5) become more numerous and these predominate on the South-west coast (Fig. 12) where the only large Type 1 beach is situated in the bay off South-west Island. The whole west coast, as viewed from the bridge of the M.V. “RSA”, has beaches of all types. Shingle, a common occurrence at e.g. Macquarie and islands off the mainland of South Georgia (Csordas and Ingham 1965; Bonner 1968) are virtually absent from all beaches visited at Gough Island.

Habitat selection and colony types

In the Otariidae polygamy and the presence of a well-developed social organization are characteristic features during the breeding season. During this time seal aggregations can usually be divided into two broad categories, namely breeding and nonbreeding colonies. Rookeries and hauling grounds designate areas which support breeding and nonbreeding aggregations of seals respectively, the former usually on the basis of adult females and their pups of the season being present.

FIGURE 10 : The example shown here is a rocky platform. It represents an open expanse of relatively smooth rock which is largely inaccessible from the sea and backed by a steep coastal cliff

FIGURE 11 : Offshore rocks (Type 6). Note the three different habitat types of the adjacent coastline; a rocky platform in the foreground, an extremely rocky section in the middle, and a jumbled rocky beach opposite the offshore rock (Stand-Off Rock) in the background

In the present study, however, social groupings are categorized according to their age and sex specific composition during the height of the breeding (pupping) seasons as well as their ultimate success as breeding or nonbreeding colonies. This is done since already during the 1974/75 season it was noted that the different classes of fur seals showed a different haulout pattern with certain age/sex groups predominating in one habitat type and almost entirely absent in another one. For example, one of the main study areas on the east coast, Admiral beach, is roughly 500 metres long and has within its confines three distinct habitat types (Fig. 13), each with a marked differently composed fur seal aggregation (colony) occupying it. These habitat types were individually censused and the relative representation of the different age and sex classes computed. All the beaches or habitat types subjected to ground counts during the week of maximum haulout (21 December 1975 – 27 December 1975) in the 1975/76 breeding season were also grouped according to the similarities and/or differences in the fur seal aggregations occupying them. However, for the purpose of delineating the colony types it was found sufficient to group together the subadult group with only the easily identifiable larger subadult males (SAM) remaining separate as a distinct group. Unclassed seals were ignored for the count, since they were present only in small numbers during the census period from which Table 2 was derived, and they had a negligible influence on the composition of the groups present on the sites censused.

On this basis four colony types, within the framework of breeding and nonbreeding colonies and subject to seasonal and diurnal variation, were demarcated (Table 2). The colony types recognized in this study are idle colonies, nonbreeding colonies, breeding colonies and established breeding colonies. Swales (1956) also found the composition of herds (colonies) to vary between different beaches and recognized five main variants on Gough Island. These included a 100 per cent breed beach, mixed breeding beach, semi-mixed breeding beach as well as a non-breeding beach and hauling ground. The present investigation on *A. tropicalis* at Gough Island confirms the existence of the populations as set out by Swales (1956). I have, however, classified both the semi-mixed and mixed breeding colonies simply as "established breeding colony".

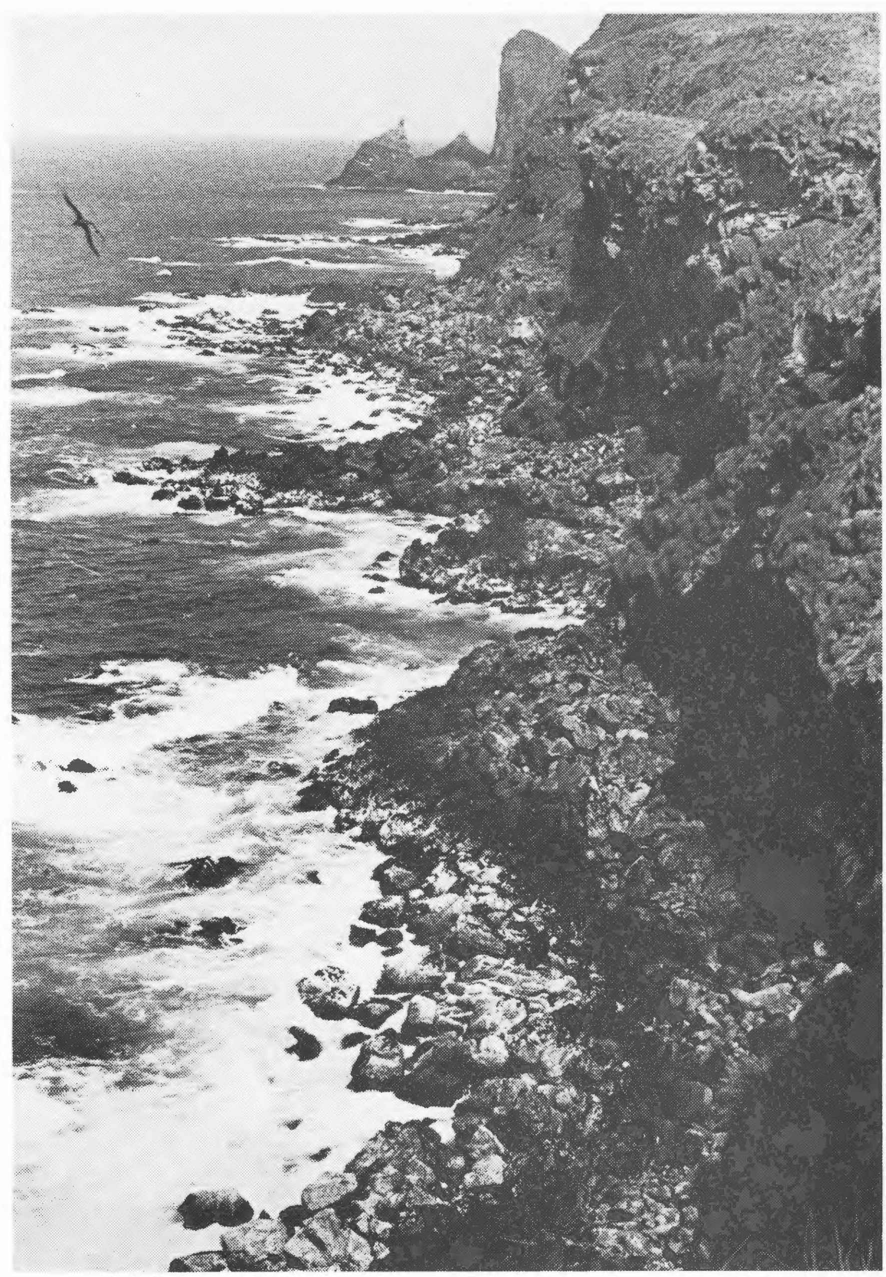

FIGURE 12 : South-west coast beaches showing the jumbled rocky beaches and extremely rocky sections at the foot of the coastal cliff with South-west Point in the background

IDLE COLONY

This colony type is primarily composed of adult nonbreeding males which form at least 70 per cent of the total number of seals found on specific hauling sites during the height of the breeding season. Subadult males in especially the older category are also included ($\overline{X}$ = 12,44 per cent). The adult males are considered idle and represent injured males which unsuccessfully attempted to procure a territory at a rookery or was evicted from one, males in prime physical condition who however apparently are not bold or strong enough to compete for a breeding site, as well as old males.

The presence of idle (nonbreeding, bachelor) males during the breeding season are recognized in other otariids as well (Rand 1956a; Bonner 1958; Kenyon 1960; Mathisen, Baade and Lopp 1962; Paulian 1964; Marine Mammal Lab. 1970; Crawley and Brown 1971; Stirling 1971a) and they are frequently found on separate hauling grounds.

The occurrence of a few adult females and pups in the count for the northern part of Admiral beach (Table 2) results from the merging of this beach (Type 1) with an intermediate type beach on its northern side; no distinct demarcation line could be drawn to separate the two beaches. The entire area was, therefore, censused as one resulting in the inclusion of the few breeders and subadults (SAU).

The habitat (beach type) occupied by this group is restricted to exposed rocky platforms and open boulder beaches, as well as stretches of open boulder beaches included in the range of intermediate types. Probably only this group occupy offshore rocks and suitable islets since those close enough inshore to be censused with reasonable accuracy through binoculars, namely Stand-Off Rock and the Midshipman, only had adult and subadult males on them. The same applies for New Zealand fur seals, *A. forsteri,* on Tamauka Island where nonbreeding males congregate on offshore stacks at the north-east side of the island (Crawley and Brown 1971).

TABLE 2: The relative representation of different age and sex classes of *A. tropicalis* in four colony types distinguished at Gough Island

Date	Type of Colony	Locality	Adult Males (AM)		Adult Females (AF)		Subadult Males (SAM)		Unidentified Sub-adults (SAU)		Total (pups excluded)	Percentage of overall total represented by pups	Final pup yield
			Number	%	Number	%	Number	%	Number	%			
23 Dec 1975	Idle	South Point Beach	1 058	90,74	0	0	108	9,26	0	0	1 166	0	0
23 Dec 1975	Idle	The Shelf	52	83,87	0	0	10	16,13	0	0	62	0	0
27 Dec 1975	Idle	Admiral Beach (North)	238	70,21	3	0,88	77	22,71	21	6,19	339	1,17	4
COMBINED RESULTS			1 348	86,02	3	0,19	195	12,44	21	1,34	1 567	0,25	4
22 Dec 1975	Nonbreeding	Archway Rocks	133	50,57	10	3,80	75	28,52	45	17,11	263	0,38	1
22 Dec 1975	Nonbreeding	Seal Beach	91	22,81	4	1,00	270	67,67	34	8,52	399	0,25	1
22 Dec 1975	Nonbreeding	Standoff area	228	59,38	10	2,60	123	32,03	23	5,99	384	2,04	8
23 Dec 1975	Nonbreeding	Cadaver Beach	99	41,42	17	7,11	78	32,64	45	18,83	239	1,24	3
27 Dec 1975	Nonbreeding	Admiral Beach (South)	69	43,13	0	0	61	38,13	30	18,75	160	0	0
COMBINED RESULTS			620	42,91	41	2,84	607	42,01	177	12,25	1 445	9,89	13
23 Dec 1975	Breeding	Ledge Rocks	5	10,64	7	14,64	4	8,51	31	65,94	47	9,62	5
23 Dec 1975	Breeding	Cave Beach	40	17,78	17	7,56	23	10,22	145	64,44	225	3,02	7
24 Dec 1975	Breeding	Cave Rocks	19	16,67	28	24,56	9	7,89	58	50,88	114	5,79	7
24 Dec 1975	Breeding	Waterfall Cove	20	16,13	68	34,68	13	10,48	48	38,71	124	28,74	50
24 Dec 1975	Breeding	South Point Beach	166	32,94	60	11,90	0	0	278	55,16	504	6,49	35
27 Dec 1975	Breeding	Admiral Beach (Middle)	16	6,18	30	11,58	0	0	213	82,24	259	3,35	9
27 Dec 1975	Breeding	Admiral Beach (North)	14	7,22	20	10,31	4	2,06	156	80,41	194	2,02	4
COMBINED RESULTS*			114	11,84	170	15,06	53	5,50	651	67,60	963	7,85	117
29 Jan 1976	Established breeding	South West Point Beach	52	20,00	195	75,00	3	1,15	10	3,85	260	78,86	1 031
29 Jan 1976	Established breeding	Repetto Bay South	48	15,58	243	78,90	7	2, 27	10	3,25	308	73,74	865
COMBINED RESULTS			100	17,61	438	77,11	10	1,76	20	3,52	568	76,95	1 896

*South Point Beach omitted from calculated representation of the different age/sex classes

NONBREEDING COLONY

In this colony one finds the presence of adult and subadult males in approximately equal numbers (42,91 per cent adult males). They form approximately 85 per cent of the total number of seals present on the colony sites. It is therefore very similar to the idle colony as previously described (98,46 per cent adult and subadult males combined). There is, however, a pronounced presence of adult females ($\bar{X}$ = 2,84 per cent) and a small number of births frequently occur. Swales (1956) also found pupped females within the confines of his "nonbreeding beaches". Paulian (1964) furthermore describes sexually mature females (mostly nonpregnant) to haulout away from rookeries but recorded births amongst them. In nonbreeding colonies at Gough Island adult females are always in excess of the total pup yield for each particular colony (Table 2) indicating that these females on the average (68,3 per cent) are primarily nonpregnant (not impregnated previous year or miscarried). Since by far the majority of seals found in these groups are nonbreeders, and the small number of births are confined to specific locations within the habitat type that they occupy which deviate from the general physical nature of the latter, I consider this to represent an essentially nonbreeding colony. Pups only represent, in average, 0,89 per cent of the total number of seals present.

Habitat types occupied by the nonbreeding colony vary between the intermediate type and extremely rocky beach.

BREEDING COLONY

This colony type has an adult male : adult female ratio of 1 : 1, 27 on average, with a preponderance of females during the height of the breeding season. Figures from South Point beach, the main study area on the junction between the east and south coast, were deleted from the calculated average value for age/sex class representation in Table 2, as this beach adjoins the large hauling site at South Point and a great number of idle males spilled over into the southern part of the habitat type occupied by the South Point beach colony. This, therefore, would have affected the calculated age/sex representation and male : female ratio. In addition, more adult females were present than the final pup yield and an average birth rate of only 50 per cent prevailed in the breeding colony. The outstanding feature of this colony type, however, is the abundance of the SAU class ($\bar{X}$ = 67,60 per cent) and the paucity of older subadult males which are usually found where present, on the fringes of such a colony. Pups on average contribute 7,85 per cent of the total number of seals counted (Table 2).

Habitat types utilized are Type 2 jumbled rocky beaches, Type 4 extremely rocky sections and to a lesser extent the intermediate Type 3, approaching Type 2.

ESTABLISHED BREEDING COLONY

This colony type represents successful breeding groups and is characterized by:

(i) the abundance of adult females which form approximately 77,11 per cent of the total number of seals present and;

(ii) exhibits a male : female ratio of 1 : 4,38 on average considering actual numbers of the adult class present at the time. Furthermore,

(iii) less than 24 per cent of the final pup yield are accounted for by adult females (most of which were away at sea for a feeding trip after parturition) on the breeding site and pups on the average represent 76,95 per cent of the total number of seals present in contrast to the low representation in the breeding colony (Table 2).

(iv) All other age/sex classes are poorly represented and virtually absent from the breeding ground.

Although the census of the established breeding colonies was carried out after the termination of the breeding season when seal numbers were on the wane, it can however still be considered to differ substantially from all other types. The subadult classes are always poorly represented e.g. Boulder Cove (established breeding colony) at the height of the breeding season only had 4,35 per cent of the SAU class present.

The relation, total individual adult females hauled out during the breeding season : final pup yield and, therefore, the presence or absence of nonpregnant females is, however, not known. This ratio would probably approach that found at Waterfall Cove breeding colony for which a birth rate of 73 per cent is calculated. This approximate values arrived at for *A. p. pusillus* (Kenyon *et al.* 1954) and *A. gazella* (Bonner 1958) which were 70 per cent and 80 per cent respectively.

However, the adult male counts for established breeding colonies (adjusted to represent their mid December strength as explained on page 48) and the final pup yield (representing the minimum number of pregnant adult females at the rookeries) give an indication of the marked difference in success between the two types of breeding colonies. Established breeding colonies have an adult male : pup ratio of 1 : 5,3 on average while the remainder of breeding colonies have one of 1,39 : 1. The same method of assessing the ratio between the adult males and parturient females was employed by Paulian (1964) and Stirling (1971a) for *A. tropicalis* and *A. forsteri* respectively. They calculated ratios of 1 : 7,5 and 1 : 6–8 respectively for the two species. Stirling (1971a) used an adjusted pup count to allow for dead pups etc. and if an adjustment is applied for established breeding colonies of *A. tropicalis* at Gough Island (a correction factor of a 25 per cent increase) a ratio of 1 : 6,6 is arrived at.

The outstanding feature of the location of established breeding colonies is their total absence from all east coast habitat types visited. This colony type is, however, well represented on especially the south-west coast. It also utilizes all habitat types with varying success, except Type 6 which is almost entirely absent on the south-west coast. Only occasionally is an established breeding colony found on easily accessible rocky platforms where jumbled rock or talus are found on the seaward fringe situated close to the waterline, but it is never present on the exposed parts e.g. in situations where a rocky platform forms an exposed headland between beaches of another type.

In summary, therefore, idle colonies are confined to beaches, rocky platforms, offshore rocks and islets, and headlands which are generally flat and exposed. Nonbreeding populations on the other hand occupy sites on the east coast that range from those that are to some extent flat and exposed, to jumbled rocks between waterline and cliff face. The limited breeding occurring in nonbreeding colonies is associated with deviations from the general physical nature of a particular site which they occupy that may make it more acceptable for the few parturient females.

Breeding colonies occur on the east coast as well as the southern part of the south-west coast, on jumbled rocky beaches to extremely rocky sections, while established breeding colonies are confined to the northerly beaches of the south-west coast (as opposed to the east coast) on habitat types of almost all categories.

The fact that breeding, therefore, is localized on the east coast subject to habitat type, and widespread and less restricted on the south-west coast, clearly indicates that although habitat type as such influences the choice of site by breeding/parturient females, other factor(s) also play a prominent role. The effect of these factors, moreover, differ substantially on the two coastlines in question for which data are available. These factors are presented below.

Factors influencing local distribution

The present study showed a number of factors to influence the local distribution of the fur seal on Gough Island, these being oceanographical and meteorological apart from the physical nature of the beaches available. These diverse abiotic influences on seal distribution have also been described for other pinniped species, as well as the effects of interrelationships of sympatric species (Bartholomew and Boolootian 1960; Bonner 1968; Ling 1969). In the present study the influence of single factors on local distribution in general, and breeding site selection in particular, could not always be clearly separated from one another and observations show that it is the combinations of determining factors that play the important role. An effort will, however, be made to discuss them as four separate entities with reference to their relative importance.

TOPOGRAPHY AND PHYSICAL NATURE OF BEACHES

Bonner (1968) and Wilson (1974) concluded that rocky habitats were preferred by fur seals of the genus *Arctocephalus* and this also applies to *A. tropicalis* at Gough Island where this habitat is almost the only one available to them. There is thus little choice other than a selection for beaches according to their degree of rockiness and general topography.

An important factor in the selection of hauling and breeding sites is their relative ease of access from the sea as well as the presence of higher ground onto which seals can haul under stormy sea conditions. Extremely rocky beaches are almost exclusively occupied by nonbreeding seals, but the few breeding seals here are on more easily accessible parts of the habitat type which provide access to higher ground or are sheltered by an immediately adjacent headland or offshore rock.

The south-west coast generally lacks the presence of large offshore rocks but many headlands break the force of the south-westerly swells (Fig. 12). Here breeding colonies also occupy the few open boulder beaches but on these higher ground, which lie out of reach of the breakers, are available, usually at the back of the beach. Narrow boulder beaches may be utilized when higher ground is available adjacent to it onto which seals haul when the sea reaches the back of the beach. On the south-west coast narrow beaches composed of poorly sorted boulders and jumbled rock are also present. Although these narrow beaches are hemmed in by the steep cliffs backing them and are with or without negotiable higher ground on the sides, they benefit from the presence of the higher range of jumbled angular rock on their seaward fringe. Under stormy sea conditions this seaward fringe of jumbled angular rock sufficiently breaks the force of the waves which result in the waves only reaching approximately two thirds of the way up the beach. Ample safe ground for the adult females and pups remains at the back of the beach whilst territorial males sometimes cling to their foremost territories which are inundated with water.

Open boulder beaches on the west coast, as viewed from the bridge of the M.V. "Hilary" had evenly dispersed animals similar to idle colonies elsewhere. These seals are considered to be adult males which, therefore, suggest that these beaches are too exposed to the sea when swept up by the predominantly westerly wind (see Table 4), and unsafe to be employed as rookeries. However, wide and easily accessible boulder beaches on the east coast are also occupied by nonbreeders even if they are relatively unaffected by high seas which is a rare occurrence on the eastern lee side of the island.

In general therefore, the topography and physical nature of the beaches on the south-west coast are less restricting to breeding fur seals, with the only requirements being ease of access and sufficient protection from high seas. On the east coast, however, only jumbled rocky beaches and accessible extremely rocky beaches are utilized by breeders. Open boulder beaches, for example, with all the benefits accruing from ease of access, available higher ground etc. are almost exclusively used as hauling sites for nonbreeders. This difference in the degree of habitat preference must, therefore, be attributed to other environmental factors and obviously, ones whose impact is different on the two coastlines in question.

METEOROLOGICAL FACTORS

Meteorological data recorded at the South African Meteorological station (Fig. 1) are depicted in Table 3. As the base is situated in the lee of the high central plateau of the island, prevailing wind speed and direction, as well as precipitation and cloud cover are surely modified and can at best only approximate conditions elsewhere on the island. The same applies to conditions on east coast beaches which lie at least 30 metres lower than the station and are sheltered from, for instance, the predominant westerly winds. Table 4 shows that wind direction predominantly have a westerly component, the wind coming from this direction 75,2 per cent of the time wind is blowing. The east coast in general therefore enjoys warmer and clearer weather than the rest of the island, similar to the conditions on Marion Island (Schulze 1971) and Grytviken Island (Bonner 1968).

TABLE 3: **Climatic data* from Gough Island (1966–1970). Readings taken at base (see Fig. 1) situated on the low eastern part of the island.**

Month	Extreme air temperatures °C					Mean relative humidity U (%)	Mean cloud amount N (octas)	Mean precipitation R (mm)
	Mean Tm	Mean max. Tx	Mean min. Tn	Mean absolute max. Txx	Mean absolute min. Tnn			
January	13,7	16,7	10,7	23,7	6,3	84	6,4	204,1
February	14,9	18,0	11,9	23,9	6,7	85	6,2	194,7
March	13,7	16,3	10,9	22,5	6,8	84	6,4	233,9
April	12,5	14,7	10,2	20,2	6,2	85	6,2	245,8
May	11,3	13,7	9,0	18,3	3,7	84	5,4	226,9
June	9,7	12,2	7,2	17,3	1,6	85	5,8	306,4
July	8,8	11,3	6,2	16,1	0,7	82	5,9	246,5
August	8,7	11,0	6,3	16,1	0,6	82	5,8	304,5
September	9,5	11,9	7,1	17,4	2,1	84	6,3	317,5
October	10,2	12,6	7,8	17,8	3,5	85	6,6	334,0
November	11,4	14,0	8,8	19,7	4,3	83	6,4	225,4
December	12,9	15,8	10,0	21,3	5,6	83	6,5	228,0
AVERAGE	11,4	14,0	8,8	19,5	4,0	84	6,2	255,6

* Data computed from the annual *Report on Meteorological Data* (1966–1970) of the South African Weather Bureau, Department of Transport.

TABLE 4: **Wind analysis *from Gough Island (1966–1970). Readings taken at base situated on the low eastern part of the island.**

	Wind direction frequency (ND)								
Year	N	NE	E	SE	S	SW	W	NW	Total
1966	89	33	5	19	29	234	315	232	956
1967	91	26	16	24	72	263	277	190	959
1968	68	43	15	33	53	261	235	151	859
1969	122	19	16	34	80	123	229	338	961
1970	124	55	30	11	43	179	277	177	896
Total	494	176	82	121	277	1 060	1 333	1 088	4 631
Per cent	10,7	3,8	1,8	2,6	6,0	22,9	28,8	23,5	–

* Data computed from the annual *Report on Meteorological Data* (1966–1970) of The South African Weather Bureau, Department of Transport.

Table 3 shows that Gough Island experiences high average daily temperatures (± 11,4°C) throughout the year when compared with islands in higher latitudes e.g. South Georgia (± 2°C), and Marion Island (± 4°), with the mean maximum being 14°C and with the mean absolute maximum being 19,5°C. Average relative humidity remains high throughout the year as can be expected for a marine climate, with the average for Gough Island being approximately 84 percent. In summer the island experiences many clear, warm, sunny days and the mean cloud cover for the year on average remains at around 6,2 octas. This probably has an influence on the fur seals during the terrestrial phase of their annual cycle since they are adapted to life in cold marine surroundings with the necessity to conserve heat. Because seals when under thermal stress on land are unable to dissipate heat effectively by physiological means alone, they have to rely on behavioural adjustments as well (Bartholomew and Wilke 1956; White and Odell 1971 and Odell 1974). High ambient temperatures, and the availability of meteorological and topographical features which could aid them in lessening adverse conditions on land would therefore, be expected to influence their choice of habitat type. Subject to this one can accept that especially breeding seals have a definite need to occupy sites with features that would moderate the effect of limiting factors to life on land. Adult males of territorial status remain on site, and maintain their territories for several weeks. The choice of a site where the effects of high temperatures are moderate would therefore be advantageous. The same applies to adult females who presumably concentrate where the survival and social maturation of their pups are optimal (see Miller 1975b) and who have to remain with their pups for considerable periods to nourish them.

Seeking of shade is recognized as one of the behaviour patterns employed by seals to escape thermal overloading under conditions of high ambient temperatures and solar radiation (Vaz-Ferreira and Palerm 1961; Bartholomew 1966; Orr 1967; Peterson *et al.* 1968; Gentry 1973). This also applies to *A. tropicalis* on Gough Island. A favourable wind could also increase the seals' tolerance under warm conditions owing to convective heat loss (Paulian 1964; Rand 1967) and they furthermore make use of evaporative cooling by wetting themselves (Bartholomew and Wilke 1956; Vaz-Ferreira and Palerm 1961; Peterson and Bartholomew 1967; Rand 1967; White and Odell 1971; Stirling 1971a; Gentry 1973).

It is significant that breeding colonies on the east coast, in the lee of the island, occupy jumbled rocky beaches pressed up against a cliff face. All open flat beaches and rocky platforms can therefore be immediately dismissed as potential breeding sites on this feature alone. The broken nature of the jumbled rocky beaches provides sufficient shelter in the form of shade from direct solar radiation, and the height of the cliff and width of the beach can concomittantly play an important role since a narrow beach backed by a high cliff will effectively reduce the angle between clifftop and waterline. This means that the site will be in shade earlier in the day because of the east/west trajectory of the sun, thus decreasing the total time (per day) that seals are exposed to direct solar radiation. That this indeed plays a significant role in breeding site selection is illustrated by the choice of a small specific breeding area on Admiral beach during both the 1974/75 and 1975/76 breeding seasons. This area is located to the south of the intermediate type section of Admiral beach and adjoins the narrow Type 2 section that demarcates Admiral beach north from Admiral beach south (Fig. 13). Although conditions here approach a jumbled rocky beach the only real difference between it and the adjacent intermediate type lies in the fact that it is tucked away at the base of an approximately 150 metre high cliff which runs almost perpendicular to the waterfront before it curves round to form the backing for the Type 2 section that runs parallel to the shoreline (Fig. 13 and 14). The trajectory of the sun and orientation of the slightly overhanging cliff result in the sun shining directly on this section only in the early hours of the summer mornings, whereas it is in shade for the remainder of the day. Moreover, harem males are strung out in a single line on the adjacent Type 2 section, but here they occur up to four deep.

The attractiveness of the above site obviously lies in the fact that the occupancy of the less favourable position far away from the waterline and its cooling effect on especially territorial males, and breeding seals in general, are offset by the availability of practically constant shade. Moreover, the first births recorded at South Point beach and Snug Harbour (Fig. 12) were all at the base of their respective backing cliffs and, therefore, on a part of the beach which is in shade longer than the remaining area or has the benefit of perpetual shade. On arrival, therefore, the pregnant females forfeit a place in the empty foremost territories in favour of the shady areas at the back which would, moreover, result in a concomittant greater effort to haul out and depart from the breeding site due to their harassment by the interposed territorial males.

Beaches on the south-west coasts, however, especially during storms face the spray-laden westerly winds. Since these winds help to alleviate thermal over loading, the necessity to occupy jumbled rocky beaches falls away and open boulder beaches can be utilized provided they comply with the prerequisites discussed above. South-west Point beach, however, lies entirely in the "lee" of the landmass formed by South-west and Rockhopper Points (Fig. 1). Since it is only backed by a low tussock covered cliff fronting the relatively low-lying neck of land connecting these points to the escarpment, this beach can still benefit from the cooling effect of the prevailing winds. Stirling (1971a) also found that at the South Neptune islands, specifically the northern one, exposure to wind was not a determining factor. This is correlated with (I assume) the small size of the island coupled with the fact that no definite island massif exists to create a definite lee.

FIGURE 13 : The example shown here is Admiral beach which includes different habitat types within its range. Note the shade cast by the slightly overhanging cliff on the left of the picture as well as the narrow jumbled rocky beach in the centre with intermediate type to open boulder beaches on either side

FIGURE 14 : The example shown here is an intermediate type beach which forms part of Admiral beach. Pupping only occurs along the base of the cliff shown on the left of the illustration

This correlation between habitat type selected for breedings and meteorological conditions was also described by Paulian (1964) for *A. tropicalis* at Amsterdam Island, where the preference for the rocky windward coast is related to their need to minimize heat stress. Although this preference by fur seals for windward coasts does not apply to e.g. Heard Island (Budd and Downes 1969), Kerguelen Island (Lesél 1968, *In:* Budd and Downes 1969) and Macquarie Island (Csordas and Ingham 1965) where seals are only found on the lee shore it should be remembered that these islands lie in much colder latitudes around the Antarctic Convergence, with protection from high seas swept up by the prevailing westerly winds being an important factor as has been emphatically stated for the *A. forsteri* population of Macquarie Island (Csordas and Ingham 1965). Thermoregulatory needs are therefore less determining factors in site selection if any at all, similar to the conditions prevailing on the south-west coast of Gough Island. The specific breeding site selection on the east coast of Gough Island in contrast can, however, be ascribed to the need to minimize thermal stress. The preference of *A. tropicalis* for windward westerly coast at Marion Island (Rand 1956b), however, remains rather obscure since even after the expansion of the fur seal colony it still is essentially absent from the lee side (Condy *pers. comm.*). Thermoregulatory needs can hardly come into play here, but other as yet undetermined factors e.g. interspecific competition may affect their distribution on Marion. On the other hand, a further increase in the fur seal population may result in the extension of breeding sites to the east coast of this island.

OCEANOGRAPHIC FACTORS

The distribution of seals is linked to the colder waters of the oceans, with the exception of the Monk seals, *Monachus* spp., which are found in slightly warmer waters (King 1964). Gough Island lies in the cold waters of the West Wind Drift with sea surface monthly average temperatures (as measured daily at the landing stage near the meteorological station) ranging between 10,3°C and 15°C (calculated for 1974).

The mean air temperature is higher than the mean sea temperature during the summer when seals are present in highest numbers on the breeding and hauling sites (Fig. 15). Moreover, since the higher range of air temperatures is considered to be the limiting factor (especially absolute maximums) one can see that the cooling oceanic effect can have an influence on the local distribution of fur seals, as well as contribute to the success of breeding colony establishment on the island's shores.

Breeding seals show a preference for areas situated on the waterline with easy access to and from the sea as has been established especially for islands in lower latitutdes. For example, Paulian (1964) found all harems close to the sea in the beginning of the breeding season. These also contained the most females throughout the breeding period. Moreover, harems diminished in size progressively the further away they were from the waterline. Orr (1967) also observed *Zalophus californianus wollebaeki* on the Galapagos islands to stay close to the water's edge and moving with the tide, and Stirling (1971a) regarded the presence of easily accessible water for cooling e.g. the sea and tidal pools, a primary factor important in the choice of a breeding location. In addition, the activities of harem males in territorial defence, maintenance of the harem etc. in the northern fur seal, *C. ursinus,* frequently result in a state of hyperthermia (Bartholomew and Wilke 1956) and male *A. forsteri* are relatively inactive during mid-day when high temperatures prevail (Miller 1974). This, however, does not apply to those males on waterline territories which have cooling agents available and these react more frequently to moving females than do inland males (Miller 1974) and can, therefore, persue breeding to the full without being restricted by thermal overloading. *A.p.pusillus,* found on a sandy shore at Cape Cross, South-West Africa in the coastal area of the arid Namib desert with its high diurnal temperatures, are confined to a narrow strip of beach bordering the waterline under conditions of high ambient temperatures and solar radiation and, therefore, derive maximum benefit from the cooling oceanic effect (personal observation).

On cold subantarctic islands, on the other hand, where dependence on the oceanic effect is supposedly minimal for thermoregulation, harems were also found to occupy vegetated hills and terraces behind the beaches (Bonner 1958, Budd and Downes 1969) and the majority of harems at South Georgia were situated on the beaches affording the best landing places (Bonner 1958). In the present

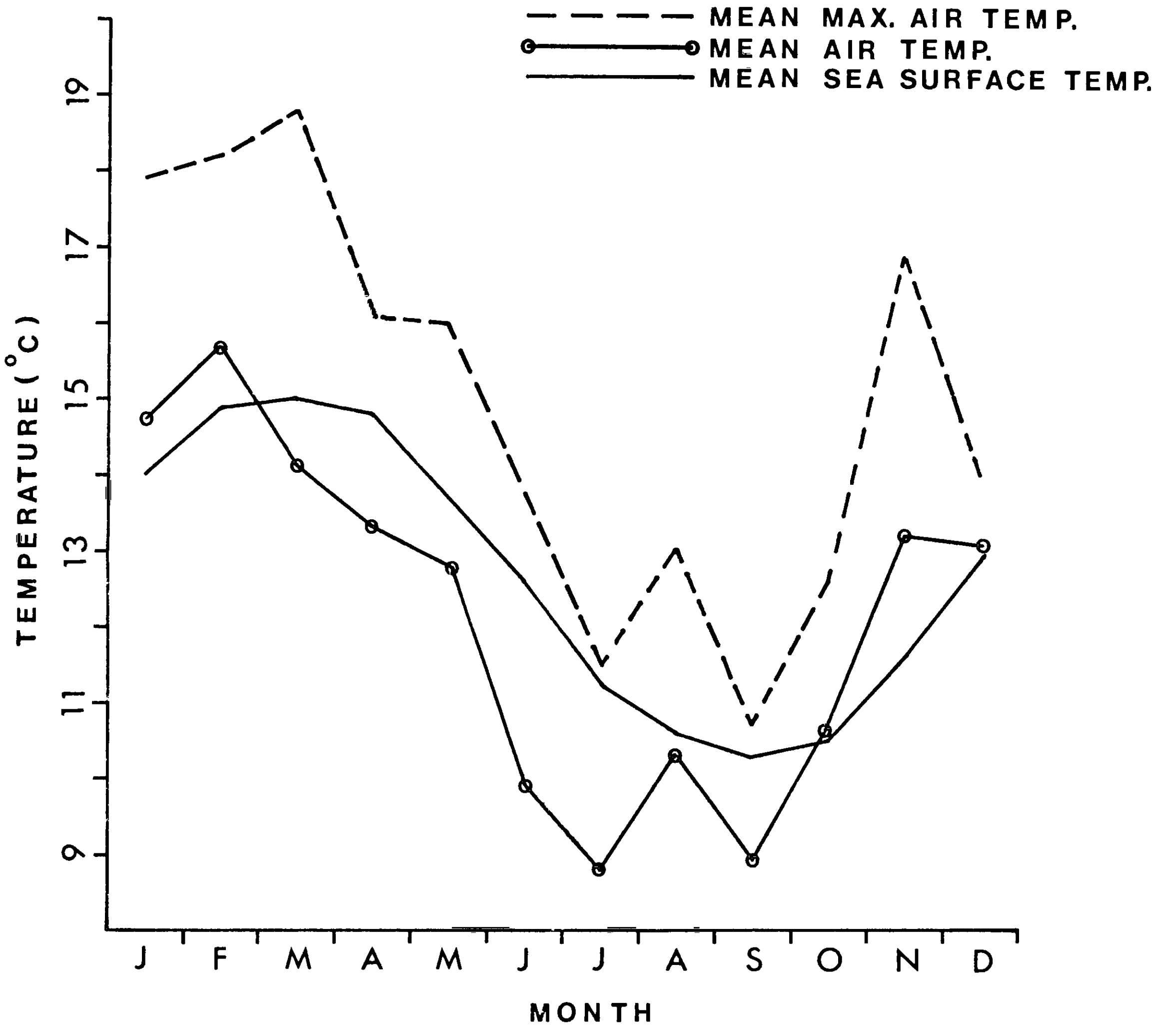

FIGURE 15 : Annual variation of air and sea surface mean temperature, and air mean maximum temperature, measured at the meteorological station on the east coast during 1974

study, however, harems were never located on vegetated and peaty areas at the back of beaches and the only areas away from the waterline occupied by them either had shade available, provided by the coastal cliffs or broken up terrain (east coast), and/or the benefit of spray laden winds (south-west coast) which would carry the cooling effect of the sea further up the beach. This also seems to be the case for *A. australis* at the Lobos islands off the coast of Uruguay, near the northern limit for this species, where harems were only found amongst the rocks where shade was available (Vaz-Ferreira *pers. comm., In:* Bonner 1958). *A. tropicalis* harems, therefore, favour Type 2 and Type 4 beaches on the east coast of Gough Island. The thermal induced restrictions on beach use on the south-west coast and for that matter on the west side of the island will be less limiting. This would also, in part, explain the favouring of the windward coast by fur seals on lower latitude islands.

Apart from the cooling effect of the ocean, the relative safety of rookeries from high seas would also affect the selection of breeding sites as has been established by Csordas and Ingham (1965), Stirling (1971a) and Budd (1972) where offshore rocks, headlands and, on islands in colder latitudes, the lee of the island with protection from westerly gales, provide this feature to such an extent that in the case of the latter even sandy beaches are used (Budd 1972). *A. tropicalis* at Gough Island also makes use of topographical features that minimize the onslaught of high seas which is less pronounced on the leeward east coast.

INTERSPECIFIC RELATIONSHIPS

Ling (1969) has made a careful study on the ecological factors affecting the annual cycle in island populations of seals and singled out the sharing of available space and food as the most significant resources for which sympatric species would compete. He concluded that in the adjusted annual cycles and different habitat requirements lie the successful coexistence between species with respect to competition on land, although interspecific contact has not always culminated in mutual toleration between two or more species. For example, on the California Channel Islands *Z. californianus* has expanded logarithmically at the cost of *E. jubatus* whose numbers dwindled. These two species occupy similar habitats and the crowding effect on rookeries favoured by the latter, but possibly also a change in water temperature and changes in the distribution of food species, initiated this phenomenon (Bartholomew and Boolootian 1960). Bonner (1968), however, considered no clear temporal separation to exist between the breeding colonies of southern elephant seals, *M. leonina,* and *A. gazella* at South Georgia. Although their habitat requirements differ substantially, resulting in a spatial separation, the wandering of juvenile and moulting adult elephant seals caused some disturbance amongst fur seals breeding aggregations which could intensify subject to an increasing fur seal population.

At Gough Island the only other pinniped species present, *M. leonina,* is not considered to compete with the fur seal for breeding space or influence it's local distribution. There is a distinct temporal and spatial separation between their breeding with the elephant seal's commencing during the second half of September, terminating at the end of October/beginning November (Bester 1976), while the earliest fur seal birth recorded was during the third week in November, peaking during middle December. Furthermore, the beach type elephant seals select for breeding is restricted to open boulder beaches on the north-east coast which, moreover, does not constitute a popular fur seal breeding area. In addition, comparatively few fur seals (36 and 80 on two respective visits during 1976) were present during the October peak of elephant seal pupping in e.g. Hawkins Bay, their sole breeding ground as far as could be determined. Only the occasional fur seal was hauled out near an elephant seal harem.

It is doubtful that a situation will ever arise where the elephant seal population of Gough will pose a threat to breeding fur seals regarding beach space since Swales (1956) estimated the total population on the island to be less than 300 and the calculated total for the 1975 breeding season is approximately 100 elephant seals (pups included). The possibility exists that the present elephant seal population is no larger than in 1955/56 since Carrick and Ingham (1962) stated that the Gough Island elephant seal population is limited because it is "on the margins of the optimal feeding zone", although it is otherwise suitable as far as adequate beach space is concerned.

During their moult elephant seals are, however, found away from the breeding ground in Hawkins Bay and occasionally they are seen on the east coast main fur seal study areas. The south coast never harboured elephant seals during the summer season of 1975/76, and this is in accordance with Swales's (1956) findings. He found them only on north and east coast boulder and sandy (Capsize Sands) beaches. They are, therefore, spatially removed from the breeding sites of the fur seals when the latter breed. Fur seals also show little interest in elephant seals and *vice versa* as shown by a few individuals of one species being unperturbed when surrounded by a close-packed mass of the other.

From the literature, human interference was also thought to be a limiting factor to the distribution of fur seals on an island. Paulian (1964) put forward a hypothesis that a defence reaction to exploitation may account for the selection by fur seals at Amsterdam Island of the rocky, wave-struck and therefore less accessible to man coast, although their distribution on the island at the time did not entirely bear this out. Segonzac (1972) supported this view, based on a study carried out 14 years later after a substantial increase in the Amsterdam Island fur seal population. Bonner (1968), however, considered this hypothesis as well as the one ascribing their distribution to body temperature regulatory needs, as unsatisfactorily since "the present distribution of fur seals represent only a fraction of the territory occupied before the onset of human exploitation". Marsallon (1969) on the other hand considered that fur seals at New Amsterdam preferred shores exposed to maximum sunshine.

It is nevertheless feasible that a remmant seal population would spread from inaccessible parts of the coastline on an island which was subjected to indiscriminate sealing operations in the past. This could be true for Gough Island with the west coast particularly unsuited for the concentrated sealing operations carried out between 1790 and 1820. Swales (1956) found the highest concentration of fur seals on this part of the coastline after a partial recovery in their numbers subsequent to cessation in sealing.

However, on islands south of the Antarctic Convergence where fur seals were limited to the lee of the island (Csordas and Ingham 1965; Lesél 1968, *In.*

Budd and Downes 1969; Budd and Downes 1969; Budd 1972) the fur seals would have little protection from sealers, especially shore parties. Neither does the occupancy of the western beaches of the cold Bouvet Island by fur seals (Holdgate, Tillbrook and Vaughan 1968) and thus with little consideration for thermoregulatory needs, exhibit an avoidance reaction to human interference. This island has negotiable beaches only on the western side (e.g. Norvegiaodden and the new platform south of Kapp Circoncision) whilst the eastern part of the island consists of an extensive ice slope and negotiable areas are extremely narrow(Muller, Schoeman and Van Zinderen Bakker sr. 1967). Moreover, at e.g. Heard Island the fur seals avoided rocky areas, occupying vegetated hills and terraces behind the beaches. Therefore the present distribution of fur seals on these islands cannot be ascribed to human interference. In addition, on Marion Island which had been subjected to sealing operations on all coasts(Rand 1956b) fur seals are still almost entirely limited to the exposed west coast (Condy *pers. comm.*). Breeding seals here also show a similar habitat preference to the Gough fur seal, which may be ascribed to thermoregulatory responses. Although the impact of the latter must be considered minimal on the Marion Island fur seal population, the island nevertheless represents the southern limit of *A. tropicalis* distribution and therefore, by comparison lies in warmer latitudes than sub-Antarctic Convergence Islands.

It can, therefore, be concluded that with an increase in population pressure the fur seals of Gough Island expanded from the west coast beaches to other parts of the coastline and that their present distribution, especially that of breeding colonies and small breeding groups within nonbreeding colonies, can mainly be attributed to the thermoregulatory needs of breeding seals which have territorial obligations. From Table 5 it is clear that the beaches censused in this study all showed a vast increase in colony size over that determined by Swales (1956). Furthermore the south-west coast still remained the most popular pupping locality in comparison with the east coast sector. In the past 20 years the east coast sector experienced a 8,7 fold population increase and the south coast one of only 1,8 (pups excluded). Nevertheless the pup yield (unadjusted) increased with only 90 on the east coast and with 6 579 on the south coast, showing the latter still to be the most popular pupping locality and still favoured by pregnant females in the absence of human interference. Subject to this on the lee of the island

TABLE 5: Historical trend in abundance of *A. tropicalis* at Gough Island

Locality	Population size		Increase	Numbers of pups		Increase	Population size (pups excluded)		Increase
	1955/56	1975/76		1955/56	1975/76		1955/56	1975/76	
Luff Point to South Point	702	6 195	X 8,8	1	91	X 91	701	6 104	X 8,7
Snug Harbour to Repetto Bay South	2 139	10 265	X 4,8	305	6 884	X 22,6	1 834	3 381	X 1,8
Total	2 841	16 460	X 5,8	306	6 975	X 22,8	2 535	9 485	X 3,7

where the less pronounced cooling effect of the wind and spray as well as the lesser threat imposed by uncommon severe storms prevail, habitat types which minimize the effect of high ambient temperatures and direct solar radiation are favoured. By contrast, habitat type as such plays a lesser role on windswept and spray laden coasts with its more beneficial climate (to fur seals) and lesser thermal induced restrictions. Here ease of access and safety from frequent high seas provided by the general topography of the beaches become the more important consideration in breeding site selection.

SEAL NUMBERS AND SEASONAL POPULATION CHANGES

Past and present numbers

Information on the population size of the fur seal, *A. tropicalis,* at Gough Island is sparse. Since its discovery in 1505/1506 and its position accurately pinpointed in 1731, little attention has been paid to the island. From 1790 to 1820 fur seals as well as elephant seals were exploited to the brink of extinction on the island, and again between 1869 and 1890 after a partial recovery in the seal stocks. The first and only reliable census of the fur seal at Gough Island was carried out by the Gough Island Scientific Survey in 1955/56 when the total number of seals was observed to be approximately 13 000, pups of the year inclusive (Swales 1956). Furthermore, most animals were encountered on the west coast with the largest breeding colonies situated at Seal Bay and Sea Elephant Bay (Fig. 1 and 2)

In my study the entire fur seal stock of the island could not be assessed, mainly due to the lack of logistic support during the time of the seals' maximum haulout. A contributing factor was that studies on behaviour and the annual cycle required my presence at the main study areas, which were confined to the South-east and South-west sectors of the island, on a weekly basis. However, approximately one quarter of the coastline between Luff Point on the east coast to the accessible beaches off Repetto Bay on the southern tip of the west coast (Fig. 1) was censused between the latter part of December and the last week in January, during the 1975/76 breeding season of the fur seals. Although the majority of beaches was censused during maximal haulout in the breeding season some were, however, counted during the decline in seal numbers immediately thereafter. The count is therefore adjusted to compensate for this departure of fur seals. The pup count reflects all pups born on the beaches in question, as derived from a census at the conclusion of the pupping season.

Although the actual figures probably give a fairly accurate indication of the population size of the censused' area, a number of factors impinged on the accuracy of a count. For example, where ample concealment was available to seals, movement through an area being censused usually started a minor stampede. Quick identification, not always possible, was required on such occasions lowering the accuracy of a population breakdown. Furthermore, inaccessible beaches (especially Type 2 and Type 4) had to be viewed from the clifftop which sometimes precluded positive identification. Many pups could have been overlooked and the whole of the beach wasn't always in view. Windless days, or where seals could be closely approached from downwind resulted in accurate counts with the reverse as true when the only approach was attempted from upwind. With high ambient temperatures and solar radiation prevailing an unknown number of seals were also at sea or in the surf zone and shallows where coat colour for identification was eliminated to a large extent. As far as possible counts were limited to the cooler early hours of the morning or late afternoon to minimize this error. At breeding sites counts were hampered by aggressive rutting harem males; a number of post-parturient females was also absent from the rookery at any one time after the onset of pupping and their numbers were augmented by the presence of non-pregnant females. Furthermore, the time of season when censuses were carried out determined the relative representation of the different age and sex classes of fur seals present.

Considering the above, a number of adjustments is made to correct the count for the census area, as well as to calculate a figure for the island as a whole. The adjustments made are as follows.

(i) The numbers of adult males on south-west coast rookeries counted after the breeding season, when their numbers were on the decline, are adjusted according to the known decrease in their numbers at study areas elsewhere at the same time. These study areas showed a 72 per cent decrease in adult male numbers (on average) between the time of their maximal breeding season haulout and the time when the south-west coast rookeries were censused. The latter's adult male count (representing 28 per cent of its total of the breeding season number) is, therefore, increased by applying the formula $\frac{28}{100} \times \frac{x}{1} = a$ (x = the number of males hauled during the height of the breeding season and a = the actual number of adult males censused.

(ii) Based upon counts of pups made before and after exhaustive searches for tagging purposes at two breeding sites, a correction factor of a 25 per cent increase is applied to the pup numbers to allow for undercounting. The correction factor approximates those employed by Bonner (1958) and Crawley and Brown (1971) who took it at 15 per cent and 20 per cent respectively under the conditions they encountered. The correction factor is not applied to areas subjected to regular censusing and where a close check, therefore, was kept on the number of births and deaths of pups throughout the pupping season (although some may have been overlooked or carcasses washed away by the sea and/or concealed amongst the rocks).

(iii) The number of pups born (dead + alive) finally arrived at will also at least represent the number of breeding females since each one only bears one pup and twins births are considered rare (Harrison *et al.* 1952; Slijper 1956; Rand 1956a; Paulian 1964; Peterson and Reeder 1966; Bonner 1968). Nonpregnant females furthermore frequent the rookeries and from counts made on south-west coast breeding colonies (maximum number of adult females hauled at any one time and final pup yield) a birth rate of 73 per cent is calculated for the adult female class. This simulates values ascertained for *C. ursinus* and *A.p. pusillus* (Kenyon *et al.* 1954) and *A. gazella*

(Bonner 1958) which was 69–80, 70 and 80 per cent respectively. The adult female class (calculated from the pup yield) is therefore increased by x $\frac{100}{73}$ in the same way Bonner (1958) and Crawley and Brown (1971) did for their studies. This adjustment is not made for east coast breeding colonies, for example, where the adult female number always was much larger than the final pup yield (up to 80 per cent larger) and the adult female numbers are taken at face value.

(iv) Accepting the figure of 60 per cent as the mortality rate of fur seals in their first year (Kenyon *et al.* 1954), the absent yearling class representing 40 per cent of the total number of pups born for 1975/76 must be added to the count (assuming that the number of pups born during the 1974/75 season was the same as in 1975/76). Paulian (1964) found the mortality amongst marked pups to be 62 per cent by January 1956 (± a month after the height of the pupping season) and that 58 per cent of pups died by drowning in bad weather. This seems very high especially since pups (and later yearlings) certainly experience more deaths later in the season. For three colonies combined Paulian (1964) estimated the mortality rate for pups to be, on average 47 per cent to five months of age.

Bonner (1968) found overall pup mortality on the beaches was 6,0 per cent but also used the figure of 60 per cent as the first year mortality (Bonner 1958).

Table 6 gives figures from the 1975/76 census for the area from Luff Point in the south-east to Repetto Bay in the south-west. The 16 460 individuals (pups included) actually counted can, therefore, be considered the absolute minimum for this area. Moreover, if one equates the numbers of pups actually counted with the number of females and adds the surviving absent yearling class, this increases the total to 28 692 after the correction factors for undercounting of pups, non-pregnant adult females and adult males are applied. The area censused is approximately 25 per cent of the total coastline (half of which predominantly supports breeding and the other half nonbreeding colonies) so that the total *A. tropicalis* stock of the island can be calculated by multiplying the observed totals by four

TABLE 6: Results of a census of *A. tropicalis* involving 25 per cent of the total coastline of Gough Island from Luff Point in the south-east to Repetto Bay on the west coast (1975/76)

Date	Locality	Adults				Subadults			Un-classed	Pups		Total	
		AM	Correct-ted[1]	AF	Correct-ted[3]	SAM	SAU	SAF		Number	Correct-ted[2]	Number	Correct-ted
27/12/75	Admirals Beach	448		94		397	634	–	0	26		1 599	1 599
27/12/75	Admiral Offshore Rocks*	31		3		18	8	13	38	0		111	111
20/12/75	South East Point	120		0		3	0	0	0	0		123	123
22/12/75	Archway Rocks	133		10		75	42	3	0	1		264	264
22/12/75	Seal Beach	91		4		270	60	12	50	1		488	488
22/12/75	Seal Beach to Stand-Off Area	228		10		123	23	–	0	7		391	391
23/12/75	Tumbledown Beach to Cave Beach	189		51		136	184	46	70	10		686	686
23/12/75	Richmond Point*	11		2		6	12	–	0	–	–	31	31
23/12/75	South Cavern Head*	135		0	–	6	0	0	36	–	–	177	177
23/12/75	Peninsula Rocks*	122		10		64	120	–	0	4	5	320	321
23/12/75	Half Shelf	52		0	–	10	0	0	0	0	–	62	62
23/12/75	Cave Rocks	19		28		9	53	5	0	7		121	121
23/12/75	South Point Beach	166		60		–	246	32	0	35		539	539
23/12/75	South Point Beach Offshore Rocks*	39		0	–	9	40	29	0	0	–	117	117
23/12/75	South Point	1 058		0	–	108	0	0	0	0	–	1 166	1 166
24/12/75	Snug Harbour South	112		97	162	37	52	40	16	118		472	537
30/1/76	Snug Harbour North	165	589	824	2 295	172	98	29	0			2 628	4 858
30/1/76	South West Island Beach	82	293	503	3 288	46	14	4	0	1 920	2 400	2 569	6 045
29/1/76	South West Point Beach	52	186	195	1 766	3	10	–	20	1 031	1 289	1 311	3 274
29/1/76	Point Bay*	51	182	314	2 055	–	–	–	0	1 200	1 500	1 565	3 737
29/1/76	Rockhopper Point	22	79	115	703	0	0	0	0	410	513	547	1 295
29/1/76	Repetto Bay South	48	171	243	1 481	7	0	0	10	865	1 081	1 173	2 750
TOTAL		3 374	4 454	2 563	12 022	1 499	1 596	213	240	6 975	8 668	16 460	28 692

Correction 1 – Compensate for 72 per cent undercount
Correction 2 – Compensate for 25 per cent undercount
Correction 3 – Adult female number = pup number; compensate for 27 per cent nonpregnant females
Total Island population – 28 692 + 3 467 (absent yearling class = 40 per cent of pup count) x 4 = 128 636 (adjusted)
– 16 460 x 4 = 65 840 (unadjusted)
*Censused from cliff-top; the remainder ground censuses

to give a figure of 65 840 (unadjusted) and 128 636 (adjusted) seals, inclusive of pups. This only applies if the uncensused west, north and north-east coast beaches have the same density as those censused in the present study. These figures are therefore slightly suspect.

Comparing present counts with those of Swales (1956) show that 2 841 seals were present from Luff Point in the south-east to Repetto Bay South at the southern tip of the west coast in 1955/56. In the present investigation the same areas (Table 5) support 16 460 seals (unadjusted counts) which constitutes a 5,8 fold increase over the 1955/56 counts. If one applies this increase to the total for the island at that time (12 904) the resultant population size comes to 74 843 which is within the range of those made for the present study (65 840 – 128 636). It is, however, likely that the population expansion was not of the same magnitude at different locations and that the west coast where 75 percent of the 1955/56 population occurred the population increase was less marked. With the apparent congestion of the breeding beaches there breeding seals would start colonizing other sites, especially if the west coast breeding beaches had reached a saturation point.

The future increase of the population at Gough Island hinges on the availability of food and beach space in the absence of commercial exploitation. It seems that the south-west coast, especially its southern part, still have breeding space available. Within the limits imposed by e.g. adult female breeding site preferences, some parts of the south-west coast are somewhat neglected for no obvious reason. The same applies more specifically to some east coast sites. Accurate pup counts for 1974/75 and 1975/76 indicate that Admiral beach showed no increase in the number of births there with both seasons' final pup yield (dead + alive) a constant 26 ± 1 with, furthermore, a single pup born at Seal beach during both seasons and five at the small tumble down beach on the westerly side of South Point. However, the area between Stand-Off Rock and Richmond Point showed a nine-fold increase in its pup yield (one to nine) and South Point beach a 2,2 fold increase (16 to 35) even after a 25 per cent correction factor for the 1974/75 count for dead and missed pups (the 1975/76 count was exhaustive for tagging purposes and no correction was made). This however, cannot with certainty be assumed to show an increase in the rate of pupping but can be attributed to small lateral displacements of pregnant females from adjoining pupping sites used previously to the above-mentioned areas.

Nevertheless, the sharp increase in pups born on these sites may be indicative of an expansion of breeding from crowded sites elsewhere since Bonner (1968) concluded that for "subsidiary beaches" on Bird Island (where up to a 99,3 per cent increase in the pup yield over that of the previous year was effective) the increase was throught not to be "due to an endogenous increase of the population on the subsidiary beaches; they must therefore represent reinforcement from the crowded beaches of the main colony". Gough Island has certainly experienced an increase in breeding sites since 1955/56 (Fig. 5) with pupping rates increasing on already recognized rookeries as well as taking place on previously nonbreeding sites.

At present nothing is known of the distribution and abundance of species on which *A. tropicalis* prey, and the carrying capacity of the range within which especially post-parturient females travel to feed, but food requirements are not thought to be a limiting factor. The present fur seal stock a Gough Island probably has as yet not numerically attained the size of the population before exploitation began.

The Tristan da Cunha group of islands, approximately 368 km NNE of Gough Island, at present also cannot be considered to support their maximum potential stock of *A. tropicalis*. Elliott (1953) mentioned them as increasing, with frequent sightings on Tristan beaches and at least 90 percent during November 1951 on Nightingale Island. He, furthermore, presumed them to be spreading from the west side of Inaccessible Island where breeding caves were present. Swales (1956) estimated the Nightingale and Inaccessible Island of this group to support 600 fur seals but during an offshore trip past the east coast of these two islands (March 1975) I sighted no seals on their eastern shores. At the same time Gough Island east coast beaches were packed with mostly nonbreeders hauled for the moult. However, since the Tristan group of islands lies within easy reach of Gough Island and *A. tropicalis* is known to have moved across the far greater gap between Amsterdam Island and Macquarie Island (Csordas 1962), it is feasible that with population pressure increasing on Gough, the Tristan group could be colonized by fur seals from here.

Bonner (1968) considers new colonizations to be representative of irregular behaviour, especially in the case of females who are unlikely to haul out away from their birthsite except for lateral displacements along the coast. He, however, has recorded recolonization to happen at South Georgia. Furthermore, the expansion of the nonbreeding stock of fur seals at Heard Island since 1955 (Budd and Downes 1969; Budd 1970), coupled with the observation that no definite evidence of breeding was found (Gwynn 1953; Ingham 1960) prior to 1963 after which breeding seals were encountered (Budd 1972), and the parallel that can also be found on Macquarie Island (Csordas and Ingham 1965; Australian Academy of Science 1967), South Orkneys (Øritsland 1960) and South Shetlands (O'Gorman 1961) show that recolonization does occur and culminates in at least the presence of incipient breeding colonies. Since Csordas and Ingham (1965) stated that new localities are prospected by nonbreeders and then as breeding beaches even before population pressure dictates expansion of range, it is probable that the Tristan da Cunha group of islands has already experienced an influx of seals from Gough Island.

No commercial exploitation of fur seals takes place at Gough Island at present although the Tristan Investment Corporation have permission (which is not made use of – P.A. Day; *pers. comm.* Managing Director) to cull 500 seals annually. Therefore, although control and protection (Wildlife Animal Protection Ordinance) came into effect between 1950 and 1952 (Elliott 1953) under which the seals at Tristan da Cunha and Inaccessible are supposedly strictly protected, Nightingale and Gough Islands were exempted and permits can be obtained to take seals there.

Annual cycle

Few quantitative data are available on the annual cycle and seasonal changes in population composition of the Arctocephalinae apart from that for the Northern fur seal, *C. ursinus* (Bartholomew and Hoel 1953; Peterson 1968). Some information is available on *Arctocephalus* species notably on the Australian (Stirling 1971a) and New Zealand (Stirling 1970; Miller 1975a) populations of *A. forsteri*. *A. tropicalis* has received practically no attention other than qualitative data made available by Paulian (1964) procured from studies involving this species on Amsterdam Island. Apart from brief data in Rand (1956b) the former is indeed the only relevant published account involving *A. tropicalis*.

The annual cycle of *A. tropicalis* at Gough Island was determined on weekly counts of the populations at Admiral beach and Seal beach on the east coast from October 1974 to October 1976. During the summers of 1974/75 and 1975/76 colonies were categorized in different age/sex groups at each census, but during the winter of 1975 and 1976 only total counts were made by members of the South African Meteorological team stationed at the island.

The outstanding feature of the seasonal change in population numbers at Seal and Admiral beach is the increased haulout during the summer months (Fig. 16). This commences during the latter part of October and peaks around the third week of December. Seal numbers ashore decline during April and May, so that only a fraction of the original numbers frequent the beaches during the winter months from June to the beginning of October. Some winter counts at Seal beach were zero but at Admiral beach, where pupping occurred during the previous breeding season, some seals were always present. Apart from the moulted pups (yearlings) born there, these included adult males, adult females and unidentified subadults during the August and September counts. The June count of Seal beach included amongst others two adult females and attending yearlings although none of the latter had been born there the previous breeding season.

This trend i.e. the increased number ashore during the summer breeding season and the subsequent drastic decline in numbers during the winter months has also been recorded for *A. gazella* (Bonner 1968) and the nonbreeding population of *A. forsteri* at Macquarie Island (Gwynn 1953; Csordas and Ingham 1965). Similarly Swales (1956) proposed that "all the fur seals spend most of the winter away from Gough Island except under one year old pups and their mothers which although at sea for some time, remain shore-based". This therefore also holds true

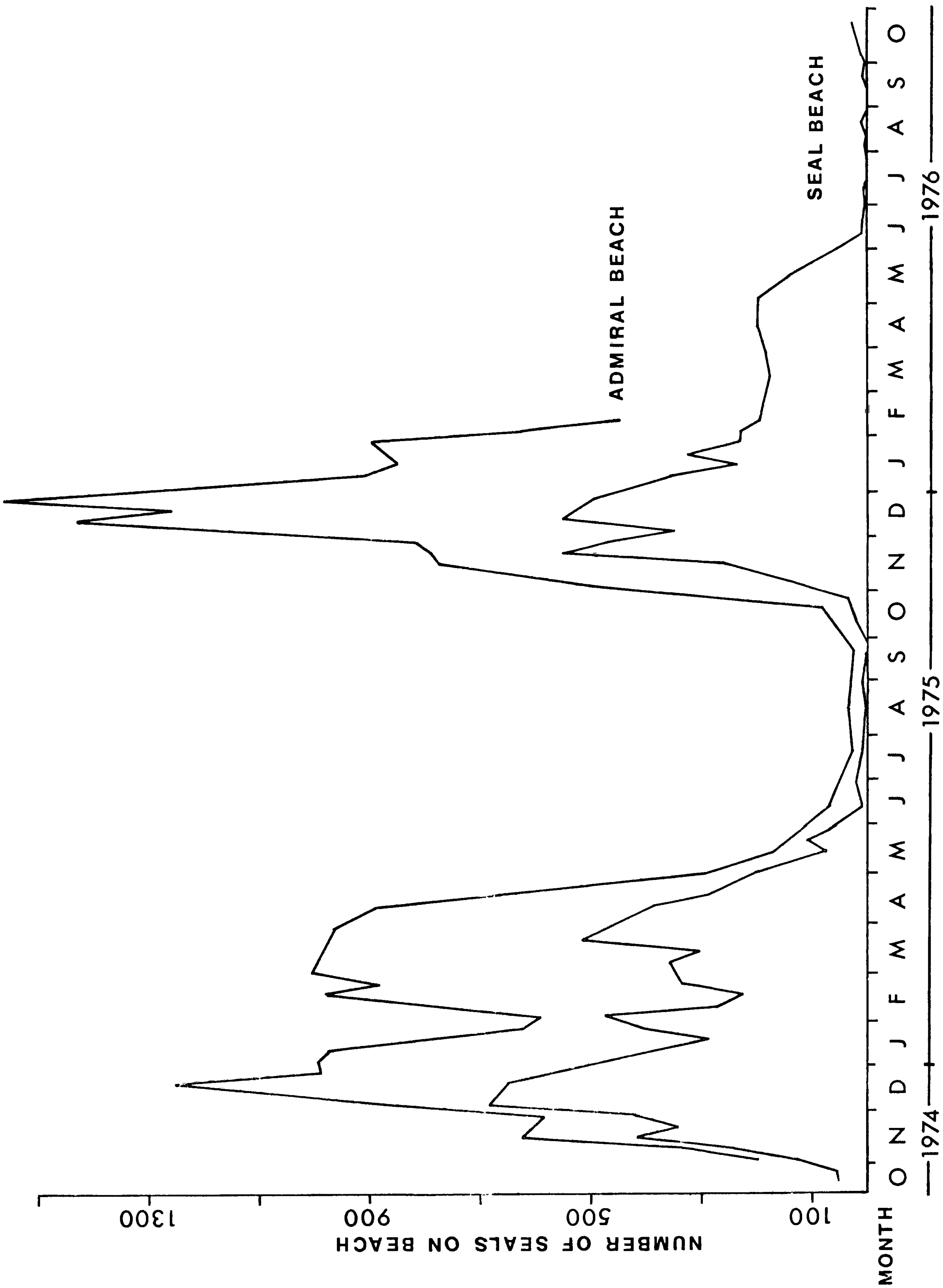

FIGURE 16 : Seasonal change in colony numbers (yearlings and pups excluded) at Admiral and Seal beach for the period October 1974 to October 1976

for west coast sites on the island which are not included in the present study. However, within the genus *Arctocephalus* this does not constitute a constant pattern. Stonehouse (1965) and Stirling (1970) found nonbreeding New Zealand colonies of *A. forsteri* at Kaikoura to attain their maximum number during winter and minimum during summer. The South Australian population (Stirling 1971a) follows the trend of *A. tropicalis* at Gough Island.

At Admiral beach and to a lesser extent Seal beach, total numbers of *A. tropicalis* ashore peak twice during the summer; first during the middle of December (after a rapid increase since the second week in October), which represents the height of the breeding season. A decrease towards the end of January is followed by an increase in numbers during February and March to a second peak during March/April. This second peak constitutes the height of the moult haulout. Seal beach, however, never clearly demonstrated the moulting peak during 1975 although this did occur during the 1976 counts from March to May. This not only applies to Admiral and Seal beaches, but also to the two breeding colonies studied on the South and South-west coast (1975/76 summer season) which were reduced to 22,4 per cent and 26,8 per cent respectively of their maximum mid-December population (pups of the season excluded) by the last week of January after which a pronounced increased haulout occurred. A count carried out during 20 February 1975 at these latter breeding colonies represented on the average a 3,6 fold increase over the minimum number of seals present end-January 1976.

A definite summer breeding as well as autumn moulting peak of *A. tropicalis* therefore occur at Gough Island as far as total numbers ashore is concerned. The inconsistant data accumulated for Seal beach are probably attributable to its being a nonbreeding site. Nonbreeders occupying it have less incentive to remain on the beach than breeding seals elsewhere during stressfull environmental conditions. Weekly counts could therefore vary according to the difference in e.g. ambient temperatures. Counts at breeding sites (or sites that at least included breeding groups within its range) however, would more clearly exhibit seasonal trends with counts showing less variation due to diurnal environmental changes. Wilson (1974) also found counts to vary more on hauling grounds than on rookeries for *A. forsteri.*

The presence of a peak in numbers ashore during breeding is common for polygynous gregarious pinnipeds. However, although the presence of a definite moulting peak is recognized, for example, for different age and sex classes of the phocid *M. leonina* (Carrick, Csordas, Ingham and Keith 1962) nowhere in the literature is it emphatically stated that it applies to arctocephalines as well, as has been determined for breeding and nonbreeding populations of *A. tropicalis.* It can, therefore, be considered to be a hitherto undescribed feature of their annual hauling and departure behaviour.

The only information in the literature on arctocephalines that could possibly indicate that a moulting peak occurs in other species of *Arctocephalus* is the presence of a double peak in adult female numbers of *A. forsteri* in New Zealand with nonmothers predominating during the second peak (Miller 1975a). The second peak occurred in mid-February, when a similar increase in numbers of mature *A. gazella* males took place following a decline in numbers at the close of the breeding season (Bonner 1968). He, furthermore, stated that such new arrivals soon began to moult. In the present investigation, however, all classes of seals were moulting by the end of February, when seal numbers were in their second increase. Indications of the moult are already present during the latter half of January.

When *A. tropicalis* stops moulting on Gough Island is not known. However, Rand (1956b) and Paulian (1964) stated that it was completed by the end of April in *A. tropicalis* at Marion and Amsterdam Island respectively, and that this approximated the situation in the Cape fur seal, *A. p. pusillus* (Rand 1956a). Accepting this to be applicable to *A. tropicalis* in the present study it would, therefore, coincide with the April/May reduction in numbers ashore when moulted animals start to depart from the island.

The important seasonal haulout/departure trends exhibited by *A. tropicalis* age and sex classes in the present study are depicted in Fig. 17 to 19. The following are the relevant points:

ADULT MALES

During both visits to Gough Island adult males were present on east coast beaches in small numbers on my arrival during mid-October. At least some of them were not on established territories since they were not resighted on subsequent visits to the particular areas. The breeding colony at South Point beach was first visited on 26 October 1975 at the commencement of the 1975/76 season and only a few males were present. They were deemed too small to succeed in holding territories when the main body of large breeding males arrived later in the season and therefore were not of territorial male status. On all beaches visited in October males were widely spaced and no indications of intrasexual fighting were detected. However, a rapid increase in adult males ashore took place during November with the first indications of intrasexual fighting (males with fresh lacerations from territorial fighting) appearing during the second week of November on breeding and nonbreeding sites alike. The frequency of occurrence of injured males increased towards the latter half of November/beginning December which coincided with the observation that larger males had evicted at least some of the territorial males at Admiral beach (middle) during the third week of November. Furthermore, at least one change in ownership of a territory was witnessed at South Point beach breeding colony during this period which in conjunction with the above observation, indicated that establishment of territories (and their maintenance) had increased. Very little territorial confrontations involving physical contact were witnessed on nonbreeding sites and most injured males hauled there and at idle colony sites probably were injured elsewhere at breeding locations. These males presumably consisted of evicted territorial males and those that unsuccessfully attempted to procure territories at the breeding sites.

Adult male numbers continued to increase at Admiral beach (Fig. 17) and Seal beach (Fig. 18) to peak middle December 1974 and towards the end of this month in 1975. Although the breeding colony at South Point beach exhibited the same trend in adult male numbers (especially since adult males from the adjacent idle colony at South Point expanded onto part of the study area at the time of maximal haulout and were included in the end-December count), Waterfall Cove breeding colony on the other hand had its maximum number of seals already

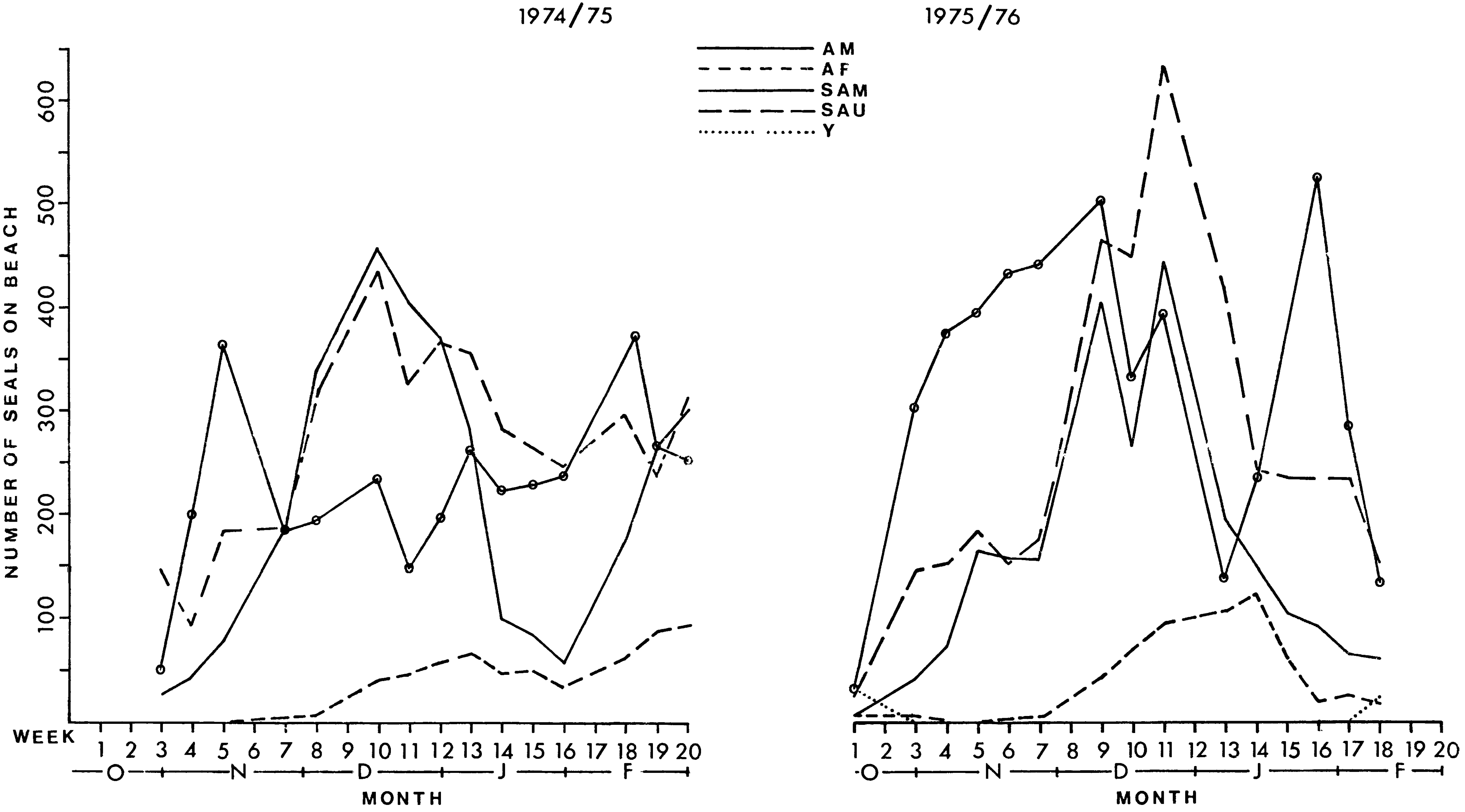

FIGURE 17 : Changes in numbers of different age and sex groups during the austral summers of 1974/75 and 1975/76 at Admiral beach

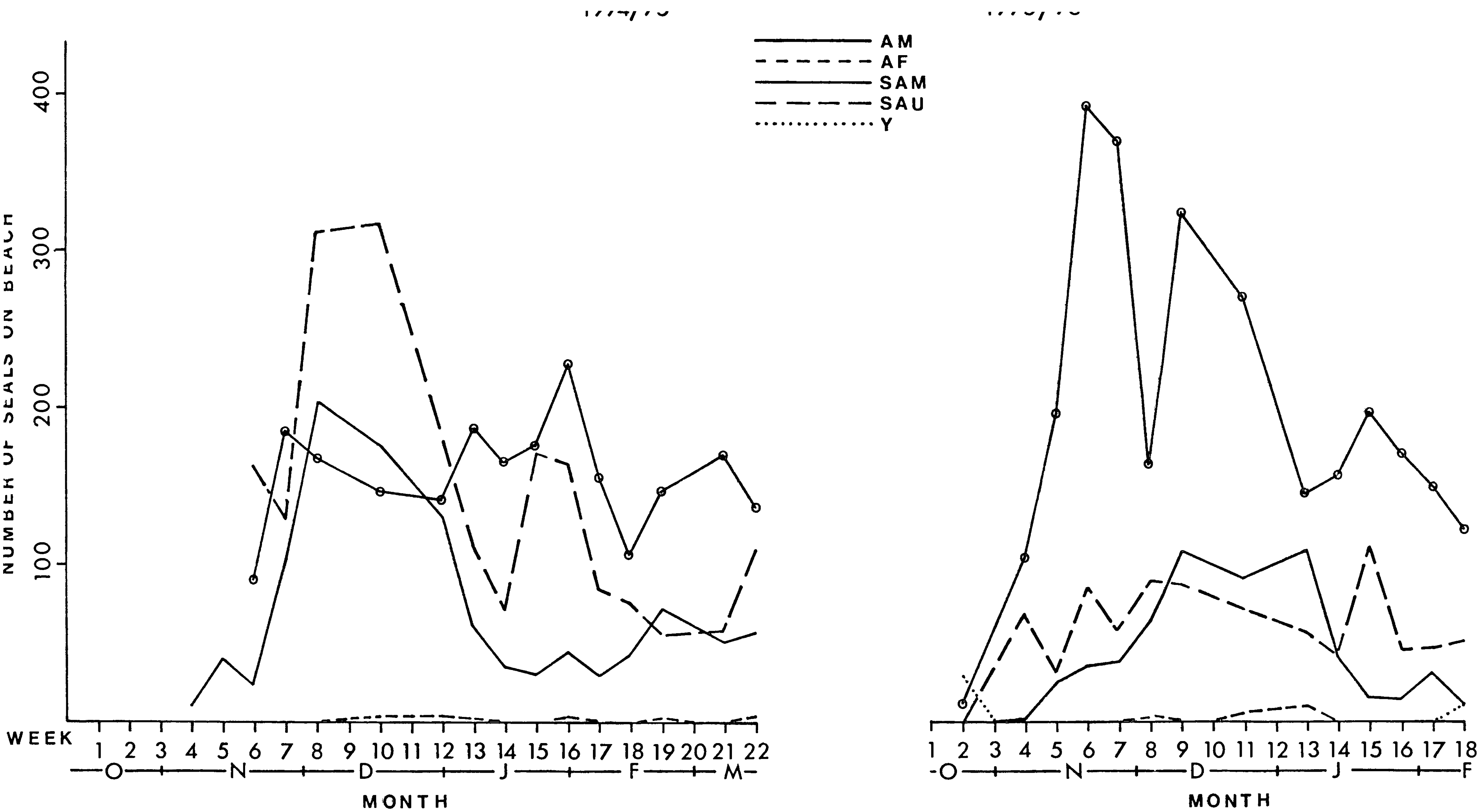

FIGURE 18 : Changes in numbers of different age and sex groups during the austral summers of 1974/75 and 1975/76 at Seal beach

towards the end of the third week in November. After this date numbers fluctuated minimally (due to the arrival and departure of a few bachelors on its eastern fringe) towards end-December, after which harem males started to depart. Only two remained at the end of January. This is hardly surprising since Waterfall Cove could only accommodate a maximum of twenty males due to their territorial requirements and this quota was, therefore, quickly filled. On the larger beaches where little breeding took place and where territorial disputes often resulted only in individual distances being kept, adult male numbers were high, e.g. in excess of 600 in the case of Admiral beach. Neither did numbers here reach a plateau as at Waterfall Cove, but adult males were assimilated into the colony upon arrival. However, numbers started declining before the beaches became very congested, probably due to the departure of individuals that had arrived earlier in the season.

At the two east coast census areas adult male numbers were on the increase once more during February 1975 up to the time the intensive population census was ceased. This was not evident for the 1975/76 season since the annual cycle was retarded by approximately two weeks (based on the difference in the haulout of females, departure of yearlings as well as pupping onset differences), and at my departure from the island only the low at the conclusion of the breeding season was reached. Seal numbers at Waterfall Cove, however, which closely followed the trend in the annual cycle at Admiral beach in 1974/75 showed an increase for the moult (Fig. 19). The earliest moulting male detected was a harem male at Waterfall Cove which abandoned his territory and clearly showed the presence of small tufts of brown underfur adhering to the surface of the guard hairs on 6 January 1976. By 28 January 1976 all known harem males which had been followed throughout the breeding season had departed and freshly hauled adult males in prime condition were starting to frequent the breeding sites and were responsible for the increase in adult male numbers. These males were considered to be those returning to land after a feeding excursion at the close of the breeding season, and they most probably originated from nonbreeding colony sites (and idle colony sites).

Territorial males that departed earlier in the month were not resighted on their previously occupied territories. Whether they do return to the sites of their

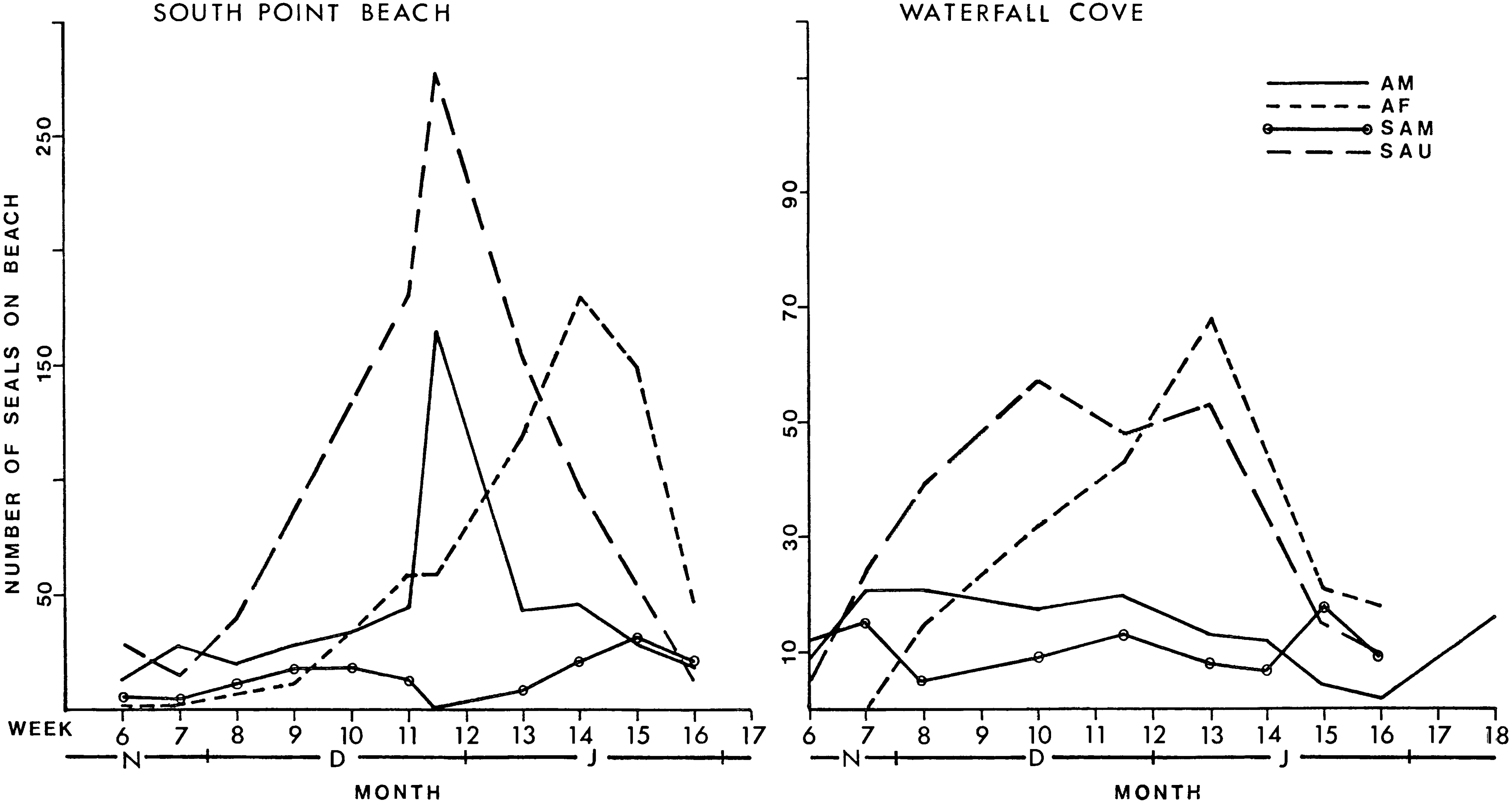

FIGURE 19 : Changes in numbers of different age and sex groups during the austral summer of 1975/76 at South Point beach and Waterfall Cove

previous territories during the moult haulout is not known. However, this is possible as Bonner (1968) reported a harem bull to have returned to his harem after an absence of about two weeks, and Miller (1975a) reported that a few territorial males returned briefly to their former territories some weeks after abandoning them.

Adult males do not entirely desert the east coast sites during the winter months and haulout there periodically. Although no data are available for Southwest coast breeding colonies during winter probably the some applies to them. Paulian (1964) mentioned that on Amsterdam Island *A. tropicalis* males of reproductive age were at sea as much as on land outside the breeding season, and Vaz-Ferreira (1956), Bonner (1968) and Stirling (1971a) all concluded that the males of the species they studied frequent colony sites only in low numbers during winter. The New Zealand breeding population of *A. forsteri* on the Open Bay Islands however, already had no adult males left as early as the middle of February (Stirling 1970). At Gough the majority of adult males leave the east coast sites at least by June as has also been described for adult males in other pinniped species during postbreeding periods (Warneke 1966; Orr and Poulter 1967; Peterson and Bartholomew 1967; Bonner 1968; Peterson and Le Boeuf 1969).

ADULT FEMALES

During the 1974/75 breeding season adult reproductive females were first sighted on east coast sites on 28 November 1974. They probably arrived before that date since they had already pupped, but were not yet present on 22 November 1974 when Admiral beach had last been censussed.

On my arrival at Gough in October 1975 a few females, accompanied by yearlings (in one instance still suckling) were seen on the east coast beaches as well as on one south coast beach (South Point beach) visited. These seals were last seen on 2 November 1975 and then left, most probably to feed. It seems therefore that at Gough Island the mother-young bond can persist up to 10–11 months, as this phenomenon was recorded the following year as well.

Numbers of adult females rapidly increased to peak, during both seasons, in the second week of January when adult male numbers were already on the decline (Fig. 17 and 19). This however, did not represent the peak pupping period which, based on the weekly increment in adult female and pup numbers at Admiral and Seal beach combined (Fig. 20) occurred during the second week of December in 1974 and the third week of December 1975. The largest weekly increment in adult females occurred towards the end of December 1975 (based on the increment per day as calculated from the increase in their numbers divided by the time lapse between censuses i.e. 4,0 per day for week 11 versus 3,45 and 2,89 for weeks 8 and 9, and week 10 respectively).

The two south-west coast breeding colonies, however, did not exhibit such a clear-cut picture; firstly because the weekly pup censuses were subject to under-counting and secondly, because the larger time lapses between counts in the latter part of the season. At South Point beach and Waterfall Cove at least 11,4 per cent and 28 per cent more pups were born (based on ground counts for tagging purposes later in the season) than the number (increments totalled) on which the weekly increments in pups were based. Here peak pupping, accompanied by a substantial increase in adult females, took place during mid-December on South Point beach, but end-December to the first week of January at Waterfall Cove (Fig. 20). However, findings for the two east coast sites and South Point beach agreed and can be accepted to reflect the true situation, especially in the combined results for Admiral beach and Seal beach which were always subjected to reliable direct counts.

The peak pupping period on the east and south-west coast, and conceivably the whole of Gough Island, therefore occurs in mid-December when adult female numbers ashore increase dramatically. However, at South Point beach the largest increment in adult female numbers occurred beginning January (daily increase) but was not parallelled by a similar increase in pups. This coincides with the maximum number of adult females counted at any one time of all four study areas (Fig. 17 and 19) and at a stage where a substantial number of post-parturient females was at sea. As the numbers of females present during this time were far more than the final pup yield this peak resulted from predominantly non-mothers frequenting the areas in question. A decrease in adult female numbers

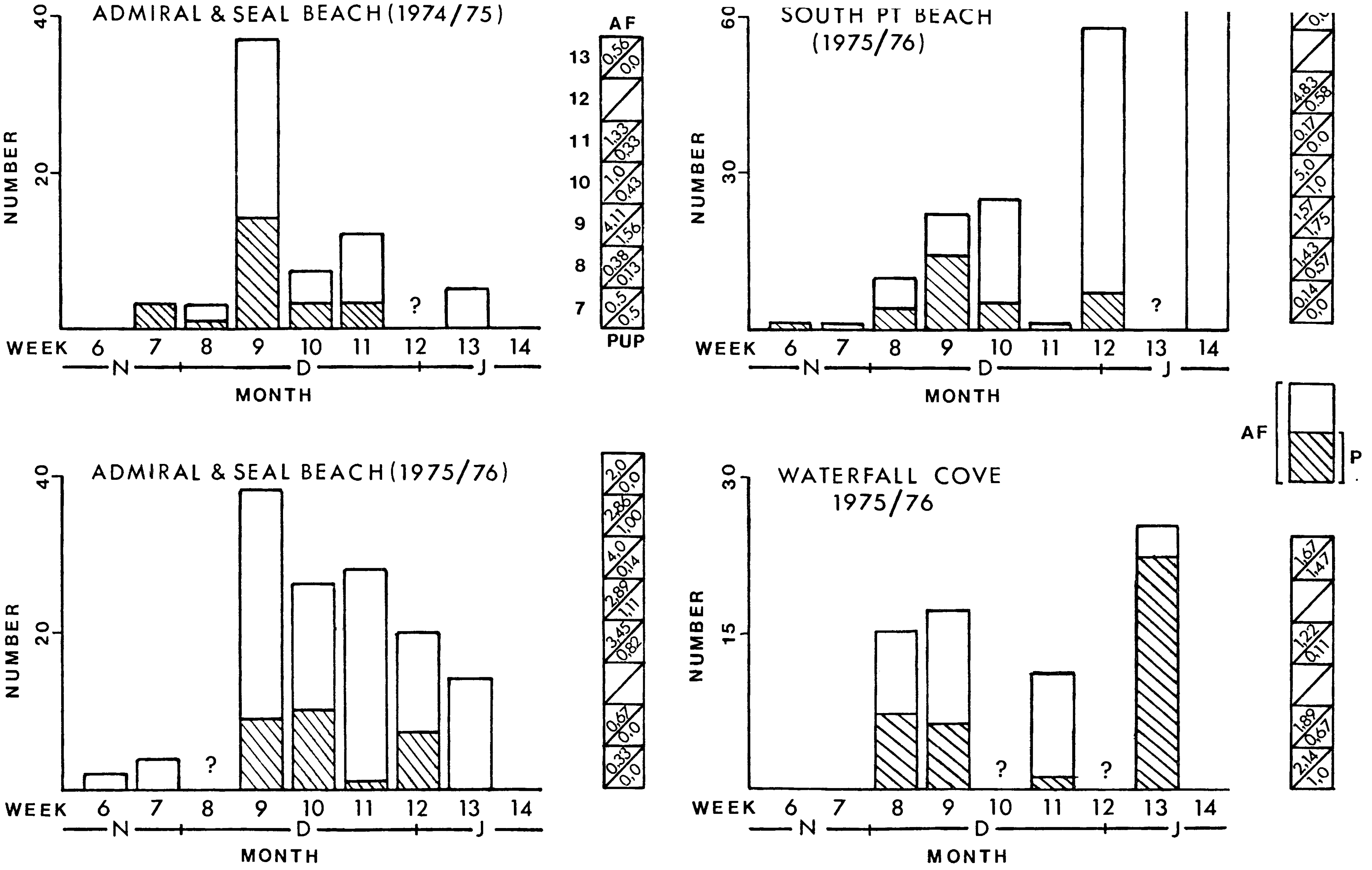

FIGURE 20 : Weekly increment in numbers of adult females and pups at Admiral beach and Seal beach combined for 1974/75 and 1975/76, and South Point beach and Waterfall Cove for 1975/76. Numbers in the columns to the right of the histograms represent the daily increment in numbers of adult females and pups (increment divided by the time lapse between censuses

to a low by the end of January ensued (Fig. 17 and 19), followed by an increase on Admiral beach in the 1974/75 season (Fig. 17) and the two south-west coast census areas by 15 and 20 February 1975 (not graphically displayed). This early February increase is considered to be for the moult since all females were moulting, indications of which were already present during the third week in January. Miller (1975a) similarly recorded a mid-February increase in adult female numbers with the abundance of nonmothers a contributary factor.

From the above it is clear that the pupping and breeding season do not occur over the same span of time. This is also the case in *A. forsteri* (Stirling 1971a) where the first copulation was recorded before the first birth. In the present investigation adult female numbers still increased after the last pup had been born and, since the majority was found to be nonmothers, it is assumed that they hauled for the purpose of being impregnated. This, however, could not be confirmed since very few copulations were witnessed throughout the study period and almost all took place during the December pupping period. However, two copulations were observed well outside the pupping period, on 17 January 1975 and 14 February 1975. This represents breeding outside the pupping period which terminates end-December/beginning January.

During the winter months adult females frequent the east coast pupping and other sites in low numbers to suckle their young. Winter-month censuses included only a fraction of the females present during the January peak, and they were always less than the number of pups (now yearlings) present on these sites. These females probably represent post-parturient females, with nonmothers probably behaving much the same as the other age/sex classes which are normally absent from the island during this period. The situation at established breeding colony sites on the south-west coast is not known. It is, however, assumed to be similar to the small breeding colonies on the east coast.

SUBADULTS

Admiral beach (mixed breeding and nonbreeding colonies colonize this site according to habitat type present) and Seal beach (nonbreeding) exhibited a fairly uniform pattern in hauling and departure of subadults for the 1974/75 census period. Subadult males were present on these sites during early October, as well as on other east coast sites visited. After a rapid initial increase during early November in subadult male numbers when adult male numbers were still slowly on the increase, the numbers of subadult and mature males on Admiral and Seal beaches were inversely related (Fig. 17 and 18).

Subadult males are well represented during the summer haulout but are to a certain extent behaviourally excluded from breeding and nonbreeding areas alike by adult males at the time the first adult females arrive. This results from adult male aggression when staking out territories, as well as competition for hauling space at sites (e.g. idle colony sites) where breeding is absent and territorial behaviour is not pronounced. This is similar to the position in *A. forsteri* during the breeding season (Crawley 1972). Subadults other than positively identified males (± 3 year and older) and grouped into a separate class (SAU), however, exhibit a different trend especially during the breeding season haulout. Seals of this group, also present during mid-October, follow the trend in adult male numbers with a peak period during mid-December and a subsequent decline followed by erratic fluctuations in numbers. Seal beach, however, exhibited a small peak in SAU numbers at the end of January, not observed for Admiral beach. This indicates that it is possible that a number of subadult males was included in this class, for the subadult male group are similarly affected at this time. It seems therefore that subadult females are better tolerated by adult on nonbreeding and breeding sites alike than is the case for subadult males.

The 1975/76 results for the two study areas showed similar trends to 1974/75 for subadult males and SAU's although their abundance differed substantially. This is probably as a result of the decrease in numbers of 19 per cent at Seal beach, and at Admiral beach an increase of 26 per cent over 1974/75 numbers at the time of maximum haulout. This decrease for Seal beach was seen in both the adult male and the SAU groups. Therefore during every census period SA males predominated. At Admiral beach, however, all classes, with the exception of adult males which maintained their numbers, showed an increase. The above trends are a constant feature for all colony types as the pattern of adult and subadult male haulout and departure is even more pronounced at the two south-west coast breeding aggregations. Subadults were present in small numbers except during early November and late January when their numbers increased over that of the adult males partly due to the departure of harem males during the latter period (Fig. 19). At the South coast study areas as well as at breeding locations within the range of Admiral beach, large subadult males occupy territories vacated by adult males by the second week in January.

A conscious effort was made during especially the 1974/75 season to identify what was considered to be second year old animals (SAs) from the rest of the subadult class. This was done since it would include females of reproductive status if the *A. tropicalis* population simulatesthe condition in *A. p. pusillus* (Rand 1955) and *A. gazella* (Payne 1977) where females first give birth in their third year. They would, therefore, have to be impregnated in their second year and therefore must be available at the breeding sites during the breeding season. Figure 21 shows that the curve for second year subadults of both sexes fits closely over the curve for adult males. They are therefore tolerated by adult males on the beaches during the breeding season and show concomittant increases and decreases during the summer haulout. Furthermore, females of this age class predominated on east coast breeding colony beaches (e.g. breeding sites at Admiral beach), whereas males were by far in the majority on nonbreeding colony sites (e.g. Seal beach) on the east coast.

It can, therefore, be postulated that second year females are found on breeding sites (on the east coast at least) and follow the hauling and departure pattern of adult males since they represent the virgin receptive females class. At least two copulations were recorded involving this age group and sexually mature males. Second year old males are, however, tolerated on the basis of their noncompetition with adult males and they are indeed often subject to herding activities of adult males at nonbreeding colony sites. Here adult males forcibly establish what appear to simulate "harems" consisting of mostly younger than three year old females. It cannot be discounted that two year old males often go unnoticed within the territory of a male in a breeding area because of their

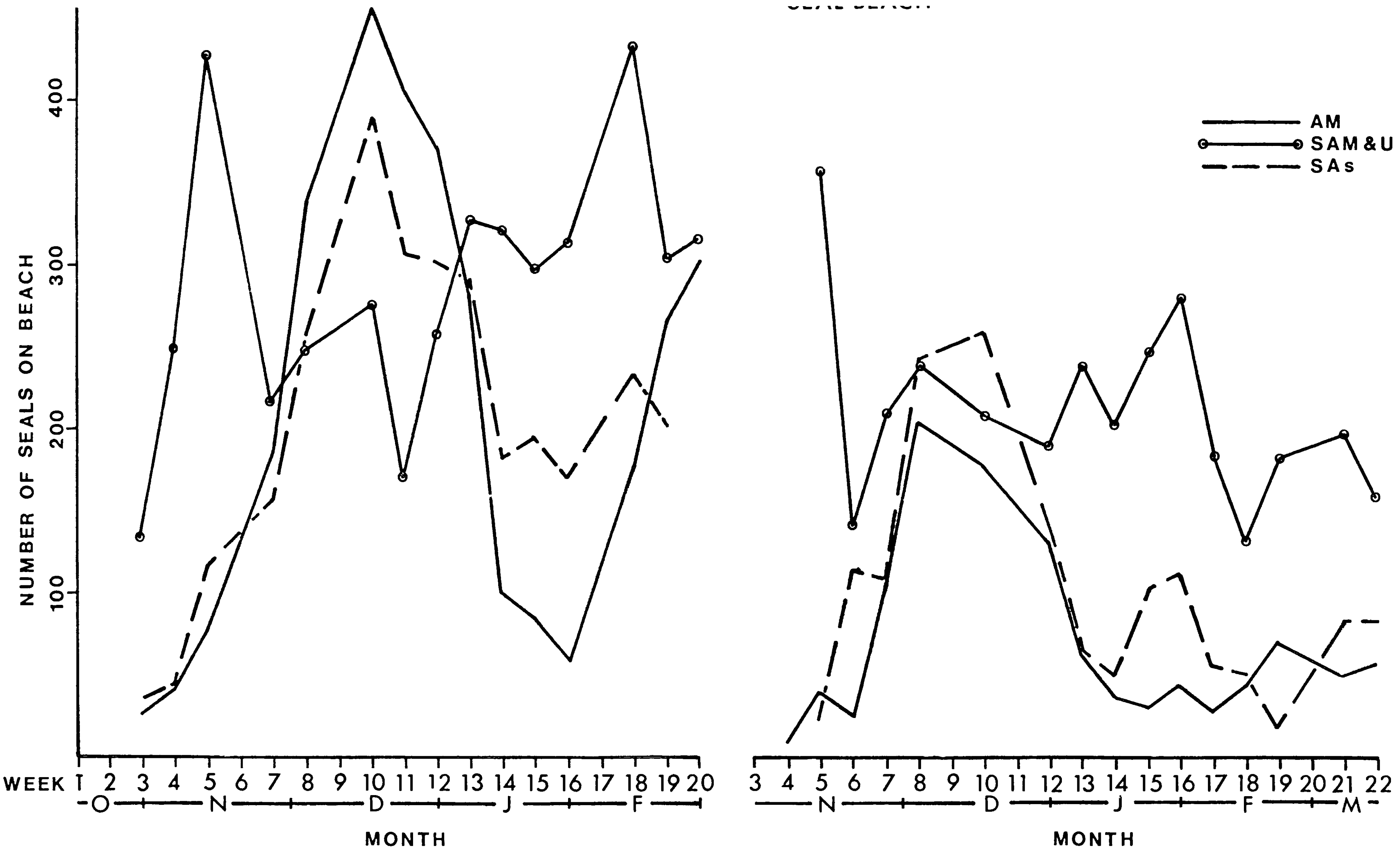

FIGURE 21 : Changes in numbers of different age and sex groups during the austral summer of 1974/75 at Admiral beach and Seal beach

submissive attitude and the absence of any pronounced secondary sex characteristics. The larger subadult males, however, are behaviourally excluded (Fig. 21). The increase in the smaller size category of the subadult class is discussed later.

YEARLINGS

Yearling fur seals are entirely absent from the island during the breeding season as is the case also for this species at Amsterdam Island (Paulian 1964) and apparently Marion Island (Rand 1956b), as well as for the New Zealand and Australian populations of *A. forsteri* (Stirling 1970 and 1971a; Miller 1975a). However, yearling *A. gazella* (although underrepresented) and *A. p. pusillus* (Bonner 1968; Rand 1956a and 1967) are found present on rookeries. In the present investigation yearlings were only weaned at approximately 10 to 11 months of age and just before the onset of the next pupping season. It was also found that the time of their departure could fluctuate. The last week in November heralded the departure of the last yearlings in 1975 but they were already absent at the beginning of November 1974. This two week difference in departure time corresponded with the difference in onset of pupping for the east coast sites in question and the delay in the haulout for the moult (Fig. 22). The significance of this, however, remains obscure.

Yearlings do not necessarily depart from the island from the immediate vicinity of their birthsites. At least some of them undergo a local post-weaning dispersal phase from their birthsites into e.g. nonbreeding colony sites. Some had already started dispersing from their birthsite when accompanying their mothers, at the beginning of March. From Table 7 it is clear that the Stand-Off Rock area, including Stand-Off Rock itself as well as Seal beach, had more yearlings during October 1975 than the maximum numbers of pups born there the previous season. They, therefore, represent weaned yearlings since a negligible number of females was located here and the instances of suckling observed can be ascribed to the still intact nutritional bond between mothers and those yearlings that have been born at these sites.

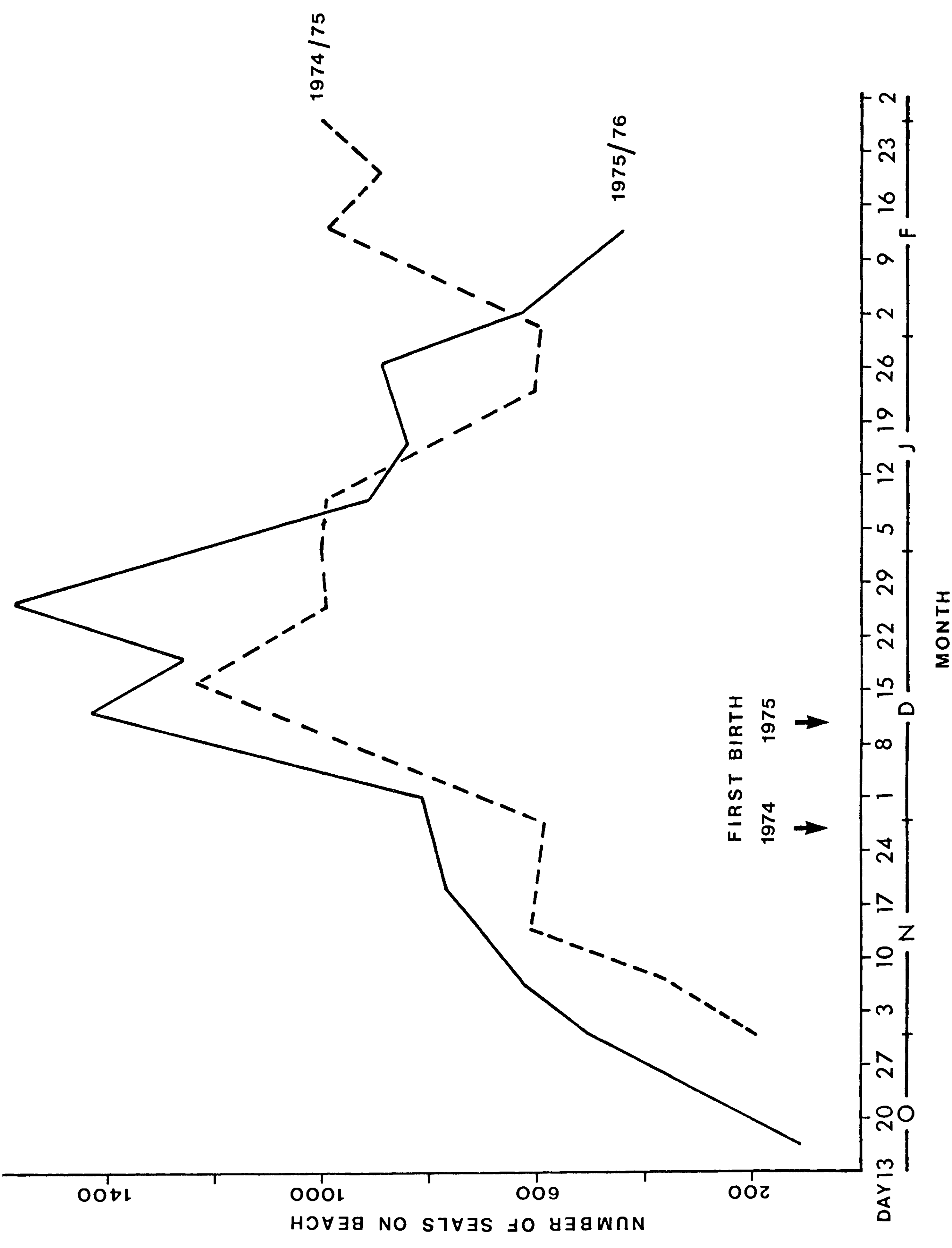

FIGURE 22 : A comparison between changes in colony numbers at Admiral beach for two successive austral summers

TABLE 7: **Counts of yearlings and adult females present at various east coast sites during October 1975 and 1976 with reference to the maximum pup yields for those areas for both seasons**

Date	Locality	Adult females	Year-lings	Pup yield
13/10/76	Stand-Off Rock area	3 +?	33	7
13/10/76	Seal beach	1	3	1
17/10/75	Admiral beach	7	33	26
20/10/75	Seal beach	0	48	1
20/10/75	Stand-Off Rock area	1	126	7
21/10/75	Stand-Off Rock area	2	112	7
27/10/75	South Point beach	1	27	35
	+ immediate surroundings			

Table 7 shows that the number of yearlings hauled at Seal beach and the Stand-Off Rock area, and the south-east coast in general experience a post-weaning influx of yearlings born elsewhere as part of a local dispersal phase before they evacuate the island for the duration of the breeding season. This phenomenon was observed for two successive seasons. The closest established breeding colonies to this area are located on the south-west coast. The single retrieval of a yearling which was tagged as a pup near Boulder Cove on the South coast 8 months previously, between Seal beach and Stand-Off Rock on 13 October 1976 suggests that at least some of them originate from south-west coast breeding colony sites. However, considering the number of yearlings found in the Transvaal Bay area and the total number of pups born on e.g. the south-west coast, coupled with their paucity on other east coast sites, the local post-weaning dispersal phase cannot be applicable to the yearling class as a whole. The bulk of the yearling class will no doubt leave the island from the approximate site of their birth within the confines of smaller lateral displacement or interbeach movement. The choice of the Transvaal Bay area, apart from its proximity to the south coast breeding colonies, is obscure since other east coast sites offer the same features that would make the former attractive.

Yearlings started to return from the beginning of February, at the latest, as partly moulted second year subadults. They were found present on breeding and nonbreeding sites alike until the time (14 February 1976) when figures for different classes ceased to be available. From information received (Peens *pers. comm.*) the majority of two year old seals depart from the island at the close of the moulting season.

PUPS

An account of the pupping season has already been given. By approximately two weeks of age pups born on the rookery started to associate with one another. This culminated in the presence of most of the pups, when four to five weeks old, at the back of the beach. This behaviour pattern can result from the aggressive attitude of others females towards pups other than their own, similar to what Bonner (1968) found in *A. gazella,* and that mothers are leaving their young for longer spells to feed.

At nearly two months of age pups first enter the surf zone and swim in rock pools. They were, however, reluctant to venture into rough water but stayed close to the foremost rocks under calm conditions. Pups in the present investigation, in agreement with Stirling's (1970) findings for *A. forsteri,* raced for land rather that the sea when disturbed. This shows that they still felt inept to cope with an excursion into deeper water. However, the familiarization with open water provided a means of inter-beach movement, apart from those evident on the beach itself. On two occasions pups were observed to haul at nonbreeding colony sites but were absent the next day having presumably returned to their place of origin. During early March (10/3/75) a pup accompanied by its mother hauled at Seal Beach, indicating that at this time breeding sites are left by at least some females with their pups. This could culminate in a more prolonged or permanent residence at sites other than birthsites. For example, what was presumed to be the same pup was found present during three censuses spanning a period of 16 days but was absent 2 weeks later as well as for 6 weeks thereafter. On 26 June 1975 two pups (yearlings then), with their mothers in attendance, turned up at Seal beach and the former remained for 2,6 months before they disappeared on 12 September 1975. At Marion Island pups also leave breeding colony beaches in favour of more secluded and less congested sites (Condy *pers. comm.*). The onset of the moult in pups was difficult to pinpoint but by middle February the first signs were detected. By the end of this month the moult definitely had set in, as was easily ascertained from the presence of hair under the nails of the pes as a result of the grooming action. By the beginning of March none had completely moulted and in essence still possessed the black natal coat. A completely new yearling coat had, however, not been attained by some at beginning May. The lack of reliable winter observations precluded determining when the moult is completed but it seems to be complete by June. Hereafter pups are referred to the yearling class. From the above it seems that the pup moult onset time is essentially the same as has been established for *A. p. pusillus* (Rand 1956a).

Colony composition changes

The annual cycle of *A. tropicalis* at Gough Island, as based on research carried out chiefly at the four main study areas, has already been described. In this section the change in the small isolated colonies demarcated according to habitat type within the range of Admiral beach will be described and compared to other breeding and nonbreeding colony sites.

NONBREEDING COLONIES

Adult male numbers for the two nonbreeding colonies censussed i.e. Admiral beach section A' and Seal beach demonstrated the typical early season increase (Seal Beach), December peak, January decrease and postbreeding (moult) increase (Seal beach + A') in concordance with the fluctuations in total number (Fig. 23 and 24).

Subadult male numbers fluctuated inversely with adult male numbers but they were always well represented, especially end-January/beginning-February, forming between 52 per cent and 62 per cent of the total population present.

The minimal representation of adult females throughout the season is evident from Fig. 23 and 24. The increased presence of females during late

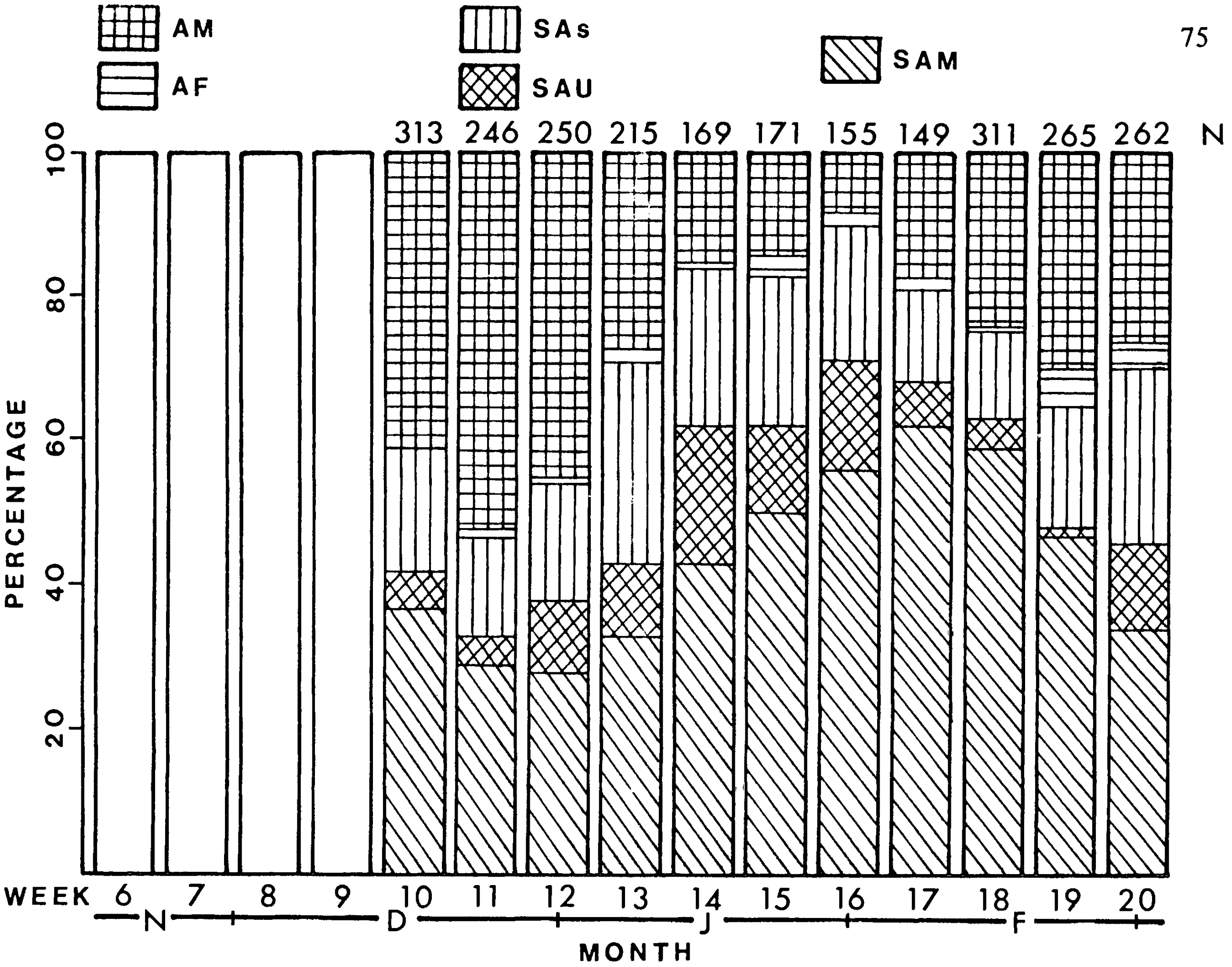

FIGURE 23 : Variation in nonbreeding colony age and sex group representation during the austral summer of 1974/75 at Admiral beach

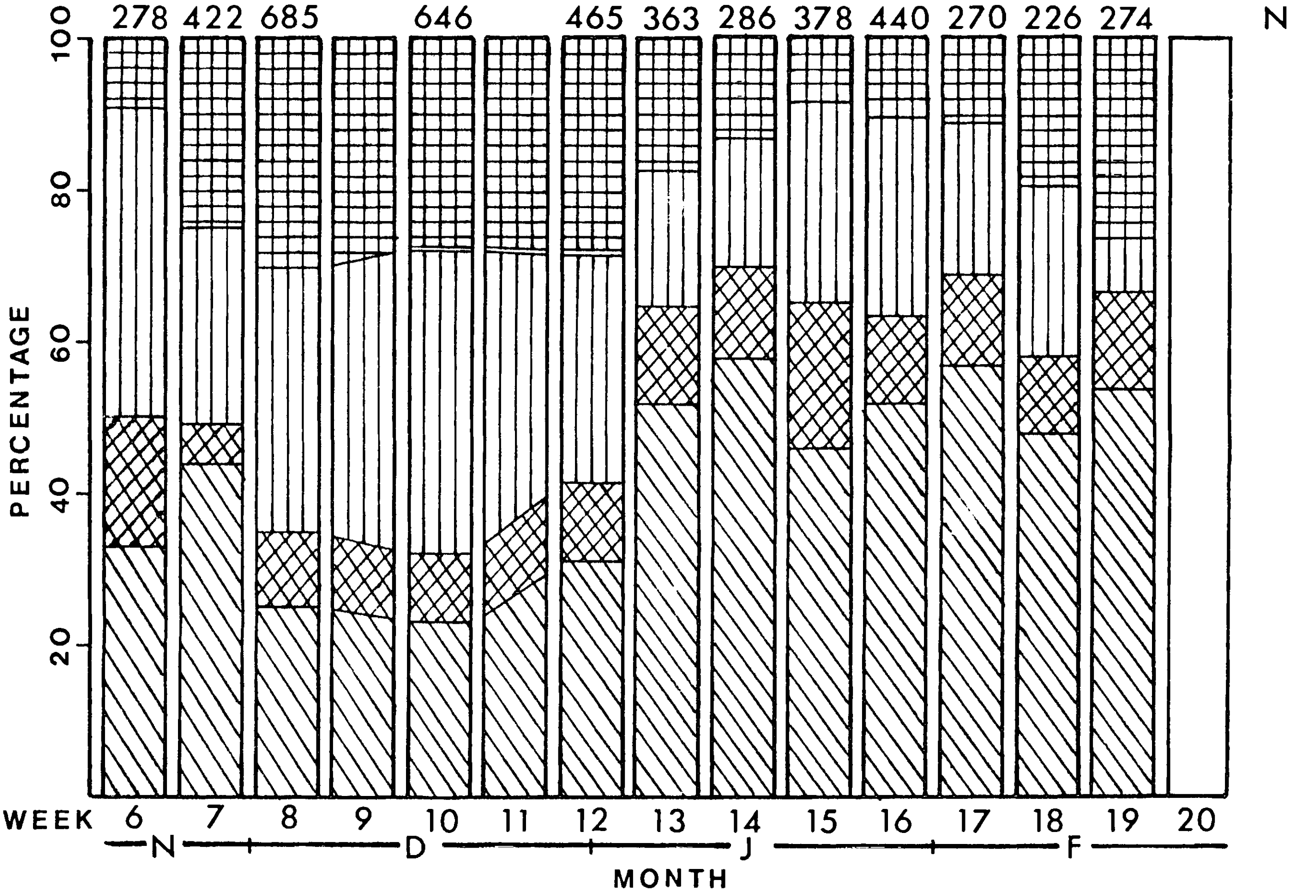

FIGURE 24 : Variation in nonbreeding colony age and sex group representation during the austral summer of 1974/75 at Seal beach

February resulted from laterally displaced pupped females (and their pups) from adjacent breeding sites, as well as the limited arrival of nonbreeding females for the moult who also utilized areas other than breeding colony beaches for this purpose.

The SAs category is fairly small in comparison with the rest but more pronounced in the Seal beach colony than in the A' population.

BREEDING COLONIES

Figure 25 and 26 show that on breeding colony beaches as is to be expected where aggregations of females occur, relatively few mature males were present. This low number (less than 20 per cent of the population) was maintained for the duration of the census period, especially during late December and onwards. At Waterfall Cove the low total number of animals present during end-November/beginning-December resulted in a high percentage of adult males, although their absolute number was much less than during subsequent counts up to mid-January (Fig. 26).

Subadult male numbers were small for the whole period but exhibited the same trend as established for nonbreeding colony sites in this study, i.e. their prominence during the early part of the season as well as late January when the reduction in adult male number increased their chances to haul onto the beach. Both colonies were, however, subject to a relatively large increase in adult females. The prominent feature here is that nonmothers predominated on A" (Fig. 25) in contrast with Waterfall Cove (Fig. 26) where they were in the minority. Based on the final pup yield and the maximum number of positively identified adult females hauled at any one time during the breeding season high, a natality rate of 0,38 (1974/75) and 0,2 (1973/76) was calculated for A" and one of 0,74 for Waterfall Cove (1975/76). This would, moreover, indicate that predominantly nonmothers frequented the east coast breeding colonies in general since similar rates were applicable for other sites there. One also, finds a good representation of the SAs group at the breeding sites in question, and although the Waterfall Cove breeding colony and the Seal beach nonbreeding colony had

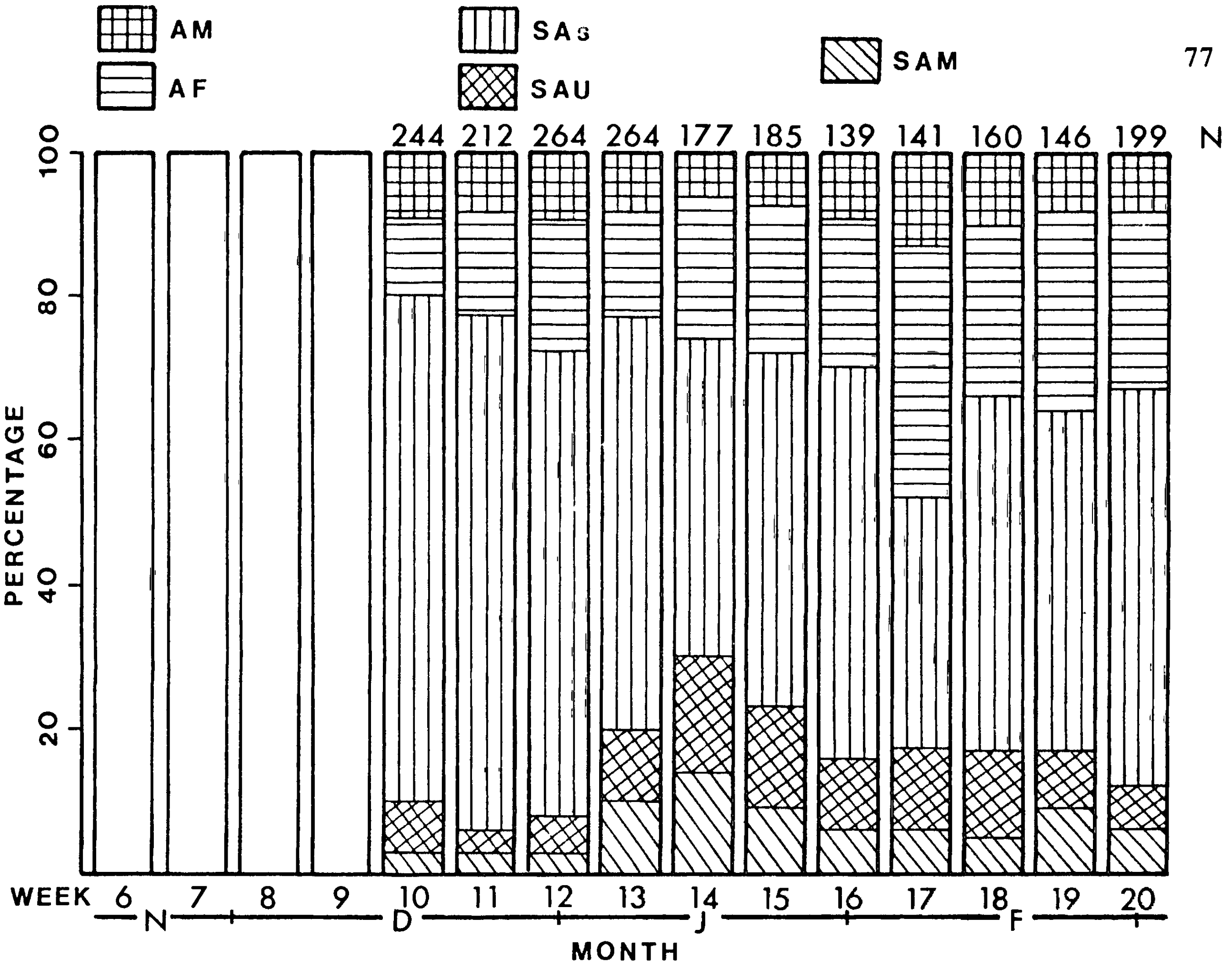

FIGURE 25 : Variation in breeding colony age and sex group representation during the austral summer of 1974/75 at Admiral beach

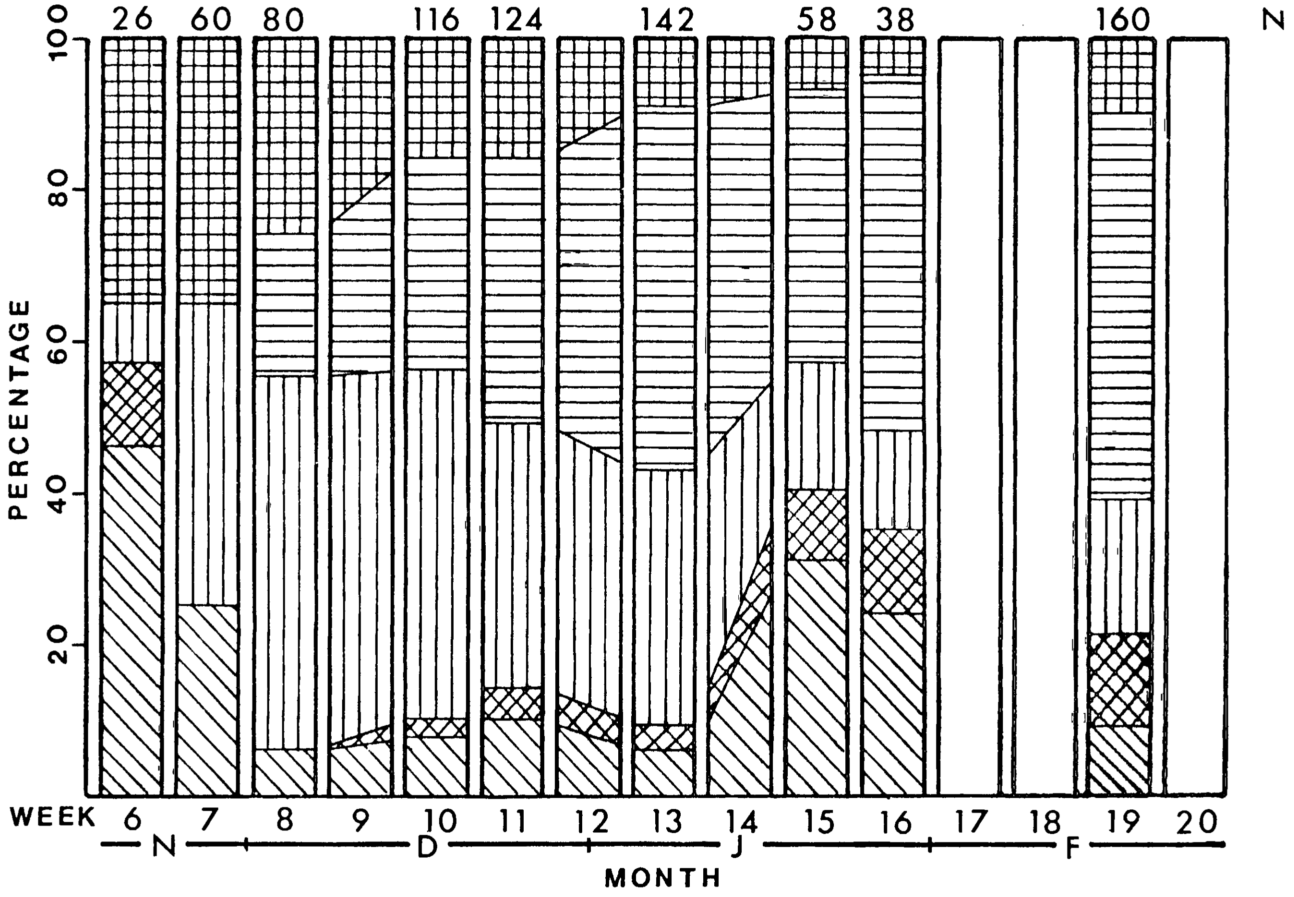

FIGURE 26 : Variation in breeding colony age and sex group representation during the austral summer of 1975/76 at Waterfall Cove. Results presented for week 19 are based on a census done during February 1975

approximately equal numbers this group was abundant on A". The latter sector as well as Seal beach in early December showed a spectacular increase in the SAs group. At A" the second week of pupping (at a time when a rapid increase in adult females ensued) showed an increase in the SAs group which was coupled with a shift of some of the SAs group from the adjacent nonbreeding colony sites.

The sex distribution of the SAs class differed at breeding and nonbreeding colony sites with females predominating on the breeding ground and males on the nonbreeding sites with a male : female ratio of 1 : 1,86 (N=20) for A" and 4,38 : 1 for e.g. Seal Beach (N=43).

The difference in the sex distribution within the SAs class illustrates that the sex ratio is in favour of females on the breeding sites. These SAs females therefore typically show the same trend in seasonal hauling/departure pattern considering actual numbers, established for this class as a whole irrespective of sex (Fig. 21). They, moreover, exhibit the same site selection as adult females. However, it appears that the south-west coast (and therefore established breeding colonies) is neglected by the SAs class and that east coast sites (including South Point beach) where, furthermore, a high percentage of nonmothers is located, possess a greater attraction but subject to female habitat requirements.

According to Payne (1977) the mean age of recruitment of primiparous females of *A. gazella* is 3,66 years with first recruitment at 3 to 5 years of age but no primiparae are older than 5 years. If the population in the present study simulates this condition it would explain the high incidence of nonmothers on the east coast in general and, furthermore, suggests that their high concentration here is the result of an avoidance of the congestion of established breeding sites elsewhere. For the same reason it would favour the presence of the smaller age/size category. Paulian (1964) also found nonpregnant sexually mature females not to land at the rookeries but to haulout alone or in small groups which are located between rookeries (breeding colony sites) and near a few males. Although this does not entirely correspond to the present situation involving the same species, the east coast breeding sites could parallel this phenomenon and approach organized, but still essentially unsuccessful, breeding populations. The low incidence of pregnancy here could possibly be ascribed to a poor serving of adult females by territorial males as well as possibly a delayed recruitment of them if virgin cows, which are in abundance here, are fertilized (Payne 1977).

Figure 27 shows colony composition and change of three breeding and nonbreeding colonies, as well as an idle colony, at selected periods (early breeding season, breeding season height, postbreeding decline) during the breeding season. For the breeding populations, especially the successful one at Boulder Cove on the South-west coast, the insignificant representations of the SAs class (A" already discussed) and the high male : female ratio and paucity of subadult males in especially mid-season, can be seen.

The nonbreeding colony adult and subadult male numbers show the same trend (rise in adult male number with concomitant decrease in subadult male numbers) as well as the low presence of adult females. The latter (presence of adult females) was more pronounced during the postbreeding total colony numbers decrease probably as a result of the regular haulout and departure of the few postparturient females between feeding trips. The early census (fourth week after commencement of censusing) at Boulder Cove occurred two weeks earlier than the others and is therefore not directly comparable. Seals and therefore the SAs class were present in low numbers which could create a faulty impression when judged against the other sites censused.. The idle population typically exhibits the complete absence of all classes except adult and subadult males for the whole breeding season and they conform to the pattern established for nonbreeding sites.

As the austral summer progresses the small east coast breeding colonies show the same pattern as the more successful ones elsewhere on the island. The major difference lies in the relative abundance of the SAs female class and nonpregnant adult females.

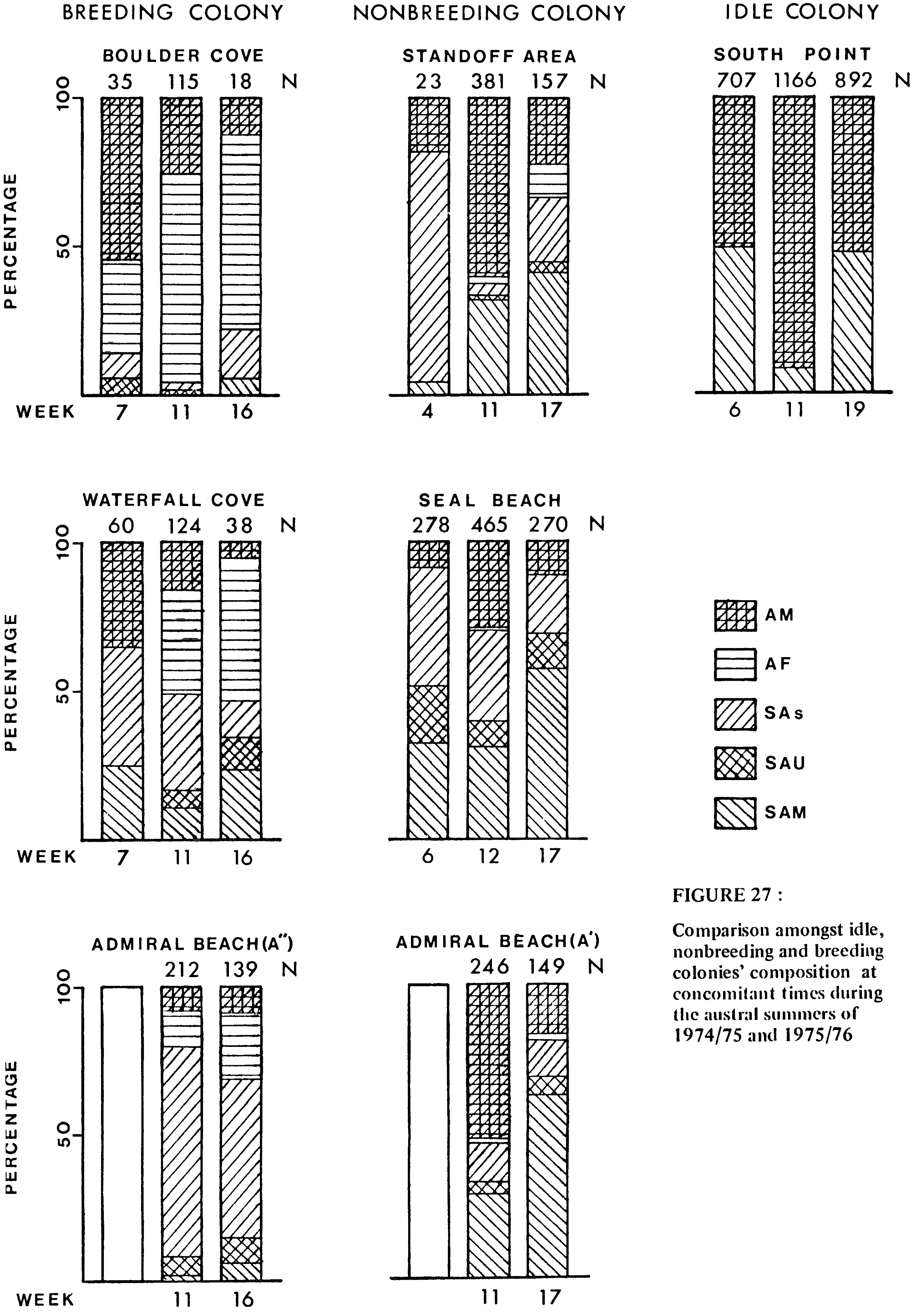

FIGURE 27 :

Comparison amongst idle, nonbreeding and breeding colonies' composition at concomitant times during the austral summers of 1974/75 and 1975/76

BEHAVIOUR

General Behaviour

HAULING AND DEPARTURE PATTERNS

Seal numbers ashore vary according to the time of day and weather conditions as established for various other pinniped species (Bartholomew and Wilke 1956; Kenyon and Rice 1961; Orr 1967; Rand 1967; Fay and Ray 1968; Stirling 1968 and 1970; Crawley 1972; Wilson 1974). In practice therefore understanding the diurnal rhythm of pinnipeds lies in the correct choice of the time of day to carry out a census.

Nonbreeding *A. tropicalis* at Seal beach, Gough Island, do not show a specific trend in daily haulout and departure patterns, although in one instance a peak between 09h00 and 10h00, followed by a steady decrease in the number of seals hauling out towards 16h00, is found (Fig. 28A). The departure pattern for the same day (Fig. 29A) shows a low but constant departure rate of seals. The remaining three observations do not confirm this or any other pattern (Fig. 28 and 29). The combined results of the four-day study period, however, show a haulout peak during the second hour of the morning observations (09h00–10h00) with a general decrease towards 16h00 (Fig. 30). Most departures occurred from 09h00 – 13h00, with a reduction in the departure rate thereafter.

The average hourly number of departures (expressed as a per cent of the total number of departures recorded for each day) was greater for the four hours before noon than the same period thereafter. Similarly, the highest hourly average of departees left during the morning except for day 4 (Fig. 29D). Furthermore, 54,89 per cent of the total number of departures over the entire study period occurred before noon versus 45,11 per cent which departed during the afternoon. Similarly, 14,74 per cent more seals hauled out during the morning than the afternoon.

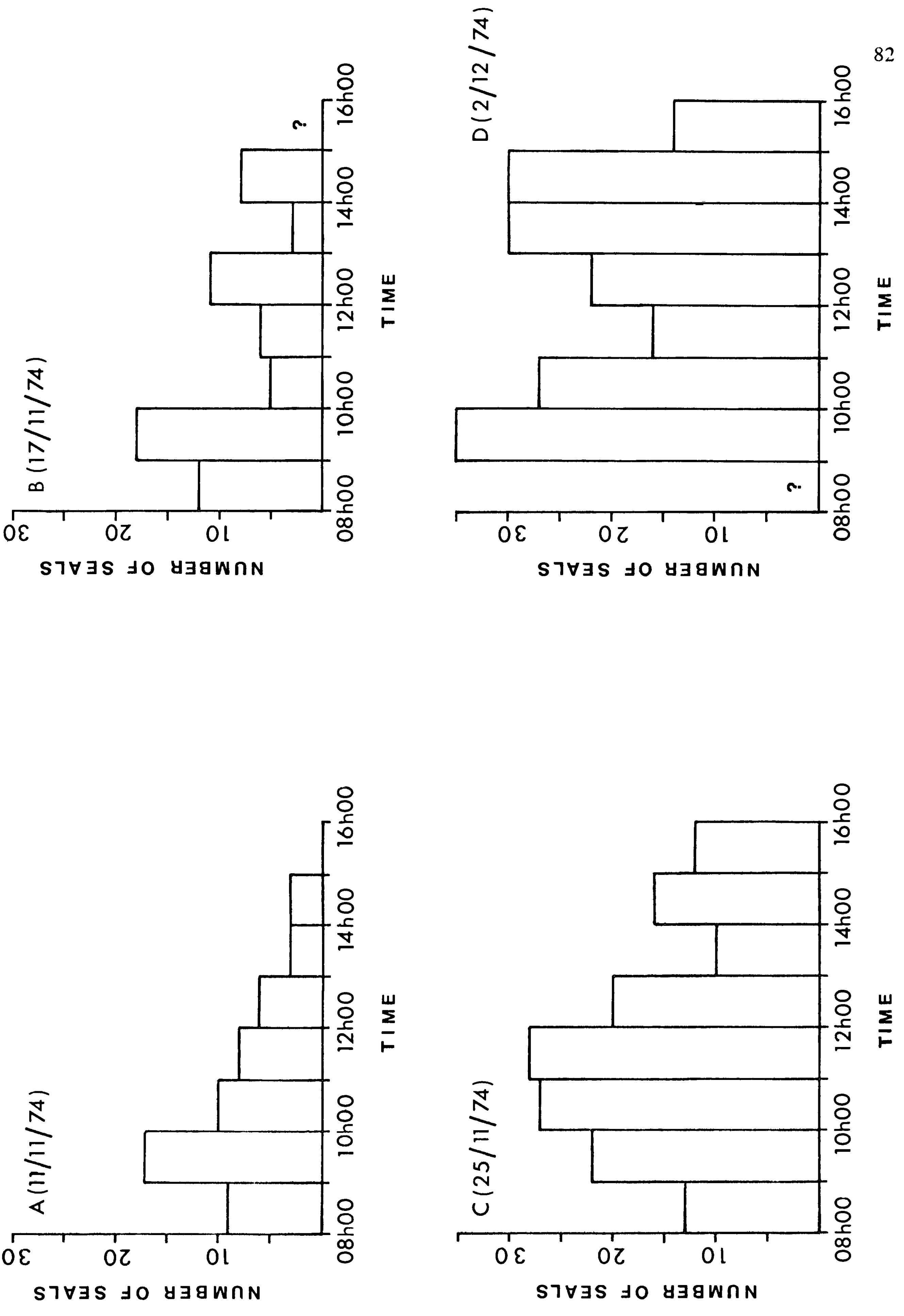

FIGURE 28 : The hauling-out pattern of nonbreeding seals at Seal beach, during four days, for the period 08h00–16h00

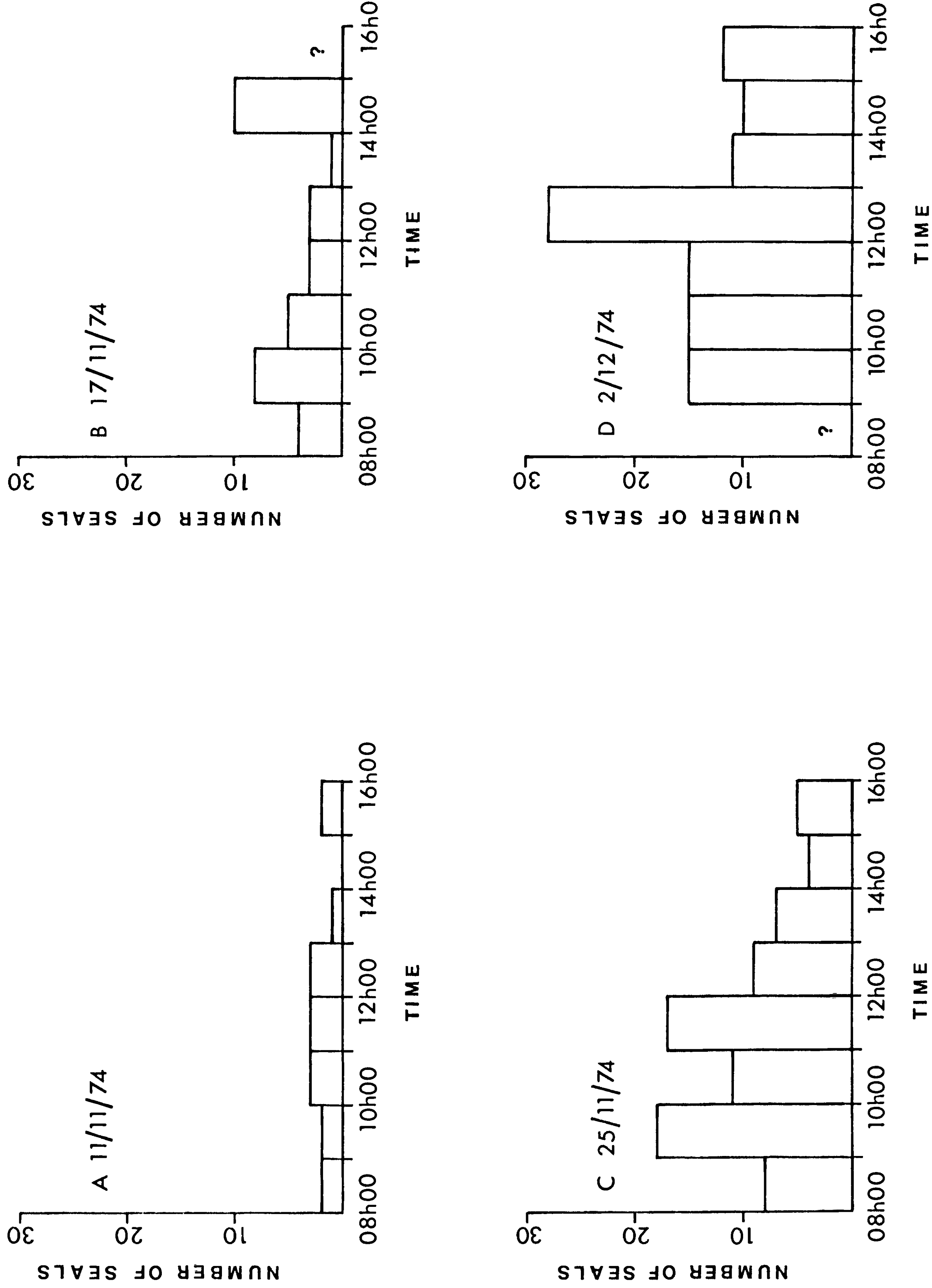

FIGURE 29 : The departure pattern of nonbreeding seals from Seal beach, during four days, for the period 08h00–16h00

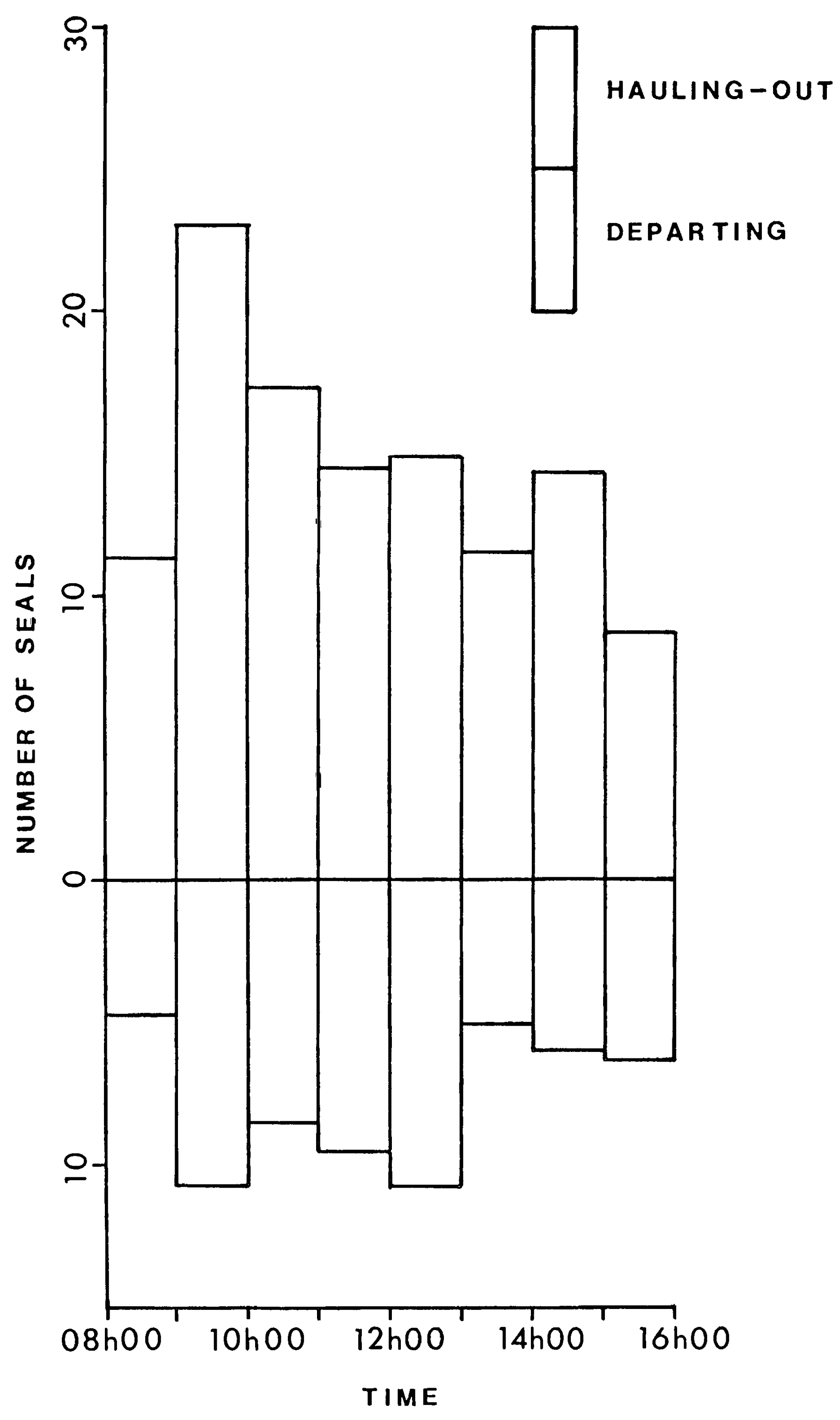

FIGURE 30 : Combined results (hourly average) of seals hauling-out onto, and departing from, Seal beach on four days for the period 11/11/74–2/12/74 from 08h00–16h00

This pattern of high departure can be related to observations on day 3 (Fig. 29C) and day 4 (Fig. 29D), when the ambient temperature was already limiting during the morning. The high morning hauling rate as an expression of the return of seals after an overnight excursion was thus parallelled by a similar high heat induced departure rate.

The daily change in the numerical size of a colony of seals depends on the difference between the influx and efflux of seals to and from the site occupied by them. Often, especially under adverse environmental conditions, the rate of departures exceeds the rate of arrivals. This is not manifest for the four-day study period described since seals could unobtrusively depart unnoticed whilst arrivals are conspicuous, they being the only wet animals on the site. Only two instances were recorded where departures exceeded the number of arrivals for the hour.

Figure 31 shows the actual number of seals present at Seal beach (dry and surf zones) at half an hour intervals, noted during three different days, from 08h30 to 16h30. On 3 March 1975, a cool cloudy day when temperature was not a limiting factor for staying hauled out, the highest number of seals was present between 14h00 and 15h00. However, on 20 November 1975 and 11 February 1975, high ambient temperatures prevailed during mid-day, with seals ashore showing signs of heat stress; the maximum number of seals counted during the day occurred between 10h00 and 11h00. A sharp decrease in numbers ensued from 11h30 to 12h30 (Fig. 31). During the afternoon hours seal numbers ashore increased once more but by 16h30 had not as yet reached the maximum number obtained during the morning. Expressed as a percentage of the morning maximum, the afternoon maximum was 92,13 per cent and 91,56 per cent respectively for the two days in question. The lowest count for these two days (mid-day counts) was 66,29 per cent and 66,23 per cent of their daily maximums. In contrast, on 3 March 1975, the minimum for the day was considerably higher at 80,58 per cent of the maximum count as a result of the absence of a temperature induced high departure rate.

The state of the tide did not visibly influence the diurnal haulout and departure pattern of *A. tropicalis* at Gough Island but affected their distribution on

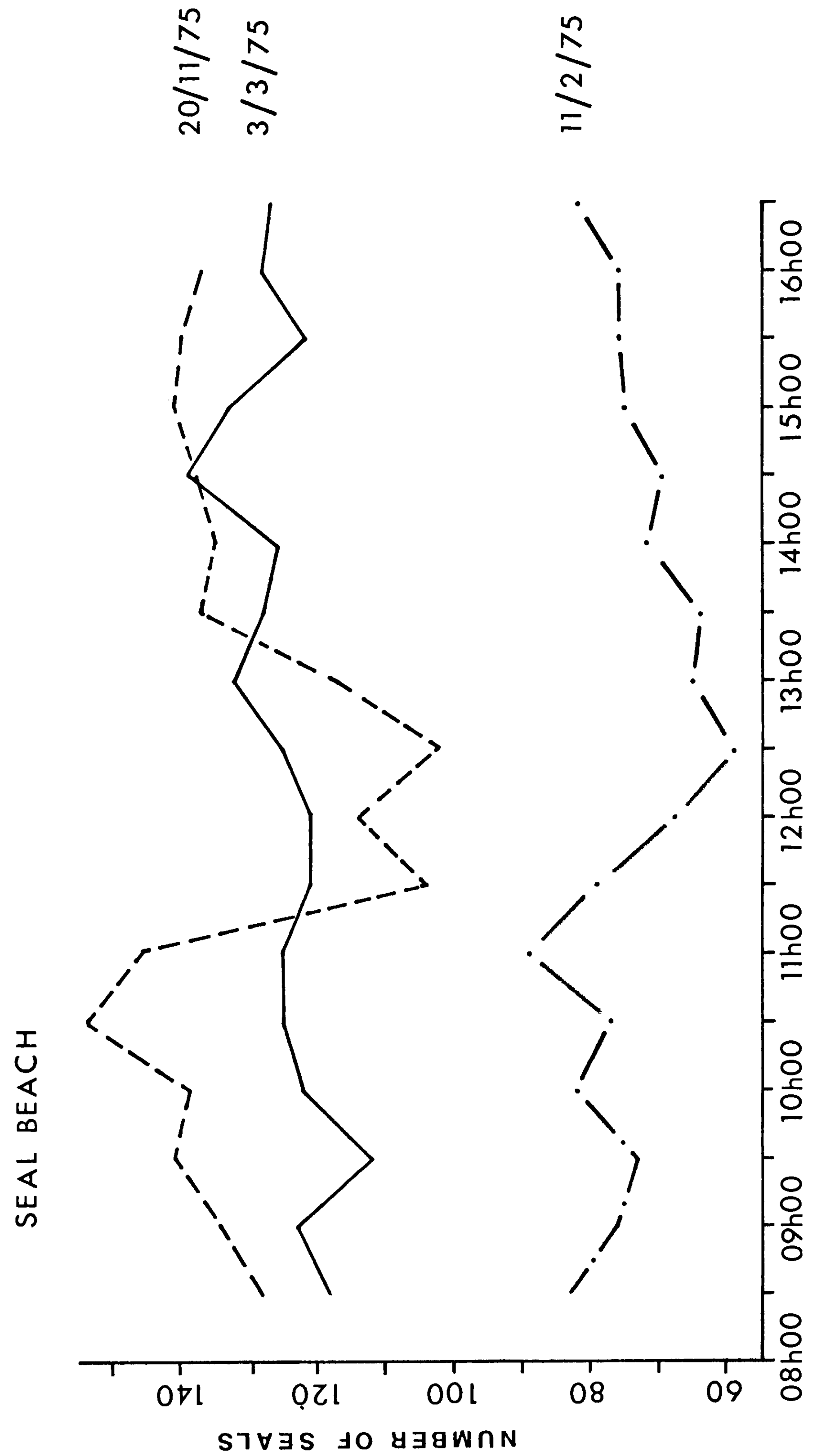

FIGURE 31 : Changes in the number of seals ashore (dry zone and surf zone) at Seal beach at half an hour intervals for three days for the period 08h30–16h30

the beach and offshore rocks. In contrast to *A. forsteri* (Stirling 1968) offshore rocks are abandoned at low tide, especially when this coincides with the late afternoon hours. At this stage, all are found on the beaches whose area is extended by the receding of the water level. However, under similar conditions but after a warm, clear day, seals utilise offshore rocks. With the flow of the tide seals simply move higher up the beach. Even under stormy sea conditions with the waves reaching far up the beach, seals did not voluntarily leave the beach but only when partly washed off their sites did they leave for open water. Occasionally adult males left under stormy sea conditions when they apparently considered it more favourable (or less cumbersome) to leave rather than move higher up the beach closer to other males inland from them.

The hauling-out rate of *A. tropicalis* on Gough Island is therefore highest during the morning, decreasing slowly towards the afternoon when maximum, or near maximum numbers are attained onshore. Stirling (1968) and Crawley (1972) also found a peak in *A. fosteri* numbers ashore during late afternoon, especially when this coincided with low tide (Stirling 1968). *A. tropicalis* throughout the day also depart from the hauling ground but generally at a lower rate than arrivals, resulting in a net gain in numbers ashore. However, under conditions of high ambient temperatures and solar radiation the hauling-out and departure rates are reversed resulting in a reduced number of seals ashore. This is especially evident for mid-day hours with the balance restored during the middle to late afternoon when temperature levels are lower. For example, on 11 February 1975, the morning temperatures varied from 13°C to 15°C (more seals arrived than departed), during mid-day varied from 17°C to 23°C (more seals departed than arrived) and was followed by a steady decrease to 13°C by 16h30 when the morning situation again prevailed. Stirling (1968) and Crawley (1972), however, did not give any indication how temperature influenced the diurnal hauling pattern of *A. fosteri* they observed.

ACTIVITY PATTERNS

Quantitative data on especially fur seal daily activity in sparse. Stirling (1968) and Crawley (1972) described the diurnal pattern of *A. fosteri* numbers ashore and Stirling (1971a) gave an account of the time budget for activity of territorial males. Miller (1974) quantified the social encounters between males and females of *A. fosteri* and referred to the influence of temperature on intersexual activity. The effects of temperature on activity levels of a number of pinniped species were also commented on by Bartholomew and Wilke (1956), White and Odell (1971) and Gentry (1973). Stirling (1971a) demonstrated the influence of time of season on male *A. fosteri* activity patterns.

In the present study on *A. tropicalis* the activity patterns of the seals and factors influencing it were given some attention. Table 8 shows the interaction frequency of fur seals occupying the nonbreeding colony site at Seal beach. The majority of interactions on the dry hauling ground (dry zone) involved at least one member of the subadult class (95,58 per cent) with 77,18 per cent of all interactions observed occurring amongst subadults themselves. In only 17,96 per cent of the cases where subadults participated, were adult males implicated. Adult males participated in 21,45 per cent of all interactions recorded with only 3,49 per cent occurring amongst adult males themselves. The paucity of adult females on the nonbreeding colony site precluded a high interaction frequency involving this sex group (Table 8). No interactions were noted between the few adult females during observation periods.

TABLE 8: Interactions occurring on the dry hauling ground at Seal beach during observations totalling 50h40 min, spanning eight days, between 20 November 1974 and 17 February 1975

	AM:AM	AM:SA	SA:SA	AM:AF	AF:SA	Total
N	28	144	619	8	3	802
Per cent	3,49	17,96	77,18	1,0	0,37	–

Figure 32 shows the diurnal rhythm in interaction frequency on the dry hauling ground from 08h00 to 16h00. The hourly percentage of the total number of interactions, recorded as an average of six days' observations, is highest from 08h00 to 09h00 with a reduction towards mid-day followed by an increase for the

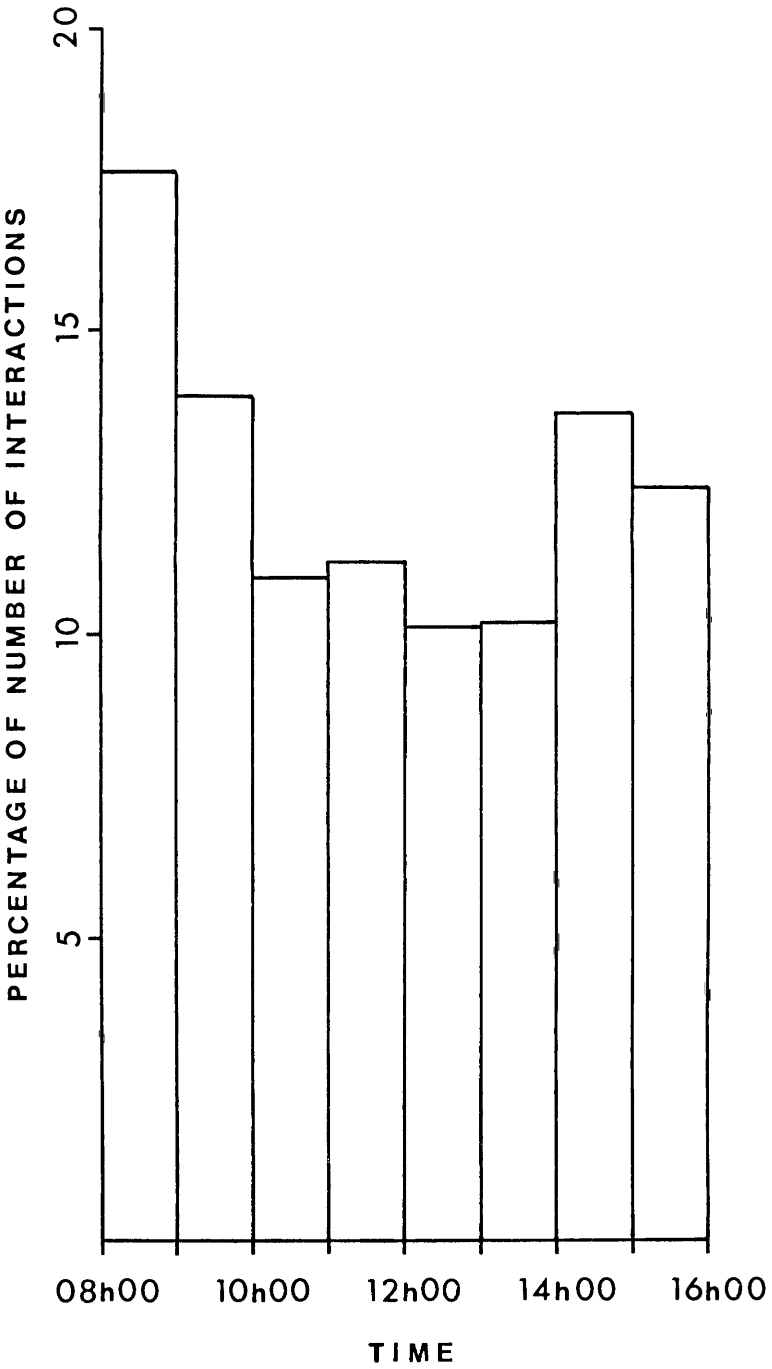

FIGURE 32 : Diurnal rhythm in interaction frequency of *A. tropicalis* on the dry hauling ground at Seal beach, compiled from observations from 08h00–16h00 on six days between 11/11/74 and 20/11/75 and expressed as a per cent of the total number of interactions scored (N = 734)

period 14h00 to 16h00. This trend follows the hauling and departure rate of the seals at this site (Fig. 30) with the morning peak in interactions associated with the high turnover in numbers ashore and when lower temperatures prevail. The afternoon high on the other hand results from the high number of seals ashore and a decrease in temperature after the mid-day high.

The lower interaction frequency for mid-day can be related to the higher temperatures that generally prevail during this time. Similarly Miller (1974) found the frequency of herding behaviour of adult territorial males to be depressed at high temperatures and Bartholomew and Wilke (1956) also observed a decrease in general activity of *C. ursinus* with an increase in environmental temperatures.

Interactions between fur seals is much higher in the surf zone than on the dry hauling ground : of a noted 2 290 interactions at Seal beach 64,98 per cent (N = 1 360) were recorded in the surf zone and only 35,02 per cent (N = 733) on the dry zone. The difference in frequencies of interactions in these two zones is especially evident during mid-day hours, from 11h30 to 13h30 (Fig. 33). The hourly frequency of interactions in both zones are highest around 08h30. By mid-day the frequency of interactions again reaches a peak in the surf zone with the dry zone interaction rate showing a further decline. Towards late afternoon interaction frequencies for the surf and dry zones converge towards each other as a result of an increase in the dry zone interaction rate and a concomitant decrease in surf zone rates (Fig. 33).

The observation that interaction frequencies were always higher in the surf zone does not imply that seals are more numerous here. On the contrary, more seals are at any time present on the dry hauling ground itself and only the interaction rates of individuals in the surf zone are elevated compared to their opposite numbers on the dry zone. On the average, 0,618 interactions were recorded per individual at each scan of the number of seals in the surf zone compared with only 0,045 on the dry zone (Table 9). This does not only apply to the interaction rate of the individuals in the respective zones but also to their activity in general.

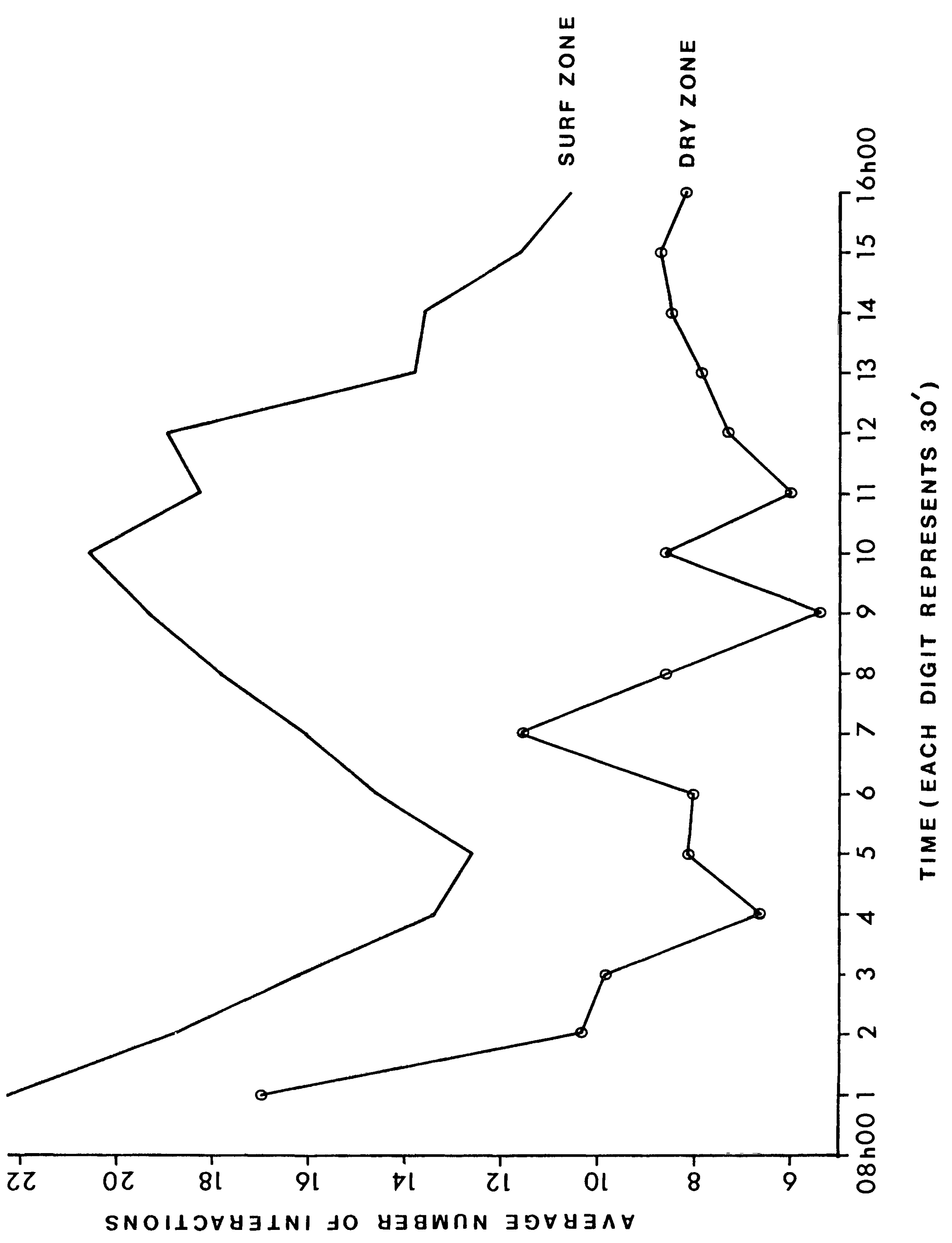

FIGURE 33 : Average number of interactions scored for each half an hour period from 08h00–16h00 on seven days of observation to show the difference in frequency of social interactions in the surf zone and dry hauling ground at Seal beach

TABLE 9: **Interaction frequencies of *A. tropicalis* on the dry and surf zones at Seal beach based on 23h10 min of observations, and expressed as the average number of interactions per individual at each scan sample**

	Interaction frequencies				
Zone	17/1/75	8/2/75	17/2/75	20/11/75	$\bar{X}$
Dry	0,046	0,042	0,022	0,055	0,045
Surf	0,805	0,589	0,425	0,632	0,618

TABLE 10: **Time budgets of subadult *A. tropicalis* on the dry hauling ground and surf zone respectively for four random hours of observation on three days at Seal beach**

Date	Dry Zone		Surf Zone		$\bar{X}$ number of seals present	
	Active %	Inactive %	Active %	Inactive %	Dry Zone	Surf Zone
7/11/75	16,88	83,12	67,90	32,10	69,5	12,5
12/11/75	6,84	93,12	76,90	23,10	50,6	24,3
14/11/75	4,24	95,76	88,65	11,35	74,5	14,2
AVERAGE	11,39	88,61	76,0	24,0	66,0	15,9

Table 10 shows the higher activity level of subadults, for example, in the surf zone when compared with the dry zone. In the latter zone, the time budget for activity of the subadult class shows that 88,61 per cent of time is spent inactive (lying motionless or sitting alert) versus only 24,0 per cent of time spent inactive by surf zone subadults. The higher activity level in surf zone subadults (interactions, grooming and walking) is related to the favourable temperature gradient that exists here.

The relative contribution of the different age and sex classes of the fur seal, *A. tropicalis*, to the interactions noted for the nonbreeding colony site (Table 8) cannot be accepted to be the norm for other colony types in the present study. The interaction pattern depends on the composition and change in the relative representation of the different age and sex classes on the colony sites. Table 11, showing the time budgets of adult males on different colony sites, illustrates this point.

TABLE 11: Time budgets of adult *A. tropicalis* males observed over 15 days during the austral summer at idle, nonbreeding and breeding colony sites

Colony type	Observation Time	Categories of Behaviour					
		Lying %	Alert %	Adult Males: Adult Males %	Adult Males: Adult Females %	Adult Males: Subadults %	Other* %
Idle	11h	94,16	1,24	0,67	0	0	3,93
Nonbreeding	90h15 min	88,95	4,37	0,73	0,18	4,0	1,77
Breeding	33h15min	81,11	12,12	1,16	3,18	1,26	1,05
AVERAGE		86,02	7,43	0,91	1,45	2,51	1,64

*Locomotion and grooming

Over a total observation period of 134 h 30 min adult males on the average spent 86,02 per cent of their time lying motionless and 7,43 percent in the alert position; therefore 93,45 per cent in an inactive state. The remaining 6,55 per cent was spent interacting with other age and sex classes as well as indulging in non-social activities such as locomotion and grooming.

Idle males have a high inactivity rate and show little interest in their surroundings which they share with the older range of subadult males. All other age and sex classes are practically absent from idle colony sites. No territories, apart from individual distances, are defended and as a result 94,16 per cent of their time is spent in a lying position or sitting alert (1,24 per cent). The only other activities recorded are interactions between adult males (0,67 per cent) with non-social activities, grooming and locomotion, occupying 3,93 per cent of their time.

Territorial males at nonbreeding colony sites, however, show an increase in activity level which can be related to the presence of especially second year subadults (which include females) and the few adult females present. These males, therefore, defend territories, especially males situated on the waterline. These are practically the only ones with adult or subadult females in their territories. As a result less time on average is spent being totally inactive (88,95 per cent) when compared with idle males and a substantial increase in the alert category is evident (4,37 per cent versus 1,24 per cent). Intermale interaction remains low at 0,73 per cent of time spent but it is an increase over that showed by idle males, as does activity directed at adult females and subadults of both sexes.

Territorial males at breeding colony sites are more active than males of the former two categories with even less time spent totally inactive (81,4 per cent). They are also much more alert (12,12 per cent). The predominance of adult females as opposed to all other age and sex categories in the breeding colony contributes to the higher percentage of time spent by harem males interacting with them (3,18 per cent) than with subadults (1,05 per cent). Intermale aggression, as an expression of vigorous territorial maintenance, is increased over that of idle and nonbreeding colony males (1,16 per cent).

These figures approximate those established for *A. forsteri* territorial males in breeding colonies; Stirling (1971a) found them to spend 72,32 per cent of time lying down with 18,82 per cent in the alert state. His combined total for inter- and intrasexual behaviour amounted to 3,12 per cent of time spent (5,61 per cent in the present study). As shown by Stirling (1971a) this percentage of total observed time spent on each of the categories varied throughout the austral summer.

The lack of territorial maintenance and involvement in breeding allows the subadult class to readily indulge in various activities not related to the above. Similarly, Rand (1967) described the subadults of *A. p. pusillus* as a boisterous class. The time budget of subadult *A. tropicalis* are given in Table 12.

TABLE 12: **Time budgets of subadult *A. tropicalis* on the dry hauling ground at Seal beach based on 14 hours of observations over six days**

$\bar{X}$ number of seals observed	Observation time	Category	Categories of behaviour				
			Lying %	Alert %	AM:SA %	SA:SA %	Other %
53,7	5 h	> 2 year old	81,87	2,26	0,17	11,46	4,24
26,6	5 h	± 2 year old	73,38	2,90	0,75	11,88	9,10
66,0	4 h	Combined	86,19	2,42	0	8,10	3,29
AVERAGE			82,29	2,45	0,22	10,21	4,83

The subadult class is on the average more active (15,26 per cent of time spent) than the adult male class (6,68 per cent of time spent) on the nonbreeding sites. The highest per cent of time spent, apart from lying motionless, involves interactions amongst members of the subadult group. Furthermore, within the subadult class, the smaller size category seems to maintain a higher level of activity compared with larger subadults (> 2 years old) which comprised mostly males. The latter group is less active and avoids the adult males with a concomitant lower interaction rate (0,17 per cent of time spent) with them. The second year old class includes females and they are frequently, amongst others, subjected to herding behaviour of adult males (0,75 per cent of time spent).

The distribution of the fur seals on a site and particularly in the case of adult males their specific location on the site, affect activity levels of the colony as a whole as well as that of individuals. For example, on 25 November 1974, 52 per cent (based on interaction frequencies) and 66 per cent (based on time budgets for adult male activity) of all interactions scored involving adult males involved only two of the average of 8,7 males under observation from 08h00 to 16h00. On 2 December 1974, two of an average of 22,8 males observed, were responsible for 42 per cent of all interactions logged. Perhaps significantly the males in question occupied preferred prime foremost territories situated on the waterline, an area favoured by all age and sex categories, especially when high environmental temperatures prevail. This area on the beach is also subjected to the hauling and departure of seals at all times during the day. Miller (1974) also described males to be relatively inactive during the hot mid-day except for those positioned on the waterline.

High ambient temperatures, especially in conjunction with intense solar radiation, have a pronounced influence on the level of activity in *A. tropicalis* colonies. Especially at idle and nonbreeding colony sites, fur seals converge onto the surf zone and into the shallows as a final reaction to excessive heat loading. Figures 34 and 35 show the change in seal numbers ashore on the dry hauling ground on two days when markedly different maximum temperatures were attained. On 3 March 1975 seals departed from and hauled onto the dry zone at Seal beach according to individual choice subject to inter-specific relationships rather than meteorological conditions (Fig. 34). By contrast, on 11 February 1975 ambient temperatures exceeded 18,5°C (the level at which the seals normally showed signs of severe heat stress) between 11h30 and 13h30. This resulted in an exodus of fur seals from the dry zone to the surf zone and at least some moved into the sea. Concomitantly the lowest number of seals on the dry zone was attained just after the highest temperatures of the day was recorded. Similarly, *C. ursinus* (Bartholomew and Wilke 1956); *A.p.pusillus* (Rand 1967), *A. forsteri* (Stirling 1970; Crawley 1972) and *Z. californianus* (White and Odell 1971) also moved into the water to escape thermal overloading. With decrease in temperature towards afternoon, seal numbers again increase on the dry zone (Fig. 35). Similarly, the activity rate fluctuates in response to the redistribution in numbers with the change in temperature. Activity, as indicated by the frequency of social interactions, vastly increases in the surf zone at ambient temperatures exceeding the 'comfortable' threshold value of 18,5°C (Fig. 36). The reverse is true when ambient temperature declines. The interaction rate also increases on the dry hauling ground when increased temperatures inconvenience seals. The number of interactions per half hour remains lower on the dry zone than in the surf zone and only increases over that of the latter at lower temperatures during the morning and afternoon when the largest number of seals is on the dry hauling ground with a concomitant increase in population pressure.

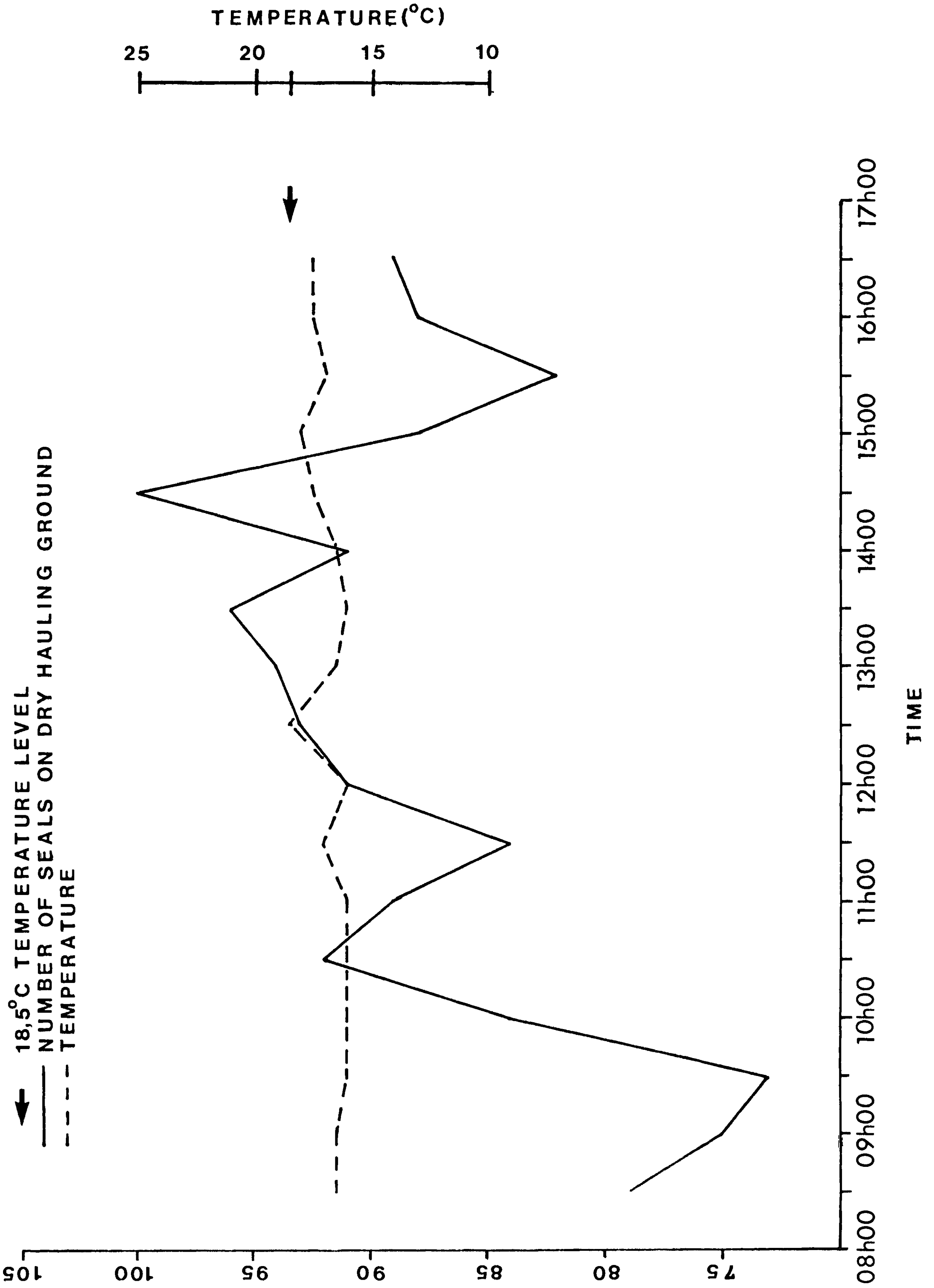

FIGURE 34 : Changes in the number of fur seals on the dry hauling ground at Seal beach during a day when ambient temperatures did not exceed the "comfortable" threshold value of 18,5°C

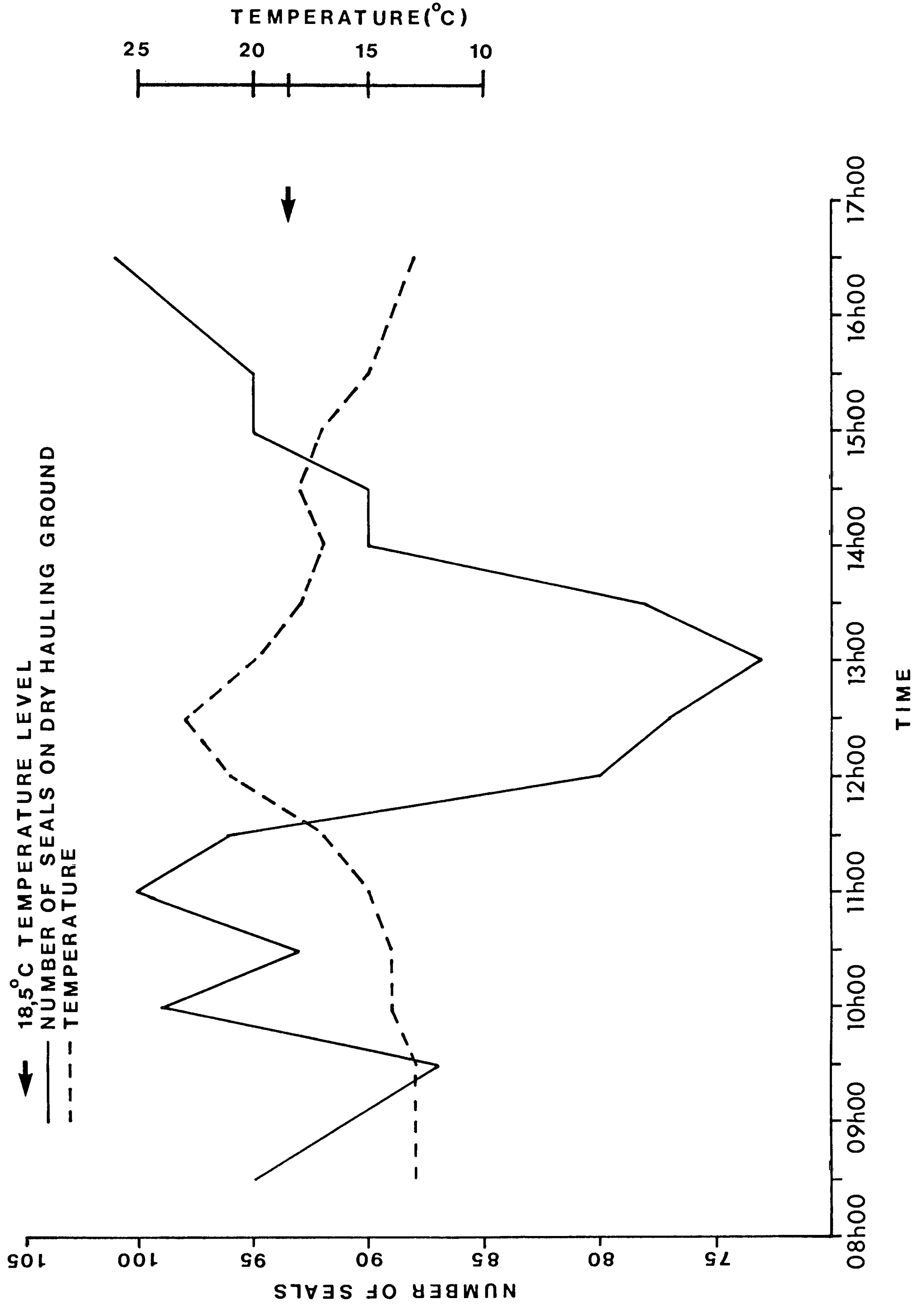

FIGURE 35 : Changes in the number of fur seals on the dry hauling ground at Seal beach during a day when ambient temperatures exceeded the comfortable threshold value of 18,5°C

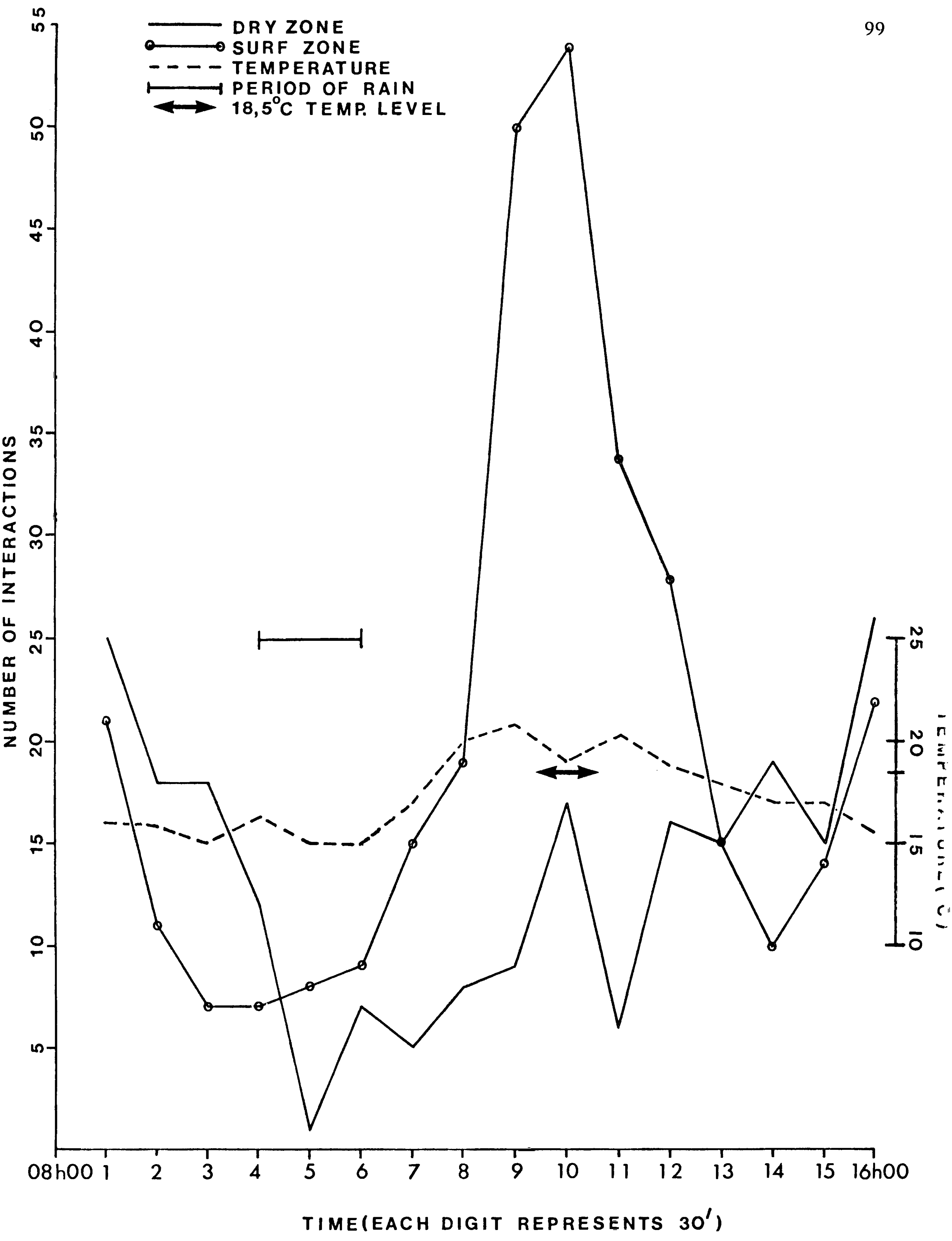

FIGURE 36 : The influence of temperature on the number of social interactions in *A. tropicalis* at Seal beach

The increase in activity on the dry zone during higher temperatures results chiefly from the movement of seals to and from the water as shown in Table 13, based on time budgets for activity of subadults. Table 13 shows that the percentage of time spent active in the dry zone is higher during temperature limiting periods than cooler periods of the same day (19,87 per cent versus 15,76 per cent). The increased activity is almost exclusively due to an increase in the time spent locomoting and also grooming. During warm conditions locomotion and grooming account for 38,58 per cent of time spent active compared with 23,40 per cent under cool environmental conditions. Very little increase in the time spent actually interacting is recorded (approximately 0,13 per cent).

TABLE 13: **Time budgets of subadults on the dry hauling ground at Seal beach at temperature limiting and cool periods during the same day (determined for five days)**

$\bar{X}$ number of seals observed	Observation time	Temperature condition	Categories of behaviour				
			Lying %	Alert %	Active %	Grooming %	Walking %
41,3	5 h	Limiting	77,45	2,68	19,87	4,39	3,28
51,7	5 h	Not limiting	80,81	3,42	15,76	1,90	1,78

The increase in the per cent time spent grooming is linked to the movement between surf zone and dry hauling ground since grooming is a normal reaction of *A. tropicalis* after leaving water. The increase in the grooming action is also evident during periods of prolonged raining or even after a short downpour. Stirling (1970) also mentioned that most extensive grooming in *A. forsteri* generally took place immediately after the seal left the water.

Prevailing weather and sea conditions also influence the activity level of the fur seal. Rain of sufficient quantity and force, especially at its onset, effectively reduces the interaction rate of seals in the dry zone (Fig. 37). This is probably the result of the percussive effect of the raindrops causing discomfort and not the degree of wetness (and heat loss) of the seals since seals in the surf

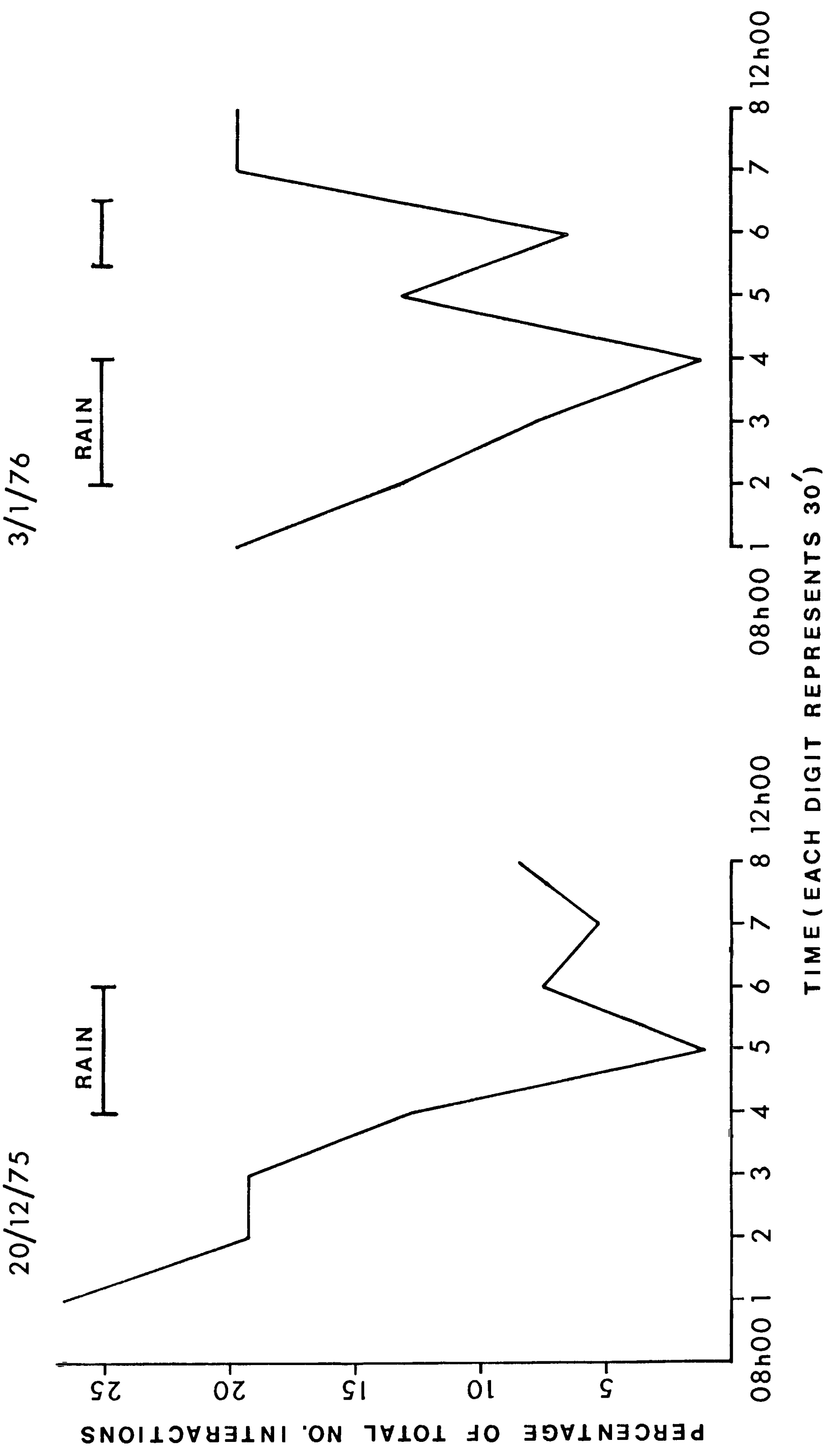

FIGURE 37 : The effect of rain on the activity of *A. tropicalis* at Seal beach

zone are similarly affected. However, activity increases once more after a short lapse of time. Bartholomew and Wilke (1956) and Rand (1967) found some *C. ursinus* and *A.p.pusillus* to take to the water under these conditions whilst others reacted by lying unconcernedly on land (Rand 1967). In the present study, a soft drizzle throughout the day does not elicit a definite response but removes the effect heat stress imposed by high ambient temperatures.

Stormy sea conditions result in the absence of seals in the surf zone as these individuals move up the beach or leave for offshore waters. The absence of the normally high activity rate in the surf zone therefore lowers the overall activity in the colony. Similarly, when a beach terminates rather abrubtly at the sea/land boundary, no large surf zone is available under calm sea conditions and activity is decreased there; when a gentle bottom gradient exists a large surf zone is usually present providing an ample flat expanse where especially the active subadult class congregate at nonbreeding colony sites.

The effect of single important events on the activity level of a colony of seals, e.g. the hauling-out of a competing male at a breeding site, or the interactions between individuals on a crowded site, cannot be discounted. Often these occurrences culminated in a chain reaction of activity involving a number of individuals. One or more seals sometimes depart from the site (especially at non-breeding sites) as a result of the disturbance. ´Rand (1956a) also stated that the sensitivity of subadults to sudden movements adversely influenced the stability of winter herds of *A.p.pusillus.* For example, the hauling-out of a single male can substantially increase the level of activity of resident territorial males at a breeding site. A territorial male's behaviour recorded for an hour prior to and after the arrival of a competitor, illustrates this point. Prior to the arrival the male spent 97,5 per cent of time lying down and 2,5 per cent in an alert position. The latter response, which occurred only once, was elicited by interactions between adjacent territorial males. However, only 71,74 per cent of the observation hour after the arrival of the competitor, was spent totally inactive, whilst 28,26 per cent of time involved the alert position or displays by the territorial male towards his adversary, as well as involvement with females present. Similarly, a male traversing a breeding colony beach is converged upon by several territorial males causing a disturbance in the colony as a whole and therefore increasing the level of activity. These events are especially evident under conditions of high ambient temperatures when thermally induced departures of males (without females) from the back of the beach often occur. In a similar situation, aggressive chasing of a male ensued in *A. forsteri* (Gentry 1973). These departures and subsequent returns and boundary displays, as well as chasing by adult males, increased the amount of aggression in the adult group by 11 to 15 per cent (Gentry 1973).

BEHAVIOURAL THERMOREGULATION

Pinnipeds are adapted to conserve heat in their normally cold marine surroundings. Their dual heat retaining pelage, a layer of subcutaneous blubber of varying thickness and a pelt of varying density and composition, are implicated to restrict heat loss to water with its high thermal capacity. However, Irving, Peyton, Bahn and Peterson (1962), stated that in fur seals very little insulation is provided by all of the subcutaneous tissues including fat. The distribution of fat in the flippers especially precludes its effectiveness as an insulator. Furthermore, Molyneux and Bryden (1975) for the first time demonstrated arteriovenous anastomoses in Weddell seal, *Leptonychotes weddelli,* skin with no significant variation in the density of these anastomoses between body and flipper skin. The majority occurred just beneath the epidermis. Their presence were suspected in hind flippers of the northern fur seal *C. ursinus,* by Tarasoff and Fisher (1970), who described them as corresponding to a 'type 2' retia mirabilia.

However, even in cold water warm body temperature extends to the skin in adult *C. ursinus* and the important insulation is provided by the waterproof fur (Irving *et al.* 1962). McGinnis, Cryer and Hubbard (1970) and Whittow, Matsuura and Lin (1970) considered the naked flippers to be the major site for heat dissipation and the rapid lowering of the temperature of the hind flippers of fur seals were considered a means to conserve body heat (Irving *et al.* 1962). The latter may be accomplished by shutting down the arterial blood supply, by diversion of the blood supply through arteriovenous anastomoses before it can reach the end of the flipper and/or by counter-current heat exchanges (Tarasoff and Fisher 1970). In all semi-aquatic mammals a heat flow system is required that prevents excessive heat loss to water without causing excessive heat retention out of the water, and that is flexible enough to compensate for sudden changes in extremes (Gentry 1973).

Pinnipeds are, however, unable to regulate their body temperature effectively on land by physiological means alone during thermal loading, e.g. *Z. californianus* (Whittow, Matsuura and Ohata 1975) and *M. angustirostris* (White and Odell 1971). This involves heat dissipation by vasomotor regulation of heat flux across the skin, cutaneous evaporation, heat storage, nonevaporative heat loss to air in the form of heat convection and radiation and respiratory evaporative cooling. Behavioural means are required to supplement physiological thermoregulation, e.g. sandflipping (White and Odell 1971; McGinnis 1975; Vaz-Ferreira 1975), flipper waving (Bartholomew and Wilke 1956; Peterson and Bartholomew 1967; Rand 1967), postural adjustments (Bonner 1968; Stirling 1970; White and Odell 1971; Gentry 1973; Odell 1974), use of shade (Vaz-Ferreira and Palerm 1961; Orr 1967; Peterson *et al.* (1968); Stirling 1970; Gentry 1973), urohidrosis (Gentry 1973; Whittow *et al.* 1975), panting and open-mouth type of breathing (Bartholomew and Wilke 1956; Rand 1967; Whittow *et al.* 1975) or resorting to water and/or wet sand (Peterson and Bartholomew 1967; Rand 1967; Fay and Ray 1968; Stirling 1970 and 1971a; White and Odell 1971; Gentry 1973; Miller 1974; Vaz-Ferreira 1975).

On land, *A. tropicalis* use behavioural and postural adjustments to combat thermal overloading under conditions of high ambient temperatures and solar radiation. The fur seal *C. ursinus* maintains a relatively constant body skin temperature under similar conditions (as a result of the constant fur insulation) and McGinnis *et al.* (1970) and Whittow *et al.* (1970) considered the naked flippers to be the major site for heat dissipation. Likewise the flippers in *A. tropicalis* are involved in postural adjustments to combat heat stress. Four types of resting postures related to the degree of exposure of the flippers are distinguished (Fig.. 38, 39 and 40). These include the curled, prone, oblique and spread postures and agrees with those in *A. forsteri* (Gentry 1973). In the present study, *A. tropicalis* resort to rest positions which conceal the flippers to reduce heat loss to the environment on cool cloudy days or when they settle down on the beach after hauling out of the sea. Similarly, *Z. californianus* (Gentry 1973; Odell 1974), *C. ursinus* (Bartholomew and Wilke 1956), *Odobenus rosmarus* (Fay and Ray 1968) and *A. gazella* (Bonner 1968) assumed a tucked flipper posture at low temperatures. At high ambient temperatures these species exposed their flippers, as does *A. tropicalis,* to increase heat loss to the environment through convection and radiation from the flipper. Cutaneous evaporative cooling may also play a part since *C. ursinus* (Bartholomew and Wilke 1956) and *Z. californianus* (Whittow *et al.* 1975) possess functional sweat glands in their naked flipper areas. These minor postural adjustments in *A. tropicalis* at Gough Island do not extent to active flipper waving documented for other species and is also in contrast to Holdgate's statement (*In:* Bonner, 1968) that it commonly happened at Gough Island.

The possible increase in respiratory heat loss through behavioural means such as panting in *C. ursinus* (Bartholomew and Wilke 1956) and *A.p. pusillus* (Rand 1967) is not apparent in *A. tropicalis.* Only as a result of prolonged physical activity (e.g. a fight between territorial males) do *A. tropicalis* resort to an open-mouth type of breathing. However, this is probably owing to a need to increase the ventilation of the lungs rather than for thermoregulatory purposes. Gentry (1973) and Whittow *et al.* (1975) implicated urohidrosis (the evaporation of urine) as a cooling mechanism. This subtle thermal response observed for landlocked *A. forsteri* adult males at high temperatures (Gentry 1973) cannot be confirmed for *A. tropicalis.* Under heat stress and when water in the form of rain pools, for example, is available on the dry zone, *A. tropicalis* wet their flippers, especially the hind flippers, as does *A. forsteri* (Stirling 1970). This could facilitate heat loss by conduction to the water, but also provides a means of evaporative cooling (Fig. 40). In direct sunshine, wet individuals may remain with their hind flippers submerged in a rainpool and with foreflippers spread although they had submerged themselves a short while previously. Therefore all these avenues for heat loss are exploited simultaneously.

Whilst *A. tropicalis* can cope with thermal loading under moderate conditions, the ultimate response to excessive solar input and high environmental temperatures is a movement to the surf zone and sea. This indicates that the limits to which their physiological and other behavioural mechanisms could extend their thermal

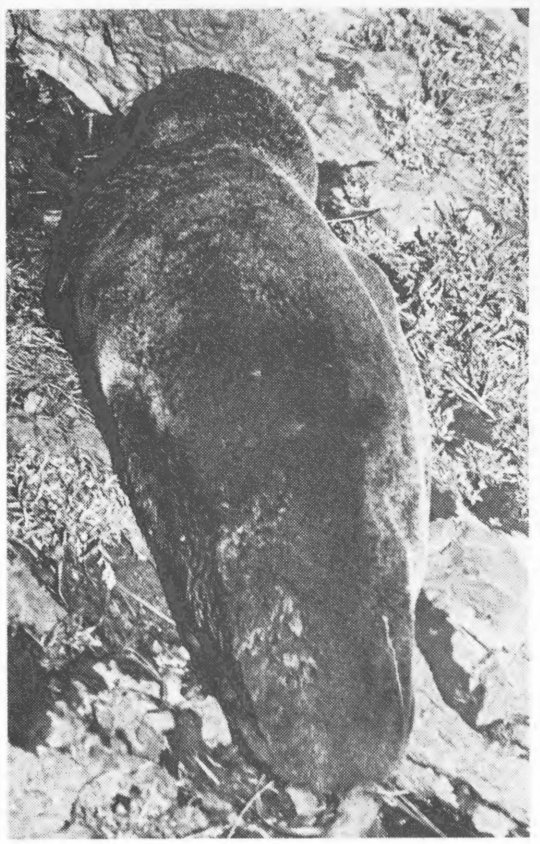

FIGURE 38 : Prone resting posture with flippers concealed

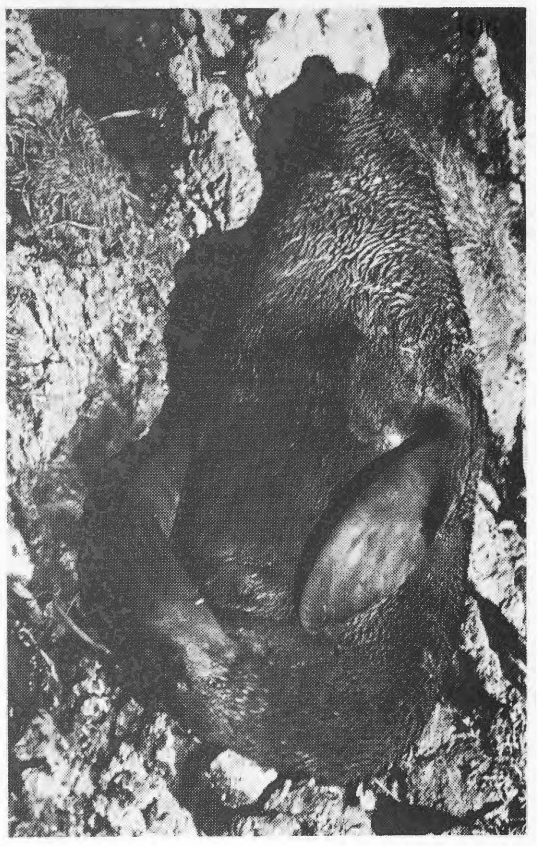

FIGURE 39 : Oblique resting posture with flippers partly exposed

FIGURE 40 : Spread resting posture with flippers maximally exposed. In the example shown the hind flippers are lowered into a pool of water to facilitate heat loss through conduction to the water

tolerance have been exceeded (Fay and Ray, 1968). This exodus is especially obvious in nonbreeding colonies (Fig. 35) involving all age classes, whilst at breeding colony sites mostly adult females are involved. The same applies to *A. forsteri* (Gentry 1973; Miller 1974). *A. tropicalis* territorial males in breeding colonies only resort to the sea under high environmental temperatures when no females are present in their territories and invariable return after absences of varying duration. This does not necessarily imply that some territorial males have a higher thermal capacity than others but simply that males in breeding colonies, away from the waterline and without the additional incentive to remain as a result of the presence of females in their territories, would more likely respond to excessive heat load by temporarily abandoning their territories. This is therefore similar to the situation in territorial males at nonbreeding sites as discussed below.

A. forsteri (Gentry 1973), *Z. californianus* (Bartholomew and Wilke 1956) and *A.p. pusillus* (Rand 1967) breeding males also at least temporarily abandon their territories under similar conditions. However, at nonbreeding colonies where adult male *A. tropicalis* exert relaxed territorial control, temperature induced departures are common (Fig. 41) with the lowest number present during the hottest time of day. These males departed and hauled throughout the day when the environmental temperatures were already above the threshold value at the onset of observations and the return rate of the seals only increased over the departure rate during the cooler afternoon. This shows that seals subject to heat stress, migrate onto the surf zone and into the sea where a favourable temperature gradient exists for heat loss. When their thermal equilibrium has been restored, they move back onto the dry hauling ground while they can still benefit from evaporative cooling. After their pelts have dried down, they again move to the surf zone unless a substantial reduction in environmental temperatures occurred in the meantime or they have the benefit of shade, etc. *A. forsteri* males show a similar pattern and up to four departures were recorded for single males per day (Gentry 1973). The movement of seals to the surf zone would suffice for thermoregulation purposes; the departure to deeper water in the present study would result from the increased population pressure in the surf zone with the concomitant increase in interaction rate (Fig. 36). Furthermore,

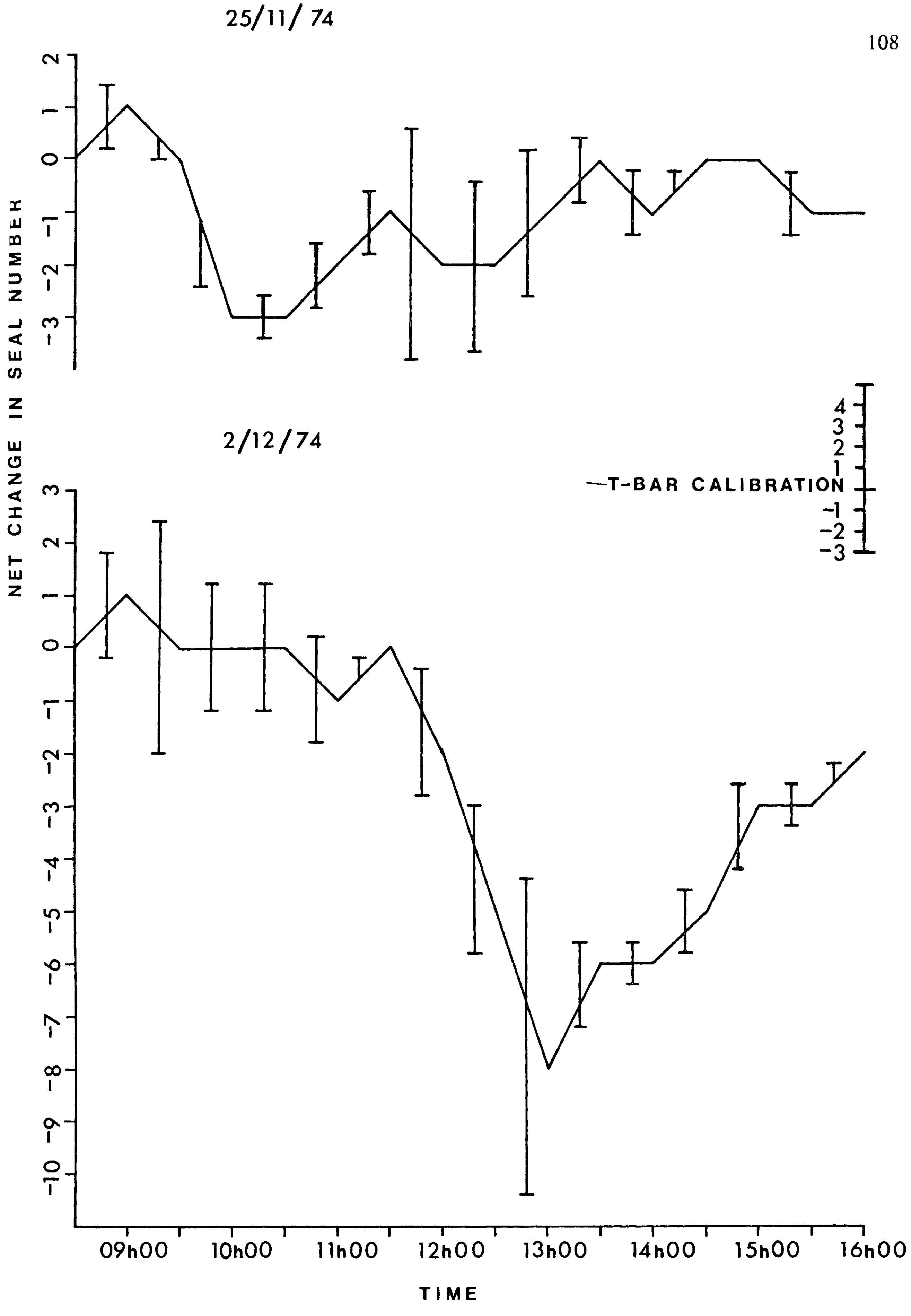

FIGURE 41 : Net change in numbers of adult male *A. tropicalis* at Seal beach with T-bars representing the change in numbers for each half an hour interval. The ambient temperatures were already limiting at the start of the observation periods

males would be behaviourally excluded by frontline territorial males (which are unaffected by exogenous thermal loading) from the surf zone and would seek relief away from the latter's immediate vicinity.

The availability of shade assists *A. tropicalis* to thermoregulate effectively on land. Rand (1956), Gentry (1973) and Stirling (1970) reported seeking of shade by *A.p. pusillus* and *A. forsteri.* Whittow, Ohata and Matsuura (1971) stated that *Z. californianus* were unable to regulate their body temperatures in the absence of water in spite of shade at the high temperatures they are subjected to in their natural environment. However, *A. tropicalis* at Gough Island benefits from shade and move closer to larger rocks and lies under tussock grass in peaty areas. Seals in the shade of the latter manage to remain when this general area is evacuated by the remainder at high temperatures. The shade cast by the cliffs especially on eastern beaches are also beneficial. Thermally induced departees will remain on the beach on their return if they haul out into this shade. If they haul short of this shady area, however, they will again depart as previously described. Seals under extreme thermal stress on the other hand, never move back into the shade cast by the cliff but respond actively to the primary urge to seek water. The above indicate that direct solar radiation is of more importance than a high ambient air temperature alone. *A. tropicalis* furthermore, sometimes reacts immediately to direct sunlight when e.g. the sun breaks through a cloudy sky in association with high ambient temperatures. *Z. californianus* and *M. angustirostris* (White and Odell 1971) react similarly and this response is thought to implicate receptors sensitive to the rate of peripheral temperature increase. The increased presence of seals during late afternoon on the dry hauling ground (Fig. 35 and 41) after a hot day can also be ascribed to the presence of shade which covers the entire Seal beach at approximately 16h00.

The high incidence of inactivity in *A. tropicalis,* especially adult males (Table 11) is related to thermoregulatory problems in heat dissipation. Stirling (1971a) maintained that the inactivity of fasting *A. forsteri* territorial males was a method of conserving stored energy reserves with the more active individuals forced to return sooner to sea to feed, and thus lowering their opportunity to mate and contribute to the gene pool. The effectiveness of this result of inactivity cannot be disputed but certainly does not provide the sole reason for this behaviour common to *A. tropicalis* and *A. forsteri.* For example, Whittow *et al.* (1975) found activity in *Z. californianus* consistently to result in an increase in deep body temperature as is also the case in *M. angustirostris* (McGinnis and Southworth 1967). In *C. ursinus* intense activity may cause a rise in body temperature several degrees centigrade above the resting level (Bartholomew and Wilke 1956). *A. tropicalis* therefore reduce the risk of overheating by inactivity and this affects adult males whatever their status (95,4; 93,3 and 93,2 per cent of time spent inactive by idle, nonbreeding and breeding males respectively). *A. tropicalis* males on the waterline are the most active as described previously and although this activity also accompany an increase in body temperature (McGinnis and Southworth 1967), the heat loss possibilities in the presence of water enable them to maintain a thermal equilibrium. The higher level of activity in the surf zone at a wide range of environmental temperatures (12°C–22°C) is evident from Table 14.

TABLE 14: The frequencies of interactions on the dry hauling ground and surf zone at different ranges in ambient temperatures

Observation time	Temp. range °C	$\bar{X}$ number of interactions per seal at each scan	
		Dry zone	Surf zone
4h	12 – 15	0,022	0,425
3h 40 min	14 – 16	0,031	0,791
4h	16,5 – 21	0,062	0,820
4h	17 – 22	0,042	0,589

The lower range of ambient temperatures apparently do not constitute a thermoregulatory problem in *A. tropicalis.* Heat loss to the environment during cold spells is restricted by assuming a tucked flipper posture when resting. Huddling, common in *O. rosmarus* (Fay and Ray 1968) and the furless sea lions *Zalophus* (Peterson and Bartholomew 1967); *Otaria* (Vaz-Ferreira and Palerm

1961) and *Eumetopias* (Gentry 1973) which would be advantageous at low temperatures, does not occur in *A. tropicalis* older than pups. Pups do huddle since their pelage is not a good heat retaining mechanism and can often be seen shivering similar to pups of *Callorhinus* and other Arctocephalines (Bartholomew and Wilke 1956; Stirling 1970). *A. tropicalis* in offshore waters, however, exhibit a need to retain heat when drifting and usually extend up to three flippers at a time out of the water similar to descriptions for *C. ursinus* (Bartholomew and Wilke 1956), *A.p.pusillus* (Rand 1967), *A. gazella* (Bonner 1968) and *A. forsteri* (Stirling 1970).

Social displays and vocalizations

In the present study *A. tropicalis* was found to utilize an array of postures and vocalizations as a means of communication in inter- and intrasexual encounters. Whereas descriptions of these on *A. tropicalis* are limited to the population of Amsterdam Island (Paulian 1964) other members of the genus *Arctocephalus* have received much more attention. Stirling (1970 and 1971a) described postures and calls of *A. forsteri*, and a comparative examination of airborne vocalizations amongst *A. forsteri*, *A.p. doriferus* and *A. gazella* is available (Stirling and Warneke 1971). Peterson *et al.* (1968) and Bonner (1968) briefly discussed vocalizations in *A. townsendi* and *A. gazella* respectively.

Stirling (1971a) described 20 postures and calls for *A. forsteri* in South Australia using terms current in the literature of pinniped ethology as well as terms coined himself. Where applicable terminology used by this author will be adhered to in describing *A. tropicalis* postural and vocal repertoires. Although much individual variation exists in especially calls of *A. tropicalis*, the following descriptions of calls and postures are representative of the norm.

POSTURES

Full Neck Display

This posture is a feature of especially adult male behaviour, but is occasionally displayed by adult females. In this position the animal sits upright with chest forward and head tilted backwards, with the nose in a vertical position (Fig. 42). This typical posture is usually assumed spontaneously by breeding and nonbreeding males alike, but is seldom seen in a conflict situation as in *A. förster*i (Stirling 1970 and 1971a) where it is used as a threat posture. However, *A. tropicalis,* subadult (young) males clearly show this posture in play-fighting bouts (Fig. 43) whilst in conflicts between adults it is at best only briefly assumed. Stirling (1970) accepted the full neck display as a demonstration of the size and dominance of a male, reducing conflict. In *A. tropicalis* this seems to be true in that a male full neck display elicits a submissive response from especially subadult male seals. Its not so pronounced role in territorial disputes suggests that it does not play an essential role. In fact, males hauling out intent on dislodging a resident male attack with little or no preliminaries.

Alert posture

This posture in *A. tropicalis* is the same as described for *A. gazella* (Bonner 1968) and *A. forsteri* (Stirling 1970 and 1971a) and is used by males and females (Fig. 44). It seems to be only a slight postural adjustment from the normal sitting posture and with the nose and head held in a pointed fashion. Adult males usually assume this posture before and after intrasexual interactions, and it is also the stance usually adopted in a full facing away display during or after an aggressive encounter. On a percentage time basis this posture is assumed more often by breeding than nonbreeding males, and it is also prominent in males on a newly acquired territory. This indicates awareness as in *A. forsteri* (Stirling 1970).

Neck-waving

This display, also described for *C. ursinus* (Bartholomew 1953) and *Z. californianus* (Peterson and Bartholomew 1967) is used in conflict situations by adult male *A. forsteri* (Stirling 1970 and 1971a). He postulated it to function as allowing an animal to size up its opponent, to prolong its display or give an advantageous position from which to attack. Typically, as in *C. ursinus* (Peterson 1968) and *A. forsteri* (Stirling 1971a), *A. tropicalis* males position themselves chest to chest (Fig. 45) and weave their heads and necks from side to side, usually

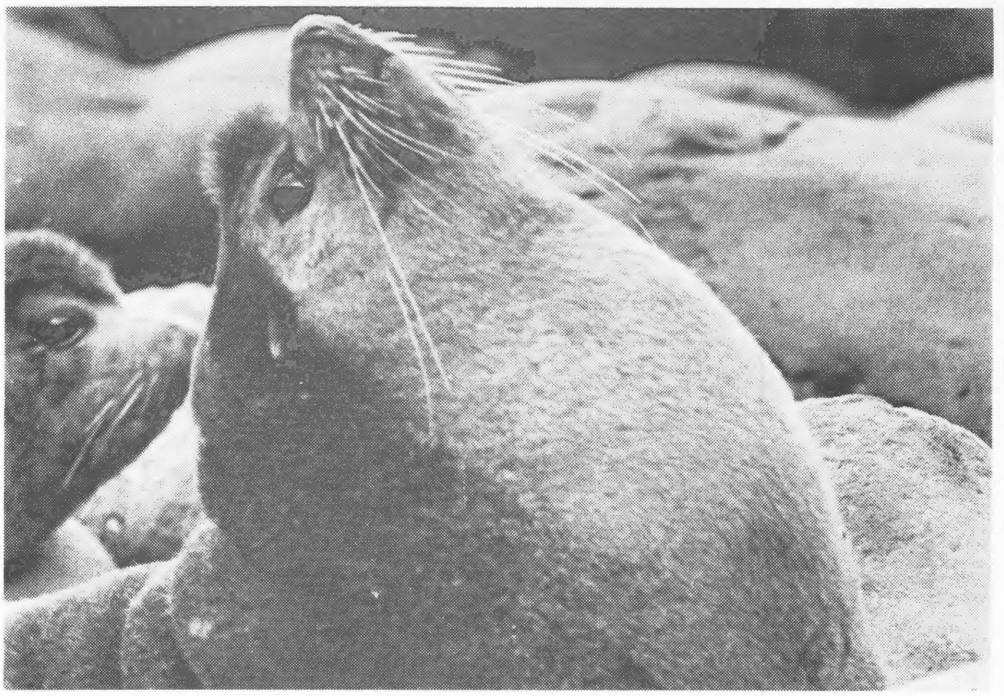

FIGURE 42 : Adult male *A. tropicalis* giving a full neck display

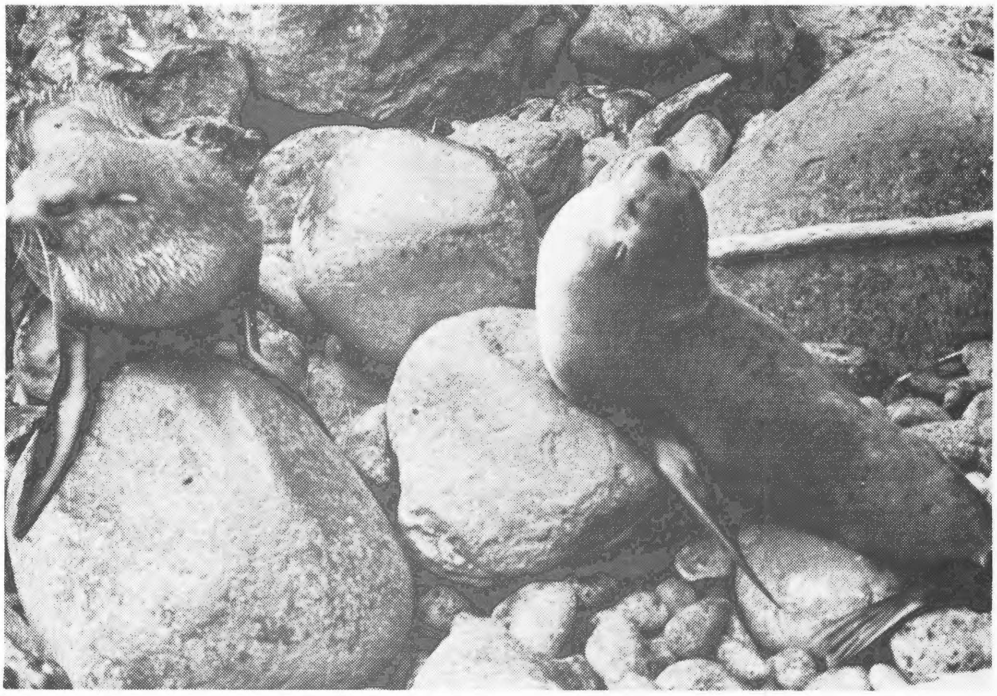

FIGURE 43 : Subadult male *A. tropicalis* play-fighting. The male on the right gives a full neck display while his opponent is facing away

FIGURE 44 : Adult male *A. tropicalis* facing away after an aggressive encounter. The male on the left sits in an alert posture while his opponent also faces away with the head held obliquely and eyes closed

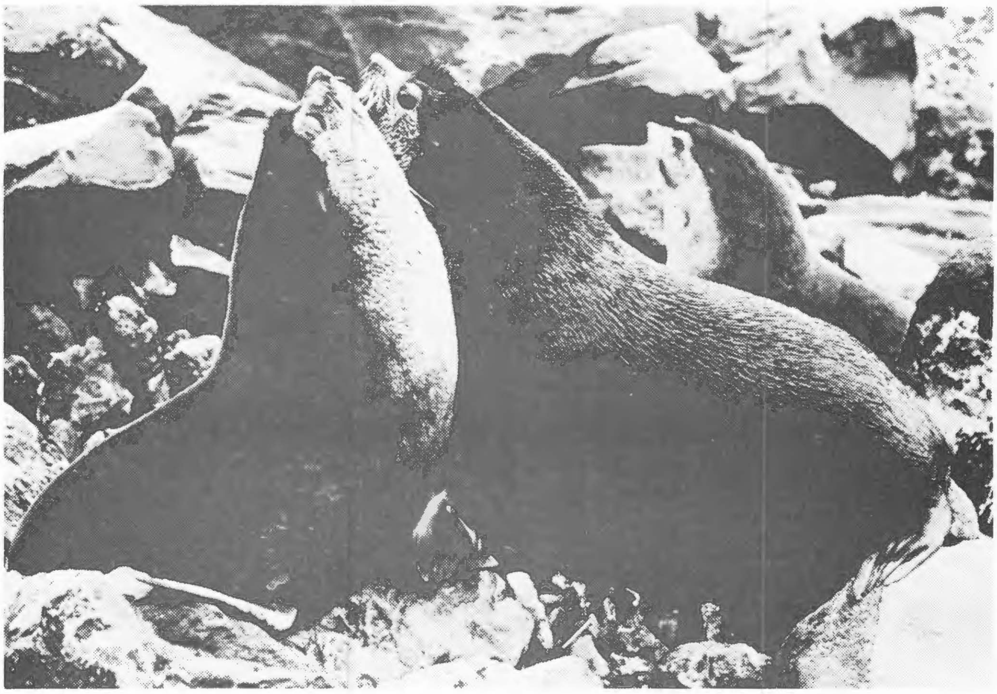

FIGURE 45 : Adult male *A. tropicalis* positioned chest to chest with their heads held high during an actual fight for the possession of a territory

out of phase with each other. This aggressive display is only used when actual physical contact is made between opponents and when a fight is imminent. Subadult males commonly exhibit this behaviour in play-fighting bouts since in the absence of serious conflict bodily contact is readily made. Neck-waving is absent in males during territorial boundary disputes, which are settled by threats alone.

Oblique posture

A. forsteri (Stirling 1971a) and *Z. californianus* (Peterson and Bartholomew 1967) males assume this posture before and after an attack and it usually follows the alert posture, full neck display, or neck-waving. *A. tropicalis* at Gough use this display extensively in especially boundary disputes and it, in short, amounts to a bunching of the neck muscles with the head and neck held obliquely to the axis of the rump (Fig. 46). The oblique posture is usually mutually assumed by contestants, in association with an open-mouth threat or just prior to a lunge at the opponent. The oblique posture is not always elaborate in appearance but often amounts only to a slight oblique squint before and after a lunge or horizontal neck-stretch. The oblique posture is a very high intensity threat display in *A. tropicalis*, similar to the condition in *A. forsteri* (Stirling 1971a).

Open-mouth display

The open-mouth display has a dual function in that it may be given either as an aggressive (Fig. 46) or submissive display. It is used in both contexes by male and female *A. tropicalis* alike and amounts to simply a baring of the canine teeth in what appears to be a threatening fashion (Stirling 1970). The open-mouth submissive display is a response elicited from an inferior male in a conflict situation, or it is given by females towards a male and is intended to reduce or forestall aggression (Fig. 47).

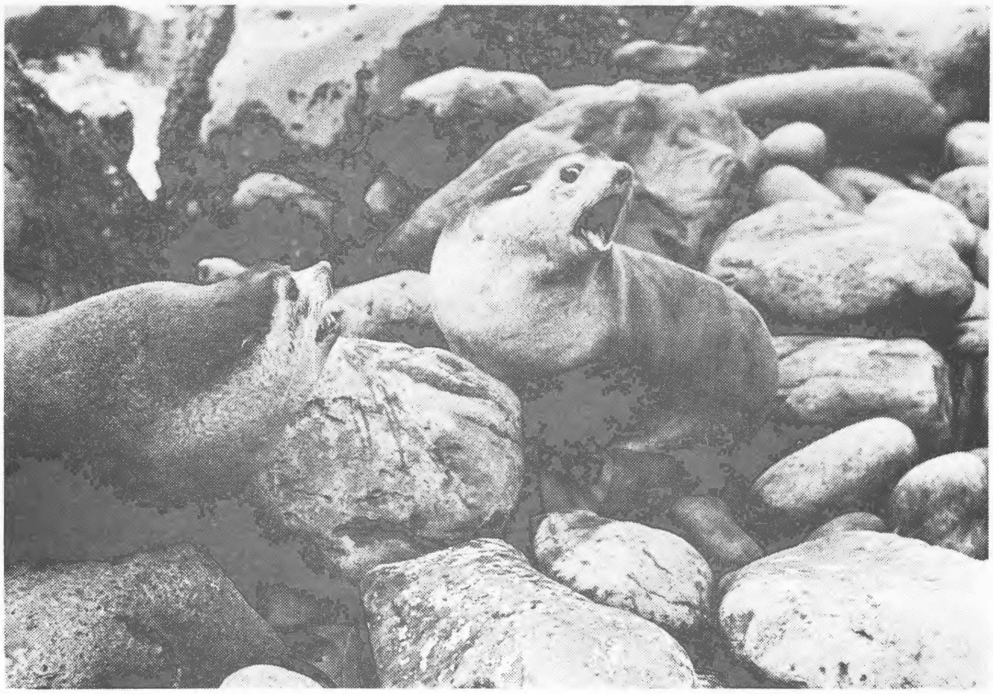

FIGURE 46 : Adult males delivering open-mouth guttural threats at each other from oblique postures, with the male on the right combining it with an oblique squint

FIGURE 47 : An adult female *A. tropicalis* giving a mild silent open-mouth submissive display at the adult male approaching her

Horizontal neck-stretch

A. forsteri (Stirling 1971a), and *A* '*tropicalis* males in this study use the horizontal neck-stretch as an intensely aggressive display. *A. tropicalis* males often throw themselves down into this position after an oblique display and combine it with an open-mouth aggressive display.

Facing away

In *A. forsteri* this display is given mostly by smaller males to larger males during or after a mutual full neck display or actual fighting (Stirling 1970). *A. tropicalis* males on the other hand regularly use this display in boundary disputes. Both opponents can use it simultaneously in a fashion similar to the "oblique stare" in *Z. californianus* (Peterson and Bartholomew 1967) during their boundary ceremony. *A. tropicalis* males may also face directly in the opposite direction than their adversaries during or at the conclusion of such disputes, pretending to be unaware of each other (Fig. 44). This display may function as an appeasement gesture (Stirling 1970) since neither *A. forsteri* nor *A. tropicalis* make use of the chance afforded during this display to attack the opponent's undefended neck.

Submissive posture

When attempting to unobtrusively depart or arrive at a site, or attempting to avoid contact with a dominant animal, *A. tropicalis* of both sexes adopt a lowered head and neck posture. This has also been described for *A. forsteri* (Stirling 1970 and 1971a).

VOCALIZATIONS

Repetitive barking or whickering

This is a call almost exclusive to male *A. tropicalis* although it is occasionally uttered by the female. The male uses it on almost any occasion, from just sitting in his territory, while moving about, and when interacting with all other age and sex classes. This is the most commonly used call and varies in pitch, duration, loudness and rate of delivery. It is usually expelled from the male throat as a high-pitched rapidly repeated sound when excited by inter- and intra-sexual contacts. Repetitive barking is described for *A.p. doriferus* and *A. forsteri* (Stirling and Warneke 1971), *A. townsendi* (Peterson *et al.* 1968), *A.p. pusillus* (Rand 1967) and *A. tropicalis* at Amsterdam Island (Paulian 1964), amongst others.

Guttural challenge

The guttural challenge is a call common to the genus *Arctocephalus*, as listed by Stirling and Warneke (1971). Paulian (1964) described it as a growl often accompanied by coughs, preceding or accompanying struggles between males. In *A. tropicalis* during the present study the guttural threat was a high intensity open-mouth threat usually delivered at close quarters by males involved in a boundary display. The guttural threat is usually associated with the oblique or horizontal neck-stretch display, and indicates a readiness to fight, and is commonly used to affirm territorial boundaries as in *A. forsteri* (Stirling 1971a). *A. tropicalis* females also use a similar call in antagonistic encounters amongst themselves, towards unwanted pups and occasionally when being aggressive towards adult males. Stirling (1970) set the female threat call apart from the male guttural challenge in *A. forsteri* but in the present study information is not sufficient to allow this separation.

Male threat call

Gough Island *A. tropicalis* males' threat call simulates the roar of their Amsterdam Island counterparts (Paulian 1964) and that of *A. townsendi* (Peterson *et al.* 1968). However, in the present study the male threat call can be separated into two completely different sounding calls given in the same situations and apparently with the same function. As in *A. forsteri*, full threat calls (Stirling 1970) are occasionally delivered from a posture where the neck and head are orientated upwards in the familiar howling posture of canids (Fig. 48), but more commonly from an (head and neck stretched forward and upwards) alert position (Fig. 49). This threat call is either a pulsed roar or a high-pitched cry rising in pitch towards the end of the call. Although neither call sounds like the *A. forsteri*

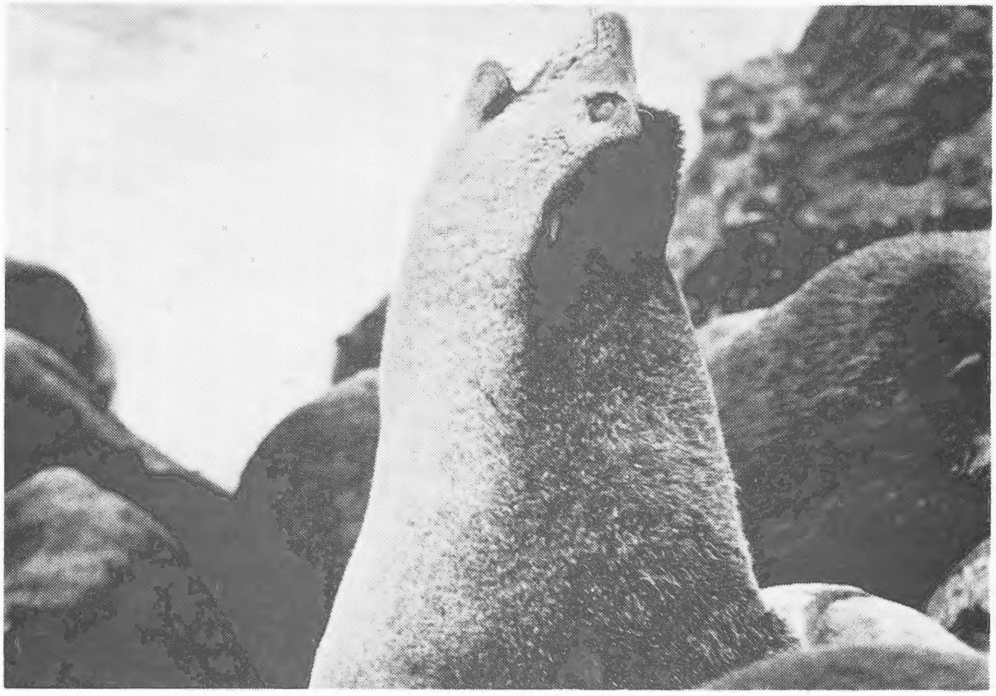

FIGURE 48 : An adult male delivering the male threat call from a posture where the head and neck are orientated upwards

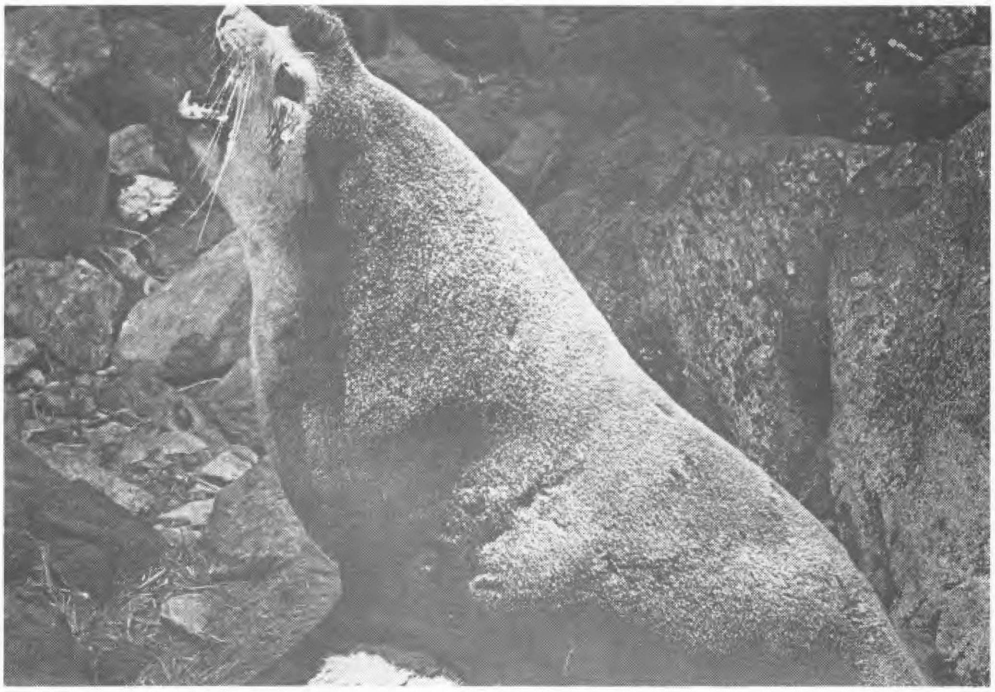

FIGURE 49 : The male threat call delivered from the more commonly observed (head and neck stretched forward and upwards) alert position

male full threat call which is in two parts (Stirling and Warneke 1971, Stirling 1971a) it is also sometimes given spontaneously. However, *A. tropicalis* males emit these calls in the majority of actual fights but more often from a facing away position after or during a boundary display. A highly agitated male normally repeats the threat call a few times in succession, interspersed with fast high-pitched whickering. This long range call elicits the same response from other territorial males on the specific location in that they also start this undirectional vocalization.

In function i.e. probable advertisement of social status, readiness to fight and individual recognition (Stirling and Warneke 1971), method of delivery (posture) and circumstances under which it is used as a high intensity threat call, the *A. tropicalis* threat call simulates the *A. forsteri* full threat call. Stirling and Warneke (1971) also recognize a male low-intensity threat call in *A. forsteri* which is simply the first portion of the full threat call. Stirling (1970) equates it with the *A. tropicalis* low roar described by Paulian (1964), however, no clear low intensity threat call was heard in Gough Island *A. tropicalis*. Calls that could be described as such simply appear to be low intensity guttural threats.

Submissive call

This highly characteristic call occurs in all other species of *Arctocephalus* that have been studied, and is uttered by male and female *A. tropicalis* as an expression of extreme submission or fear when threatened by a dominant animal. It typically involves a high-pitched modulated sound almost like a scream.

Female and pup-attraction calls

These seem to be identical to those described for *A. tropicalis* at Amsterdam Island (Paulian 1964) and found in other Arctocephalines as well (Stirling and Warneke 1971). These calls are like high-pitched whines.

The adult male at colony sites

TEMPORAL CHANGES IN ADULT MALE TERRITORIAL EXPRESSION

Seasonal transition to and from rigid territoriality is recognized for pinnipeds by various authors. Less intense territorial behaviour during early summer is noted for fur seals *A. forsteri* (Miller 1975b), *A. tropicalis* (Paulian 1964), *C. ursinus* (Kenyon 1960; Peterson 1968) and sea lions *Neophoca* (Marlow 1968) and *Eumetopias* (Gentry 1970, *In:* Miller 1975b). A late summer decrease in territorial behaviour intensity occurred in *C. ursinus* (Peterson 1968), *A. gazella* (Bonner 1968) and *A. forsteri* (Stirling 1970; Miller 1975b).

Adult male *A. tropicalis* frequent Gough Island east coast and presumably west coast colony sites in low numbers during winter, from end May to September. During mid-October 1975 at least some of them were in association with single adult females before the latter's departure prior to the onset of the imminent breeding season. Similarly adult male *A. forsteri* were found present with up to three adult females at breeding colony sites on the Open Bay Islands during mid-September (Stirling 1970). In both *A. tropicalis* and *A. forsteri* males, the areas where they were located were not defended, although some *A. tropicalis* males were present on the same site for at least a few days in succession, even when no females were present. These males were widely spaced and maintained ill-defined "areas of influence" (after Miller 1975b) in contrast to smaller and vigorously defended territories later in the summer. Some *A. tropicalis* males were not site bound but relocated themselves during the early stages of the breeding season since they did not remain on the sites where they were first sighted.

Miller (1975b) suggested that male *A. forsteri* can to some degree predict which localities will contain females and would haul out there. However, few adult male *A. tropicalis* are present on prospective east coast breeding colony sites during late October. This is evident even when adult females are still present on breeding colony sites and therefore providing a cue where oestrous females would be present later, during the breeding season. Adult males are predominantly found on characteristically open and flat east coast nonbreeding colony sites even during late October when ample beach space is still available at e.g. the South Point breeding colony beach. Therefore, although male *A. tropicalis* may have the ability to predict breeding colony site locations, this is not evident early in the austral summer.

During early November competition for beach space increases with the increase in adult male numbers. Territorial behaviour i.e. "the establishment and maintenance of a preserve delineated by threat displays with adjacent males around the perifery and encroachment upon which precipitates a fight" (Gentry 1975) though still not intense, is increasingly evident during the second week of November. The first territory changes occur and the first wounded males, a sign of physical contact in fighting, observed. Adult males also show increased aggression towards human intruders. At nonbreeding colony sites where only some males exhibited explicit territorial behaviour, territory changes can still be accomplished by threat displays alone without actual fighting.

During the third week of November the first large males of territorial status arrive at nonbreeding colony sites. At the same time adult male numbers on west coast breeding colony sites are still relatively low, with predominantly the larger sized males present, occupying and defending foremost territories.

At the end of November most resident adult males on east coast sites are replaced by larger males of territorial status. Territorial behaviour is intense and the west coast breeding colony site at e.g. Waterfall Cove has already attained the maximum number of uniformly large territorial males exhibiting rigid territorial maintenance behaviour. Territory changes through fighting occur on all sites where territories are present. Similarly during November uniformly large and aggressive male *A. forsteri* held territories on Open Bay Island breeding colony sites and these were usually gained or lost through fighting (Miller 1975b).

In *A. tropicalis* the expression of intensified territoriality coincides with the arrival of the first adult females during late November/early December. Considering the timing of events, adult males of territorial status therefore arrive approximately a week prior to adult females. Similarly adult males of *A. gazella*

(Bonner 1968), *A. tropicalis* at Amsterdam Island (Paulian 1964) and *A.p. pusillus* (Rand 1967) arrived approximately a week before adult females. During the first week of January rigid territoriality begins to wane and a more relaxed use of the available area sets in. Fighting to gain access to territories by challengers now occur only infrequently. Small east coast breeding colony sites experience the first departures of territorial males and these are replaced by inferior males. At least some of the territorial males here abandon their territories temporarily and of their own accord. On their return they easily reclaim their territory by threat displays alone. This occurs especially when large subadult males, to a certain extent tolerated in the vicinity of territorial males at this time, have moved onto their site. Also during the first week in January the first territorial males at South Point beach and Waterfall Cove breeding colony sites depart voluntary, and their former territories are not claimed by new arrivals. Neighbouring territorial males simply incorporate the vacated areas into their own territories similar to *A. forsteri* males (Miller 1975b). These expanded areas are not rigidly controlled but considerable overlap between neighbouring territories is evident.

Territorial males increasingly start departing and by end January all the known ones which were observed throughout the season, had left. Unscarred males in good condition start arriving at breeding and nonbreeding colony sites alike. These events coincide with a low in adult female numbers, as well as an overall reduction in adult male numbers. During mid-January already at least one east coast breeding colony site was totally abandoned by resident territorial males.

With the second increase in adult male numbers (for moulting) inter-male aggressiveness is evident once more and new males at breeding and nonbreeding colony sites exhibit loose territoriality. Infrequently adult males sport fresh wounds, indicating that fighting still occurs but at a low frequency level. Adult males are not defiant to humans any more, in contrast to especially the mid-breeding season, but are however, reluctant to trespass onto neighbouring males' areas of influence.

Adult males at idle colony sites, throughout the breeding season as well as thereafter, never exhibit territoriality but maintain individual distances. Even during postbreeding periods they never lie together as did *A.p. pusillus* (Rand 1967, Fig. 13).

No information is available for Gough Island *A. tropicalis* regarding territoriality during the autumn maximal haul out and for the winter months. Presumably during the latter period loosely defined winter territories exist, as described for *A. australis* (Vaz-Ferreira 1956), Amsterdam Island *A. tropicalis* (Paulian 1964), *A. gazella* (Bonner 1968) and possibly *A. forsteri* (Stirling 1971a).

PERIOD OF TERRITORY TENURE BY ADULT MALES

The period of territory tenure by territorial males could not be pinpointed since the colony sites could not be visited daily. The breeding colony sites at South Point beach and Waterfall Cove were first visited on 21 November 1975 and again on 28 November 1975. If it is assumed that the 15 known territorial males followed throughout the breeding season establish their territories during the latter half of November, when males of territorial status start arriving, and depart shortly after the last census when they were still present and before a subsequent census, an approximate duration of territory tenure can be calculated. On this basis these males remained on their territories for a period of 35–56 days, with a mean of 45,4 ± 6,7 days (N = 15). This is comparable to the approximate lengths of territory occupation observed for 16 male *A. forsteri* which showed a range of 21–54 days with a mean of 36 ± 9,7 days (Stirling 1971a). One *A. tropicalis* male for which the exact date of territory procurement is known stayed on site for between 48–56 days. Similarly Vaz-Ferreira (1956) recorded two male *A. australis* on station for 50 and 58 consecutive days.

TERRITORY TYPES

Territories can be classified according to their location on the beach, their time of formation and duration of maintenance, and their success in attracting females. In general territories are classified with respect to their position relative to the waterline.

In *A. tropicalis* frontline territories are normally first established (Fig. 50) although some males, as in *C. ursinus* (Kenyon 1960), haul farther up the beach with space still available on the shoreline. *A. forsteri* (Stirling 1970 and 1971a), *A. gazella* (Bonner 1968), *A. tropicalis* at Amsterdam Island (Paulian 1964) and males of mainland herds of *A.p. pusillus* also first established territories on the waterline. In *A. tropicalis* the turnover in territory ownership subsequent to the arrival of size-related dominant males later in the season also involves foremost territories. Subsequent haulers either dislodge territorial males here or when repulsed, being inferior to the front rankers, occupy territories farther inland. In general late arrivals usually land up towards the back of the beach although males that arrive earlier may also be located here. For example already during the third week of November a male of territorial status was located at the back of the beach against the cliff. He maintained his position with ease before voluntarily abandoning it during mid-January. Therefore, unlike *A. forsteri,* permanent territories do not depend on the availability of water (Stirling 1971a) although no doubt it would be an asset for an adult male active in territorial maintenance to have water available to cool himself.

Inland territories are numerous on wide beaches as is the case in *A. gazella* (Bonner 1968). On narrow east coast breeding colony sites, however, available space often only permit the establishment of frontline territories in single file along the beach. Frontline territories and those just inland from them are usually established before the arrival of adult females, but of course subject to change in ownership as the austral summer progresses.

At breeding colony sites the larger territories are inland since the foremost territories, being the most sought after, are subject to contraction as more males arrive to compete for a site adjacent to the sea. The converse is, however, true at nonbreeding colony sites. Here only frontline males usually express explicit territory maintenance behaviour owing to the presence of subadult and a few adult females. Inland males, especially during the maximal haulout of adult males, are more or less evenly spaced apart and had smaller areas of influence.

A third type of territory is those of back fringe males. Located far back up the beach on wide breeding colony sites, these males initially do not exhibit definite territorial behaviour. Only when acquiring a female(s) do they express definite territoriality. This type of territory is therefore formed upon the arrival of a female. Yet a fourth territory type may be recognized. It occurs infrequently during the breeding season, and is formed at hauling sites (and therefore away from the recognized breeding colonies) during the infrequent arrival of a female. Upon the arrival of a female the closest male immediately exhibits territorial behaviour with the result that his area of immediate influence is pushed out into a typically controlled territory. A parallel can be found in *A.p. pusillus* (Rand 1967) and similarly in *E. jubatus*, where a single female is adequate stimulus for territorial behaviour to be shown by an adult male (Sandegren 1970 *In:* Miller 1975b).

Male *A. tropicalis* do not hold aquatic territories as in *Z. californianus* (Peterson and Bartholomew 1967) and *A.p. pusillus* (Rand 1967). Neither are roving aquatic males recognized as in *A. gazella* (Bonner 1968). Only once was a male observed to intercept and chase an adult female in offshore waters when she left a beach. This is similar to *A. gazella* roving aquatic male behaviour (Bonner 1968). However, as in *A. forsteri* (Stirling 1971a) and *A. gazella* (Bonner 1968) adult males defend temporary, usually small territories on exposed areas at low tide or seaward of established front rankers (Fig. 51). In *A. tropicalis* these territories are formed at approximately mid-December when breeding sites attain their maximum in numbers of seals ashore. These males' attention is directed at females hauling onto and departing from the beach and females are only temporarily confined to the territories through the males' herding activities.

Territorial behaviour constitutes a goal for access to females (Miller 1975b) and in this respect frontline territory owners are the most successful, especially earlier in the breeding season. Frontline territorial males in *A. tropicalis* come first into contact with females hauling onto the rookery, intercept them and endeavour to restrict the females to their territories. However, with the increased haulout of adult females inland territories get their share; during their maximal presence ashore, females are found continuously from the waterline right to back

FIGURE 50 : Southern part of South Point beach breeding colony site showing frontline territories. The example shown represents a transitional zone between the jumbled rocky beach of the breeding colony site (foreground) and the rocky platform of South Point (background). Note the presence of very small subadults within the territories. Pupping only occurs amongst the jumbled rocks on the beach

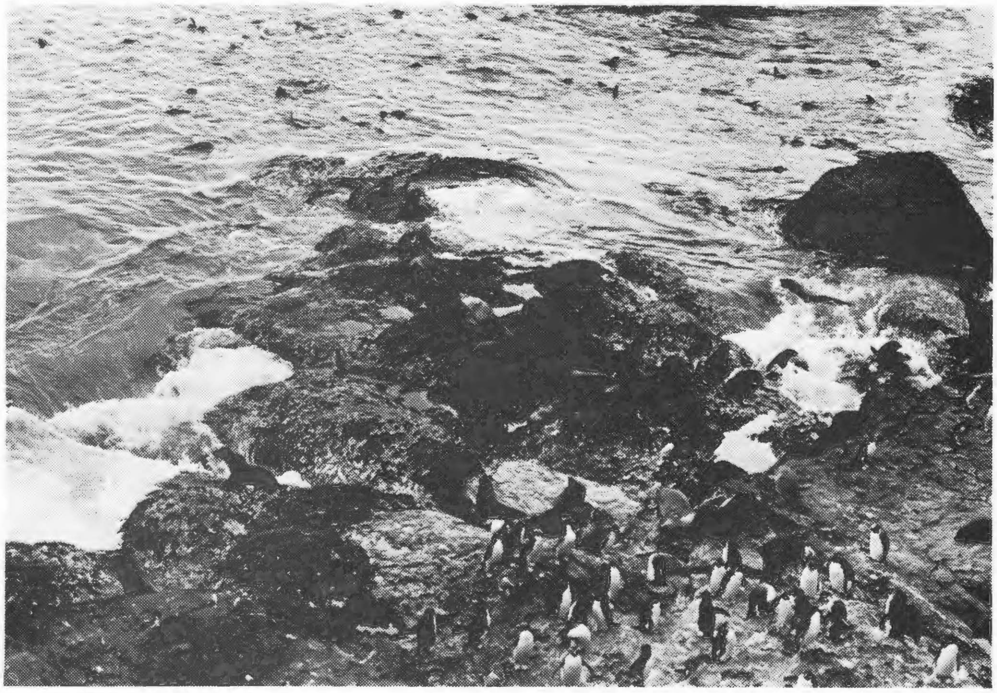

FIGURE 51 : An intertidal territory exposed at low tide and calm sea conditions

fringe males. At this stage the generalization that females are more numerous on frontline territories with their number diminishing farther up the beach, falls away. With maximum numbers of adult females ashore a redistribution in their location, due to environmental conditions, becomes evident. At high ambient temperatures and solar radiation females are most numerous in frontline as well as back fringe territories, when the latter are in the shade during the afternoon hours. During high seas, especially under cold cloudy conditions, most females are at the back of the beach probably to avoid the high surf and spray. The fact that pups, approximately 3–4 weeks of age, tend to congregate at the back of the beach may also contribute to the increased presence of females here since females tend to remain where they have located their pups after an excursion to sea. The above all contribute to the position that sometimes even territorial males in prime positions at least temporarily are without attending females whilst sub-dominant males have access to large numbers of females.

TERRITORY CHARACTERISTICS

Fur seal territory boundaries tend to be delineated by natural topographical features, e.g. large rocks, boulders, ledges, etc. This has been described for e.g. *A. gazella* (Bonner 1968), *A. forsteri* (Miller 1975b) and *A. tropicalis* (Paulian 1964), and territories are therefore more or less geographically fixed as in *C. ursinus* (Peterson 1968). That this pattern is not constant for pinnipeds is clear since e.g. in *Z. californianus* the territories shift in location with time of day, temperature, level of the tide and location of the females (Peterson and Bartholomew 1967).

As jumbled rocky beaches are preferred locations for breeding in *A. tropicalis,* natural boundaries to territories are especially evident there. Territories are often completely delineated by rugged topography, similar to the case with isolated males of *A. forsteri* (Miller 1975b), and precise boundaries within which a territorial male range occur. Only in relatively flat areas with a regular open profile are territorial boundaries less well defined. In this case territorial males tend to vary the distance tolerated between themselves and their neighbours before resorting to threat displays. In *A. forsteri* tolerated trespasses similarly occurred more often over topographically poorly-defined territories than over those that were topographically well-defined (Miller 1975b).

The shapes and sizes of adult male *A. tropicalis* territories are influenced by topography, thus being dependent on the position of physical barriers and their position relative to each other. Where conspicuous physical boundaries exist close to one another the territory may be small, but when these are far apart the territory may be considerably larger. Table 15 illustrates this point and shows that the territory sizes range from 5,0 m^2 – 63 m^2 with an average size of 23,1 ± 14.2 m^2 (N = 43). Territory sizes may also vary between non-breeding and breeding colony sites and are not always related to topographical definition. Therefore territories on nonbreeding colony sites, more or less with a much less pronounced rugged topography, were on the average smaller than those on breeding colony sites (13,8 ± 4,1 m^2 versus 20,1 ± 11,8 to 28,3 ± 13,9 m^2). Furthermore, territory size may also vary according to location on the beach with, in general, permanent ones bordering on the sea being smaller than inland and back fringe territories. Moreover, territory sizes may vary with time of season, with territories held earlier in the breeding season being subject to a decrease in size. They are usually larger than those defended during the mid-breeding season as a result of increased competition. Conversely late in the season territories may expand due to the incorporation of adjacent territories (abandoned) into existing ones.

The average territory size, determined for all permanent territories maintained during the breeding season ($\bar{X}$ = 23,1 m^2, N = 43), is comparable to figures given for *A. forsteri* ($\bar{X}$ = 23 m^2, N = 12) by Gentry (1975). His figure, arrived at for territories on a rookery of *A. forsteri*, falls mid-way between the average territory size measured for two *A. tropicalis* breeding colony sites (Table 15) and is exactly the same as the combined average of the two.

TABLE 15: **Territory sizes in *A. tropicalis* during the height of the breeding season, on nonbreeding and breeding colony sites at Gough Island**

	Territory size (m^2)			
Colony type	$\bar{X}$	Range	S.D.	N
Nonbreeding	13,8	8,5 – 17,5	4,1	10
Breeding	20,1	5,0 – 41,5	11,8	17
Breeding	28,3	12,5 – 63,0	13,9	16
AVERAGE	23,1	5,0 – 63,0	14,2	43

The effective space on a beach actually available for the demarcation of territories may also vary between different colony sites. In this context effective space available for territory demarcation is defined as the sum total of the area on which territorial males actually move and does not include the whole area where their influence is evident, which obviously is much larger. On this basis, e.g. at Waterfall Cove, the effective space used by 20 territorial males amounted to an approximate area of 566 m^2 (20 x 28,3 m^2). Since the beach area occupied by these males totalled approximately 1 040 m^2, an estimated 474 m^2 of beach area was not utilized by territorial males in territorial maintenance. This area constitutes mostly inaccessible topographical features serving as territorial boundaries. This effective area for territory demarcation would obviously be larger on open boulder beaches (e.g. South-west Island beach) than on jumbled rocky beaches. The physical nature of a beach therefore also contributes towards the number of territories that can be formed.

However, in *A. tropicalis* at Gough Island no accepted pathways through territories exist where males are safe from attack when they want to gain access to a beach or leave for the sea. This is similar to the situation in *A. forsteri* (Stirling 1971b), *A. gazella* (Bonner 1968) and *A. tropicalis* elsewhere (Paulian 1964), but unlike the situation at colony sites of *A. australis* (Vaz-Ferreira 1956) and *A.p. pusillus* (Rand 1967) where such avenues exist. On the other hand "pathways of least resistance" were seen during the present study. These depend on opportunity and are available only to a small number of males present. In short, where topography is such that an elevated area (provided by large rocks serving as territorial boundaries and forming a continuity) is available, a back fringe male on his way to the sea may utilize it. He would then wind his way towards the sea as far as is permitted before making a dash through frontline territories. More often, if a beach is flanked by a rocky ledge, a territorial male situated there may use this as a pathway to gain access to the sea so as to avoid a dominant male(s) located between him and his destination. At least two inland territorial males were observed to use such a natural topographical feature to gain access to the sea as well as to return to their territories. Such pathways of least resistance are, however, only utilized by males whose territories have such features as boundaries. The majority of males, however, have to contend with overt aggression from neighbours when departing from or returning to their territories after an excursion to the sea.

TERRITORIAL ESTABLISHMENT AND MAINTENANCE

A. forsteri (Miller 1975b), *A.p. pusillus* (Rand 1967), *C. ursinus* (Peterson 1968) and *Z. californianus* (Peterson and Bartholomew 1967) exhibit two types of inter-male interactions during territory establishment and maintenance. These interactions involve actual fighting usually during the time of territory establishment, as well as territorial displays during territory maintenance. The latter were also described as boundary ceremonies (Peterson and Bartholomew 1967) and ceremonial threatening (Peterson 1968). Miller (1975b) regarded threat displays between territorial males not as disputes but recurring at points in space accepted by both participants, and furthermore rarely involving physical contact. In *A. forsteri,* more encounters occurred per hour during the period of territory establishment than the period thereafter (Stirling 1971a) and similarly in *A.p. pusillus* fighting decreased as territories were recognized (Rand 1967).

In *A. tropicalis* fighting ensues in an attempt to defend or procure a territory. Once a territory becomes established neighbouring territory holders tolerate each other, indulging only in boundary displays. In the present study 158 interactions recorded on a time basis were analysed. Of these, 156 involved threat displays by territorial males, all except one being on territory boundaries. In only two instances did resident territorial males depart submissively upon the arrival of a size-dominant male and then only early in the breeding season.

Physical contact involving biting in inter-male interactions occurs in only 8,86 per cent of interactions. In boundary displays physical contact involving biting takes place in 8,39 per cent of cases. This is markedly different from the situation in *A. forsteri* where Stirling (1971a) found 30,9 per cent of "territorial disputes" to be resolved by fighting. This difference however may be the result of his classifying certain threats amongst territorial males as fights, as Miller (1975b) pointed out. In contrast to Stirling's (1971a) findings, *A. forsteri* males observed by Miller (1975b) and Gentry (1975) were involved in physical contact in threat displays across territorial boundaries in respectively only 2,88 per cent and 5,0 per cent of cases recorded. These two figures for *A. forsteri* therefore are closer to those obtained for *A. tropicalis* in my study (8,39 per cent).

The stimulus that elicits a threat display vary substantially in *A. tropicalis* (Table 16). These boundary threat displays do not always involve neighbouring territorial males but also temporary trespassers hauling for the purpose of gaining a foothold on the beach, as well as predominantly back fringe males during their thermal induced departures and subsequent return journeys.

Threat displays by territorial males resulting directly from temporary trespassers hauling onto and departing from the rookery account for respectively 33,3 per cent and 15,4 per cent of all inter-male interactions (N = 156). Therefore, 48,7 per cent of threat displays by territorial males result from this stimulus (Table 16). In 6,6 per cent of threat displays thus evoked physical contact involving biting occurs. A temporary trespasser rarely reciprocates a threat display from a resident male, and then only when hauling intent on procuring an already occupied territory (2,7 per cent of displays resulting from arrivals and departures). Back fringe males departing are always submissive to those inbetween them and the sea and are rarely bitten when in transit. Although not seen during the observation period, this was evident during casual observations at other times. The fact that a challenger to a male's territory usually comes from the sea may be the reason why haulers, however submissive, are more often bitten than trespassers moving in the opposite direction.

TABLE 16: The relative representation of stimuli effective in *A. tropicalis* territorial male aggression observed for nine days between 9 November 1975 and 17 December 1975

		Stimulus to territorial male				
	Undetermined	AF present	AM present	Another AM hauling	Another AM departing	Other
N	36	35	4	52	24	5
Per cent	23,1	22,4	2,6	33,3	15,4	3,2

In 3,2 per cent of threat displays across territorial boundaries by adjacent territorial males the reason was indirect i.e. from the disturbance caused by resident males interacting with temporary trespassers. Furthermore, inter-male activity not related to the former but simply as a result of other males interacting accounts for 2,6 per cent of interactions involving territorial males. Therefore 5,8 per cent of all interactions involving territorial males result from disturbance caused by inter-male activity.

Territorial *A. tropicalis* males interacting with adult females within their territories at Gough Island also stimulate other males to interact. This is especially evident when a territorial male persues a female moving away from his territory to the territorial boundary. Under these circumstances boundary threat displays become very intense and frequently involve physical contact through biting. Territorial male interactions resulting from male (themselves or others) interaction with adult females account for 22,4 per cent of interactions noted. Of this category of interaction 20 per cent culminates in at least one male biting his neighbour.

For 23,1 per cent of inter-male threat displays no obvious factor was responsible although it may have gone undetected. However, at least some of these apparently non-exogenously motivated encounters can probably be related to a need on the part of a territorial male to advertise his territorial status and to reaffirm his territory boundaries. Only 2,8 per cent of these threat displays involved physical contact through biting.

Considering the total number of physical contacts involving biting, recorded for territorial male interactions, those resulting from male:female interaction account for 4,5 per cent of the total (N = 156). This is followed by those coincident with interactions as a result of inter-male activity of all types (3,8 per cent) whilst those resulting from undetermined stimuli amounted to 0,64 per cent.

In all inter-male interactions recorded (N = 158) the outcome of 48,7 per cent of them resulted in stalemate being reached. This is the typical outcome of a boundary display between neighbouring territory holders. In 48,7 per cent of interactions the temporary offender (a hauler or trespasser and therefore not territorial whilst in transit) moved away. Only 0,63 per cent of interactions resulted in a territory being shared whilst in 1,9 per cent of cases a territorial change ensued (Table 17).

TABLE 17: **Outcome of encounters between adult male *A. tropicalis* observed for nine days between 9 November 1975 and 17 December 1975**

	Trespasser evicted	Stalemate	Sharing of territory	Territory ownership change
N	77	77	1	3
Per cent	48,7	48,7	0,63	1,9

BEHAVIOURAL PATTERNS IN ADULT MALE CONFLICT

Adult male interactions in *A. tropicalis* vary in intensity and due to circumstances. In a size-based dominance relationship a mild threat alone by the larger male may often be sufficient to displace a lesser opponent, or elicit submissive behaviour from him. Often, however, intense fighting ensues during competition for the possession of a territory, especially at breeding colony sites. For the Otariidae Paulian (1964), Peterson and Bartholomew (1967), Rand (1967), Bonner (1968), Peterson (1968), Stirling (1970 and 1971a) and Gentry (1975) for example, described interactions between territorial males. Definite behaviour patterns, therefore, is evident in otariid male conflict.

Few fierce fights between adult male *A. tropicalis* were observed in the present study. An adult male hauling-out onto a rookery may give a brief guttural challenge or a rapid whickering, before stiffly walking up, in an alert position, to the resident male. The head is held high and combined with an oblique squint just before contact is made. This is reciprocated by the defender who turns to meet the challenger when becoming aware of his presence. The opponents position themselves chest to chest (Fig. 45) before mutual neck-waving may start, presumably to gain an advantageous position from which to lunge and inflict a bite on the opponent. However, males may lunge at each other without these preliminaries. A forward lunge from one contestant is deflected with the neck and chest by his opponent. These lunges and slashes may be repeated a few times before the contestants briefly disengage, or when one succeeds with a bite on the face or neck of his opponent. If the bite results in a firm grip being obtained a visible contest in chest pushing ensues in which the one that obtained the firm holdfast tries to push his opponent over, or force him backwards. This results in a contest of strength with the bitten male reciprocating. Intermittantly the male with the advantage violently shakes his opponent, with the result that the latter's skin tears at the point of contact. The male held fast in the jaws of his opponent may try to break the hold by lowering his head and pulling it through to the opposite side. At this stage they may disengage to resume a head-held-high alert position, squinting obliquely whilst emitting rapid whickering and/or threat calls. If the male that makes first contact gets a grip low down on his opponent's neck he is similarly bitten low down on the neck, and males thus locked in combat alternatively shake each other until exhausted whereupon they release their grips (Fig. 52).

Whereas during the early stages of a fight the bites are directed anteriorly towards the face and neck, attempts can be made to inflict a bite on the flipper areas. If a male obtains a hold here he also strains forward, pushing with his neck and shoulder against the chest of his adversary.

Males do not always manage to get a firm hold on their opponents but in rapid lunges brief contact can be made which send fur and whiskers flying. Between clashes one animal may assume a full neck display, but with head held obliquely to keep the opponent within his field of vision (Fig. 53), whilst the other may crouch in a oblique posture. This full neck display does not conform to the more exaggerated one typically used spontaneously or occasionally at the conclusion of boundary displays (Fig. 42).

The outcome of a fight and the reason for its termination may vary. At any point during a fight one male may back away submissively. When persued it may give an open mouth submissive display and be put to flight into the sea. A dislodged male may also move inland and since he has presumably already established dominance over his former neighbour (earlier in the season), claim this territory when met with little or no resistance, as has been observed in the early breeding season. In the abovementioned combat for ownership of a territory the initiator of the interaction established his superiority without any doubt. However, at least one adult male after being evicted from his territory returned three times shortly thereafter to try and reclaim his territory, eventually at least temporarily establishing himself on an intertidal territory just below his former one. Therefore, the new owner of this particular territory only established his superiority after defeating several attempts by the former owner to regain his possession and not outright as in the previous instance.

Prolonged fighting between adult males for the possession of territory may leave both contestants exhausted, without one gaining the upper hand. In such cases a territory is shared, and the discontinuation of the fight may relate to not only the fact that they are well matched but also that they are probably becoming hyperthermic through the prolonged and intense activity.

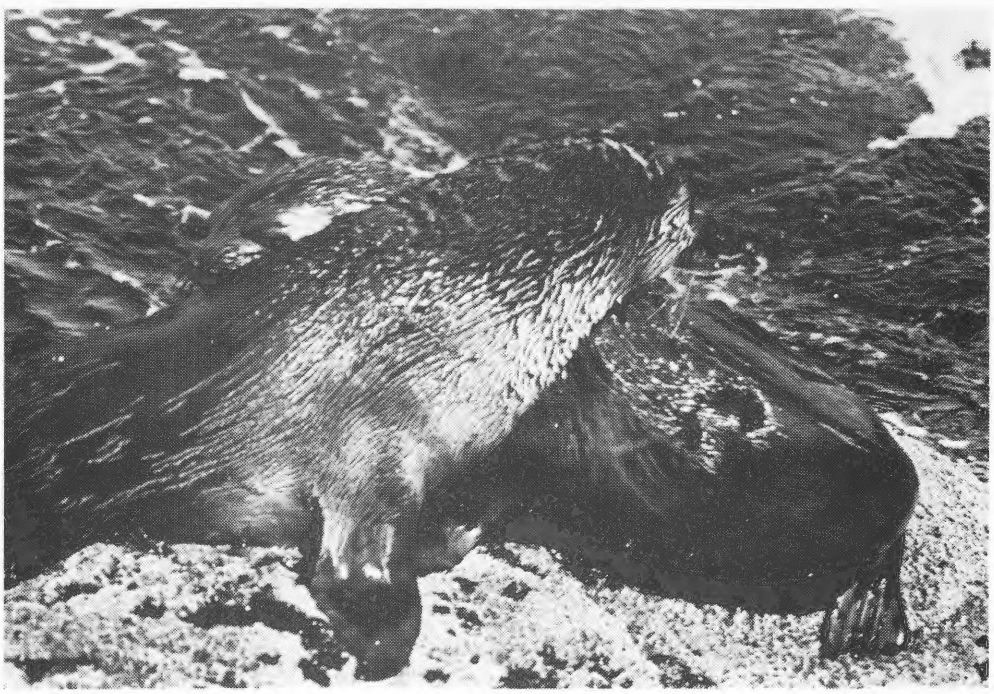

FIGURE 52 : Subadult male *A. tropicalis* involved in a play-fighting bout. The example shows a situation where both contestants have procured holdfasts on each other's backs typical to the situation which may develop in adult male fights

FIGURE 53 : The illustration shows the postures that may be assumed by adult males during a lull in a fight or during a boundary display. The male on the left crouches in a oblique posture, delivering a guttural threat while his opponent sits obliquely in a head-held-high position combined with an oblique squint

In at least one instance an outside factor settled the fight in favour of the resident male. As a result of the chest pushing contest the resident male forced his opponent to the territorial boundary where the neighbouring territorial male hovered. The latter immediately joined in the fight by biting the intruding male on the rump, shaking him vigorously. The latter disengaged the fight in the face of these odds and fled to sea, giving an open-mouth submissive display in conjunction with submissive calls.

Boundary displays never culminate in prolonged fighting in *A. tropicalis* at Gough Island. Similar to the boundary ceremony in *Z. californianus* (Peterson and Bartholomew 1967), elaborate threatening in *A.p. pusillus* (Rand 1967), ritualized threat displays in *A. forsteri* (Miller 1975b) and patterned boundary displays in *C. ursinus* (Peterson 1968), explicit boundary displays between *A. tropicalis* territorial males follow a predictable pattern.

In *A. tropicalis* a territorial male usually walks or rushes up to his boundary with an accompanying whickering when stimulated to do so. The male comes to a standstill in an oblique posture and simultaneously emits an open-mouth guttural threat(s). This is reciprocated by his neighbour and often results in mutual oblique open-mouth threat displays (Fig. 46). At the conclusion of this display the males usually sit up in a half facing away position, pretending to ignore each other although fully aware of each other's presence. One or both males may also give the guttural threat from an alert position, squinting obliquely (Fig. 53). Sometimes a male may fling himself down in a horizontal neck-stretch position, with an accompanying open-mouth threat display, after briefly assuming the oblique posture. This horizontal neck-stretch posture differs from a lunge in that the open mouth falls short of the opponent and is therefore not intended to inflict a bite. In appearance the horizontal neck-stretch posture simulates the boundary puff described for *C. ursinus* (Peterson 1968). During intense threat displays one or both males may use a quick facing away posture between threats (Fig. 43).

During boundary displays slashes are often directed at the opponent's face and chest whilst quick lunges from the oblique posture are usually directed at the insertion of the front flippers. The lunges are followed by a rapid lateral movement of the head in the process of withdrawing the neck and head, which is exposed during a lunge (Fig. 54). *A. gazella* males for the same reason made similar quick lunges at the flipper areas of opponents to avoid being bitten in the back (Bonner 1968).

Boundary displays are concluded when males resort to an almost full facing away display, and sitting either in an alert posture or occasionally giving a full neck display (Fig. 44). Intermittantly threat calls interspersed with whickering are emitted at such times. These threat calls are delivered from the same position as the full threat calls described for *A. forsteri* (Stirling 1971a) and illustrated in Fig. 48 and 49 of the present study. In *A. tropicalis* an elaboration of the facing away posture entails a male lying down, completely facing away from his neighbour even when the latter wants to resume the boundary display by directing a guttural challenge at him.

Facing away postures may be assumed even before the onset of a boundary dispute. For example, a male rushing at one of his neighbours which is involved with an adult female near the territory boundary, will stop in his tracks after covering about half the distance to his neighbour and assume an alert posture. Only subsequent to this will the boundary display be resumed. Often a male exhibits vacillation between an impulse to indulge in a boundary display and to prevent an adult female from leaving his territory. In this situation a male on his way to his territory boundary would make an incomplete approach to his neighbour and in the act of delivering an open-mouth threat display (even before he could vocalize) would abandon the effort to intercept an adult female leaving.

Group aggression where two or more territorial males simultaneously or concurrently involve themselves with a trespassing male were described for *C. ursinus* (Peterson 1968), *A. gazella* (Bonner 1968), *A. tropicalis* at Amsterdam Island (Paulian 1964) and *A.p. pusillus* (Rand 1967). Peterson and Bartholomew (1967) did not find this in *Z. californianus* and Stirling (1971a) found that more than one male *A. forsteri* seldom entered a fight with an intruder.

In *A. tropicalis* on Gough Island "group aggression" on breeding colony sites especially is a common occurrence. In fact, group aggression contributes largely

FIGURE 54 : **Adult male lunging at his opponent, directing the bite at the latter's front flipper area**

to the high percentage of male interactions (48,7 per cent) as listed in Table 15. However, as also apparently in *C. ursinus* (Peterson 1968), territorial males converging on an intruder at their common boundary intersects stay within their own territory limits. As a result little interaction amongst adjacent territorial males ensues after an intruder has passed (3,2 percent of territorial male involvement).

A temporary intruder hauling or departing exhibits stereotyped submissive behaviour. Usually when confronted by a territorial male the intruder gives an open-mouth submissive display with or without submissive calls, whilst rotating his body in such a way that he faces the quarter from which he is threatened. The open-mouth submissive display is also accompanied by nipping at the dominant male's chest and face and serves as a form of appeasement. During such an encounter the intruder backs away in the general direction of his intended destination, whether to sea or the back of the beach. When the encounter is broken off he may turn to resume his flight or repeat the above-mentioned sequence when confronted by the next male. However, even extremely submissive behaviour on the part of the intruder does not safeguard him from being injured, as has been described elsewhere. A male hauling to move to his back fringe territory is similarly harassed and this elicits the described submissive response from him. However, once he arrives on his territory this behaviour ceases and he immediately becomes pugnacious. Similarly *A. forsteri* and *E. jubatus* males never gave submissive displays whilst in possession of their territories (Gentry 1975).

The response of territorial males to a temporary trespasser entails threat displays but apart from the occasional physical contact through biting, they may also chest push the intruder out of their territories. Curiously enough on occasions a territorial male would pin an intruder down by pressing with his chest across the intruder's back in an attempt to, I presume, immobilize him. This occurs even when the intruder is on the verge of departing across the territory's boundary and does not constitute an attempt to prevent the intruder from crossing into the owner's territory.

Adult males detected before hauling out amongst the foremost territories can be discouraged to do so only by a mild vocal response from a frontline territorial male. Those intruders that gain a foothold on the beach itself by sneaking onto the beach in a lowered head and neck submissive posture, may upon detection start a headlong rush up the beach, or with silent open-mouth submissive display slide back into the water.

WOUNDS AS AN INDICATION OF FIGHTING TECHNIQUE

Male *A. tropicalis* on rookeries have numerous wounds sustained in territorial fighting. This is also evident at nonbreeding and idle colony sites where males haul out when defeated elsewhere. By recording all fresh wounds evident on adult males an indication can be obtained where most wounds are inflicted, as well as which body areas are sought after to obtain a holdfast by combating males. Furthermore, the distribution of wounds, as well as their frequency of occurrence in the different body zones demarcated, supplements the information on fighting technique employed by males in combat.

Considering the relative number of zones which have one or more fresh wounds on it, by far the majority is sustained around the insertions of the front flippers, as well as on these flippers themselves. In 115 adult males one or more wounds were present in 200 instances on the five zones demarcated for the body surface area of adult males. Of these 41,5 per cent occurred in the foreflipper zone (Table 17), 21,0 per cent on the neck, 20,5 per cent on the back and rump and 17,0 per cent on the throat, face and chest combined (Table 18). These figures accord very well with the relative percentage of the actual number of wounds sustained in these zones expressed as a percentage of the total number of wounds noted (Table 18).

From these figures it is clear that those body areas on the forequarters of an adult male, and therefore within reach of the weaponary (teeth) of a challenger in a fight, receive the most wounds. Of these the face, throat and chest receive the least damage (17,0 per cent of the total) being only slightly lower than that recorded for the neck region (21,0 per cent of the total). These figures are almost half of that recorded for the front flipper zones (41,5 per cent of the total). The predominance of injury to the flipper areas versus those of the face, throat, chest and neck is accentuated by the fact that most wounds sustained on the front flipper zone occur on the small areas around the insertions of the flippers (Fig. 55). These areas represent only a fraction of the surface areas of the other zones recognized. The back and rump injuries approximate the values obtained for e. g. the neck region (20,5 per cent versus 21,0 per cent). The back and rump are also susceptible to damage and spectacular wounds may be inflicted here (Fig. 56).

TABLE 18: The distribution frequency of wounds sustained by adult male *A. tropicalis* in intrasexual fights.

	Zones					
	Throat and face	Chest	Flipper areas (Front flippers)	Neck	Back and rump	Total
Number of damaged zones	21	13	83	42	41	200
Per cent	10,5	6,5	41,5	21,0	20,5	–
Number of wounds	26	26	138	70	82	342
Per cent	7,6	7,6	40,4	20,5	24,0	–

From the above it is clear that in intrasexual fighting bites are more often delivered, and contact made, at the insertions of the foreflippers. More significant though is the observation that these areas are more susceptable to damage than for instance the neck with its heavy fur and thick skin. Furthermore, a firm grip on the front flipper zones is more likely to swing the fight in favour of the male that inflicts this bite, as well as bring it to an earlier termination than for instance when a grip is acquired on the neck region of the opponent. As in *A. forsteri* (Stirling 1971a) even after prolonged shaking and pulling such a bite may not open a visible tear in the skin of the neck. A bite delivered to the neck would therefore be of less immediate concern to a male on the receiving

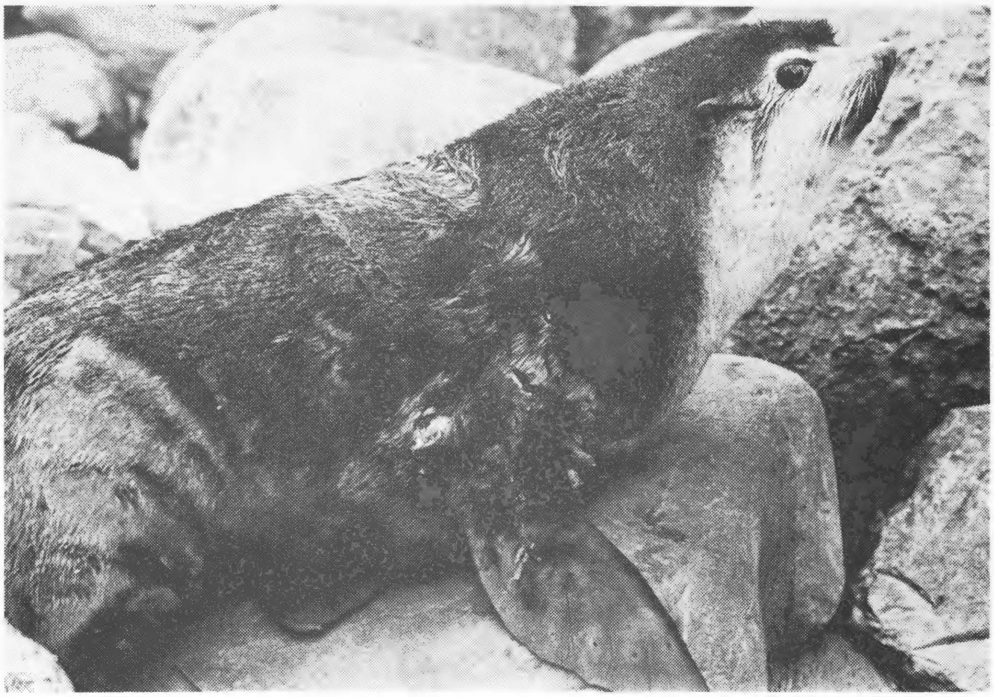

FIGURE 55 : An adult male *A. tropicalis* with deep gashes around the insertion of the front flipper sustained in intrasexual fighting

FIGURE 56 : A serious wound sustained on the rump by an adult male. This wound could be fatal since the underlying musculature was torn away with the skin, and the male could hardly move

end than a bite to the flipper area. This is substantiated by the observation that if a male is firmly bitten on the unprotected flipper area, and especially the flipper itself, he may almost immediately start to emit high-pitched submissive vocalizations and try to discontinue the fight. The fact that the male, successful in obtaining such a grip, leaves his neck unprotected for retaliation do not seem to be of concern as discussed above. Furthermore, a wound received on the flipper articulation may practically immobilize an animal especially if the wound becomes inflamed at a later stage.

Stirling (1971a) concludes that for *A. forsteri* the neutralization of the opponent's weapon system is as critical a goal in attack as is actual wounding. Furthermore, similar to e.g. all otariids biting is predominantly directed at the opponent's head and neck. This can also be accepted for *A. tropicalis* in the present study, especially during the early stages of a fight where the emphasis is on physical strength in pushing the opponent over or towards the territory boundary. Failure to resolve the fight at this stage apparently leads to seeking the vulnerable areas to gain the upper hand, although bites directed at flipper areas may already occur during the early stages of a confrontation.

Social behaviour between adult males and females

The term "harem" is usually used to designate a group of females associated with a single male (Peterson 1968). However, female pinnipeds seem to aggregate without regard for the males (Peterson 1968; Gentry 1975) and female choice of sites where they pup apparently are not based on male attributes, but rather on position in the rookery (Miller 1975b). Similarly *A. gazella* females' choice of site is influenced by the presence of other females as well as the condition of the beach (Bonner 1968). Furthermore, females do not go back to the "harem" after a feeding excursion to sea in any regular manner but tend to stay where they find their pup (Paulian 1964). Females may also move through harems very easily (Bartholomew 1953). The discontinuities in female aggregations on the beach, and therefore their local patchy distribution relate to the territorial behaviour of the males around the perimeter of the territories (Peterson 1968), and their territorial activities and herding behaviour (Gentry 1975). These discontinuities in female distribution are not absolute (Gentry 1975) and indeed in *C. ursinus* (Peterson 1968) and in the present study involving *A. tropicalis*, female aggregations become continuous when the number of females on the beach is very high. As in e.g. *C. ursinus* (Peterson 1968) and *A. forsteri* (Miller 1975b) no pair bonds seem to exist and the term "harem" is therefore a misconception as pointed out by Peterson (1968), with the term "aggregation" being perhaps more appropriate. It is within this context that adult male : adult female social behaviour must be seen.

A. tropicalis on Gough Island exhibit seven categories of adult intersexual behaviour. These are not always distinct since interactions may be stimulated for one reason but may culminate in, or include behaviour typical to another category. However, the transition from one type of interaction to another will be indicated where appropriate. The seven categories of intersexual behaviour are herding, crowding responses, displacement, olfactory investigation, peacekeeping, copulation, and vocal and visual contact.

HERDING

In herding the territorial male endeavours to prevent an adult female from leaving his territory. This herding response to contain a female (s) within his territory boundaries usually entails him interposing his body between the female and her line of departure. This response may commence upon the movement of a female in his territory without her actually moving towards the boundary. Typically the male blocks the female's path with his neck and chest whilst whickering incessantly with the whiskers in an erect position. When he has brought her to a halt he may place himself in an upright posture in front of her and with rapid "headflicks" i.e. rapid ventro-lateral movements of the head, try to make her desist. He may also, through physical contact with the head in an upright alert posture combined with an oblique squint, force her back into his territory.

The female's reaction towards the male is predictable since she always gives a submissive open-mouth display even before the male reaches her (Fig. 47). In a mild submissive open-mouth display the whiskers are not erected. When the male moves closer to her the female may start nipping at his chest, face and occasionally at his flanks and even flippers, and/or bite lightly into his chest fur. If she backs down and desist in trying to leave the territory, the encounter usually terminates at this point. However, if the female persists in trying to leave the male he becomes increasingly aggressive, emitting rapid high-pitched whickering intermittantly interrupted by an open-mouth guttural challenge from a head held high and slightly oblique position. Headflicking may intensify at this stage.

The degree of submissive displaying by the female intensifies as the male's aggression mounts, and she rapidly jabs at his face with an open mouth and bites into his chest. In extreme submission she strongly erects the vibrissae with her open mouth directed at his face, and may emit submissive vocalizations when hard pressed by the male. She eventually remains in the territory at least for the time being, or after prolonged herding the male may let her go.

Males herding females trying to leave their territories account for 20,3 per cent of all interactions between males and females (Table 19). Similarly Miller (1974) recorded 16,2 per cent of social encounters between adult male and female *A. forsteri* as herding (approach-herding) responses.

TABLE 19: Summary of social encounters between adult male and female *A. tropicalis* observed on seven days between 5 December 1975 and 6 January 1976

Category	N	Per cent
Herding	55	20,3
Crowding responses	69	25,5
Displacement	5	1,9
Olfactory investigation	98	36,2
Peacekeeping	21	7,8
Copulation	3	1,1
Vocal and visual contact	20	7,4
TOTAL ENCOUNTERS	271	–

The most extreme herding behaviour recorded for *A. forsteri* entails the male pinning the female down by throwing himself on top of her (Miller 1974). This constitutes less vigorous and aggressive behaviour than recorded for *C. ursinus* (Bartholomew 1953; Peterson 1968) and is similar to that reported for other *Arctocephalus* species (Bonner and Laws 1964; Paulian 1964; Bonner 1968). However, *A. tropicalis* on Gough Island do not conform to this pattern of milder herding behaviour responses. In this the Gough Island population of *A. tropicalis* even differs substantially from its counterparts on Amsterdam Island. (Paulian 1964) but matches the extremes in herding resorted to by *C. ursinus* (Peterson 1968). Male *A. tropicalis* may bodily lift a female persistent in departing and carry her back well inside his territorial boundaries. Furthermore, a male may even bite a female in the rump and drag her back even if she has just crossed into a neighbouring territory. He himself, however, does not venture into a neighbouring territory in pursuit. However, a frontline territorial male will chase after a female that has already fled his territory into the sea. For example, on one occasion the male dived into the sea after the female, and still submerged, caught her approximately 8 metres offshore and surfaced with her rump firmly clasped in his jaws. He then proceeded to carry her up onto the beach (Fig. 57) and upon releasing her, herded her back into his territory. The male may also chase a female along the shore and back onto the beach further along. In one instance a male doing this was confronted by another male at the new location, and thereupon chased the female back to his territory along the same route they had come. As in *C. ursinus* (Peterson 1968) these extreme herding responses occurred as a result of human interference during e.g. ground censusing, but although infrequent, occur under natural circumstances as well.

A female, when picked up by the male, also bites firmly into his back (Fig. 58). Although this biting seems to be aggressive behaviour on her part it has submissive undertones and she at any time may resort to explicit submissive behaviour to appease him.

Under the above circumstances the females do not inflict wounds on the male and in land-bound herding responses a female's wet mouthing marks can be seen on a male's chest. On the other hand females on the rookery occasionally have

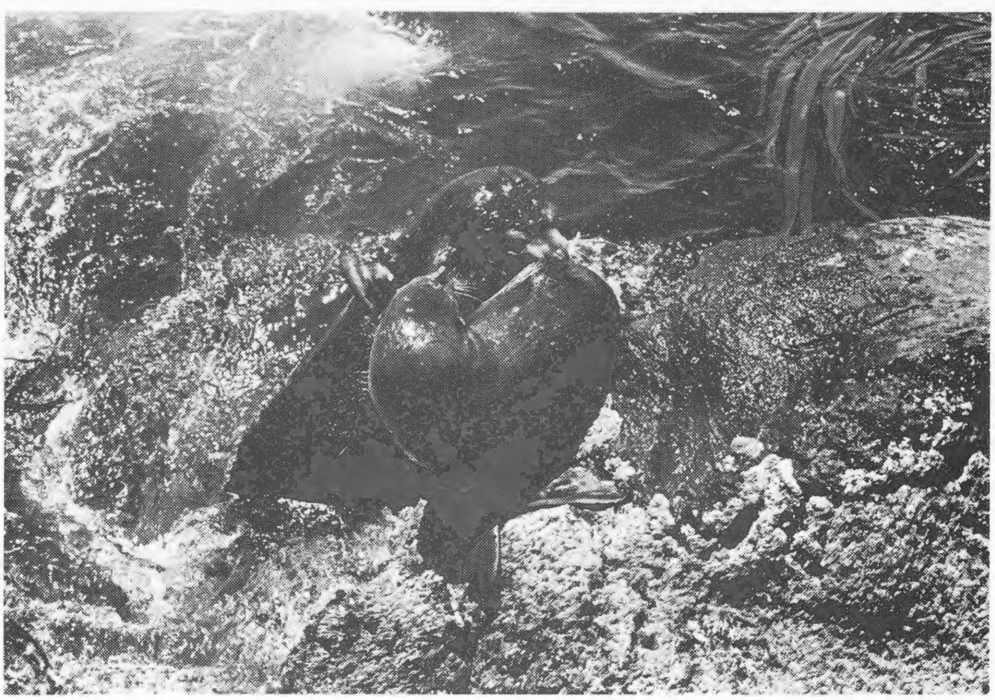

FIGURE 57 : An adult male *A. tropicalis* carrying an adult female back onto his frontline territory, after catching her in offshore waters and subsequent to her escape from his territory

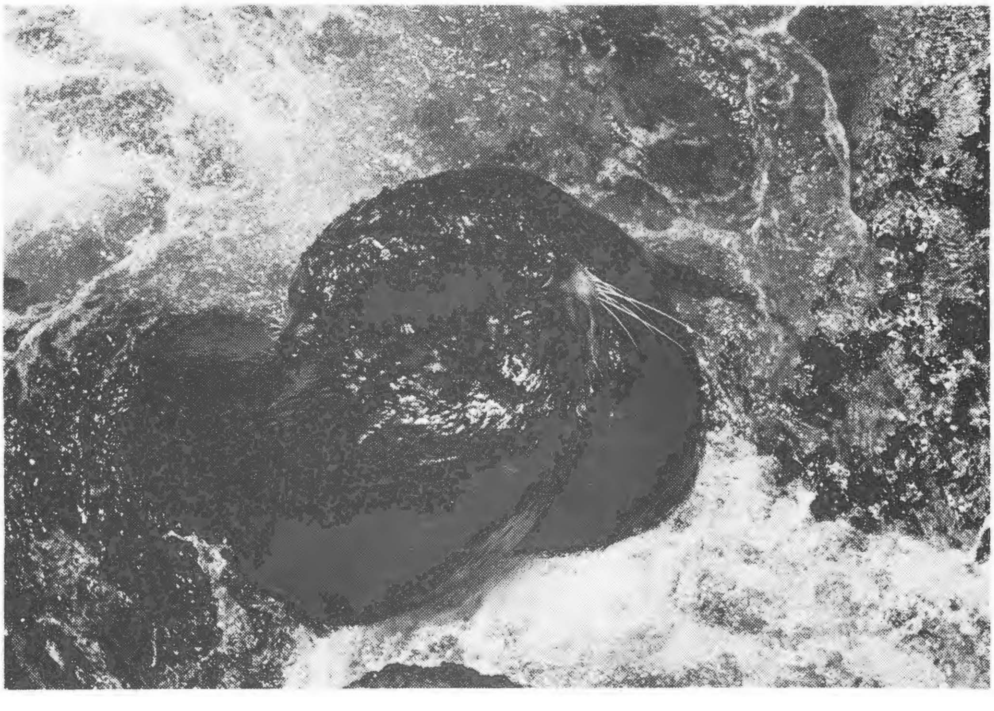

FIGURE 58 : Adult female counteracting male's efforts to carry her back onto his territory by biting him firmly on the back

lacerations on the neck, back, rump and flanks, although rarely more than one at a time, which can be connected with extreme herding behaviour by the male. These lacerations presumably occur when the female is practically suspended by her full weight from the single contact point with the male's jaws.

Herding behaviour by *A. tropicalis* males seldom results in an effective containment of adult females. A persistent female always manages to escape, even after prolonged herding by the male. Furthermore, the numbers of females on territories may fluctuate considerably from one day to the next, as well as during the same day. Therefore females manage to move through territories although males endeavour to restrict their movements by herding behaviour.

As the breeding season progresses males often have only a passing interest in adult females. Especially from late December onwards females may haul up the beach practically undisturbed. Already from the second week of December do different males show different responses to females crossing their territories. For example, a female may be vigorously herded by one when she moves through his territory, but the neighbouring territorial male may only vocalize at her when she escapes the herding male and move through his territory towards the back of the beach.

CROWDING BEHAVIOUR

In the present study crowding behaviour is defined as interactions between males and females, similar to herding, but not resulting from the female trying to move away from a territory. Crowding entails a male moving towards a female and upon reaching her assuming an alert posture. He then pushes against the female in the manner typical in herding, so that the female is forced backwards. Crowding behaviour by a male is accompanied by headflicks and whickering, but these have less aggressive overtones than in herding. In fact, crowding may be performed in an amicable manner.

The stimulus leading to a crowding response is obscure. Approximately 1,5 per cent of crowding responses result from the female simply changing position.

This may be related to herding since the male may interpret such a movement on the part of the female as an attempt to move away. Aggressive interactions between females and pups also account for 1,5 per cent of crowding responses by the male and may be related to peacekeeping although males usually ignore female:pup interactions. In 2,9 per cent of cases females elicit a crowding response through interacting with the male by submissively stretching forward with head and neck in conjunction with a submissive open mouth display. Restlessness in adult males, resulting from border displays involving neighbouring males culminate in at least 7,3 per cent of crowding behaviour. Similarly Paulian (1964) noted the involvement of males with females after male interaction.

For 87 per cent of crowding behaviour no definite outside stimulus is evident. Miller (1974) reasoned that since herding seldom succeeds in containing females it may have a communicatory value; it may serve to advertise certain attributes of the herding males. Since there is no good evidence for mate choice in pinnipeds (Peterson 1968; Miller 1975b) it seems likely that this feature of male behaviour provides herded females with a criterium for recognizing "normal" males, as abnormally active male *E. jubatus* may repel females (Gentry 1970, *In:* Miller 1974). This assumption seems applicable to the present study, especially for crowding responses, although some other cause may be effective here. For example, at least 14,5 per cent of crowding responses include olfactory investigation of the female, presumably to assess her reproductive status, although this did not appear to be the male's original intention when commencing the crowding behaviour. Furthermore, 18,2 per cent of true herding behaviour culminates in, or includes olfactory investigation chiefly of the perineal area. This presumably depends on the female's reproductive state so that the male's vigour in containing her may fluctuate. Moreover, some females attract the most attention from an adult male, even in the face of his losing other females from his territory. Therefore, the extreme herding responses which *A. tropicalis* males exhibit are correlated presumably with the reproductive condition of the female and not with the intention of communicating with her. These herding responses occur in an effort to contain the female in the territory at least until the male has copulated with her.

OLFACTORY INVESTIGATION

In 36,2 per cent of adult male:female interactions these are directed at either nuzzling the female's face (21,8 per cent) or smelling her perineum (14,4 per cent), but this may culminate in one or more interactions of another type. Male *A. gazella* identified oestrous females by their odour, and nuzzling (sniffing the nose), often followed by perineal investigation, served this purpose (Bonner 1968). Similarly olfactory investigation to assess the female's reproductive state occurs in *A.p. pusillus* (Rand 1967), *A. tropicalis* (Paulian 1964), *A. forsteri* (Miller 1974) and *C. ursinus* (Bartholomew 1953; Peterson 1968). Bartholomew and Hoel (1953) observed male *C. ursinus* to mount a female after only smelling her face.

In the present study the importance of olfactory investigation of females by male *A. tropicalis,* in assessing their reproductive state, is shown by the observation that at least 48,3 per cent of all male:female encounters involve this reaction at one stage or another. Barring the 7,4 per cent of all interactions involving only vocal and visual contact, and, thus apparently not used for the recognition of oestrous females, the occurrence of olfactory investigation amounts to 52,3 per cent of the total number of male:female interactions.

Females dislike being subjected to perineal investigation. They always try, at least initially, to prevent the male from reaching down with his nose by biting him in the chest and rotating their hindquarters away from him. When faced with overt resistance from the female, the male may let her go and be content to smell the rock on which the female lay. However, when males persist in their efforts and are continually foiled by the females, they become very aggressive and bite at the female, threaten her or hammer sideways at her with the head (exaggerated headflicks). At this stage the females usually show the open-mouth submissive display at the male, snapping at his whiskers apparently to appease him, but when he resumes his effort to smell her perineum she may interpose her head and neck. This results in him repeating his aggressive behaviour in an effort to make her move her head and neck out of the way. Sometimes a persistent male pins the female against a rock in an attempt to immobilize her and in one instance a male lifted a female almost completely off the ground with his jaws clasped around her perineum.

DISPLACEMENT

This involves the eviction of a female from the particular spot she lies on. The male moves towards her in an upright posture combined with an oblique squint and whilst whickering, head flicks her and also deliver guttural challenges until she moves away. Displacement accounted for 1,9 per cent of all adult male:adult female encounters. One instance observed involved a male on an intertidal territory rushing forwards, biting a female in the rump, and then flinging her back. He then proceeded to lie down in the position formerly occupied by her. This is abnormal behaviour in displacement and probably was the result of the male being highly agitated by the presence of two frontline territorial males inland from him.

Another form of displacement activity which may be included here is the very infrequent occurrence of an action where a male simply drags a female closer or displaces her by biting her in the back or rump. On rookeries this could be termed "stealing" of females, since in one instance a female thus treated lay just inside a neighbouring male's territory' boundary. This behaviour is however more often seen on nonbreeding colony sites and is directed at the subadult female class. In this form of displacement the male does not claim the female's position. This has not been described for other *Arctocephalus* species. However, displacement of a male by a female in an effort to claim her resting place on a site has been described for e.g. *A. forsteri* (Miller 1974).

PEACEKEEPING

Peacekeeping i.e. the intervention of a male in a dispute between adult females, accounts for 7,8 per cent of all adult intersexual encounters, in contrast to only approximately 2 per cent in *A. forsteri* (Miller 1974). This behaviour pattern was also recorded for *A.p. pusillus* (Rand 1955 and 1967), *A. australis* (Vaz-Ferreira 1956), *C. ursinus* (Kenyon 1960) and *Z. californianus* (Peterson and Bartholomew 1967; Shusterman and Dawson 1968). Although termed peacekeeping, this behaviour is probably not intended to terminate inter-female aggression but rather is a response by a male to heightened activity (Peterson and Bartholomew

1967, Miller 1974). Similar to *Z. californianus* (Peterson and Bartholomew 1967) "peacekeeping" by adult male *A. tropicalis* ensues even when a female and pup interact. Indeed, this accounted for 9,5 per cent of the total number of peacekeeping encounters noted in the present study.

COPULATION

Copulations and attempted copulations represent 1,1 per cent of the total number of adult intersexual encounters (Table 19). Few copulations were witnessed for the whole study period and only three from start to finish. Female response to a male intent on copulating with her varied between her being resistant throughout the attempted copulation or resisting only at the end of copulation. In the few copulations witnessed the female did not solicit the male although this is highly probable. On occasions soliciting by a female was observed although it did not terminate in copulation. Males mount the females dorsally as in *A. forsteri* (Stirling 1971a, Miller 1974), *A. gazella* (Bonner 1968) and *A.p. pusillus* (Rand 1955) although ventro-ventral copulations occasionally occurred in the latter two species. There is little preliminary behaviour in *A. tropicalis* before the mounting phase, although one male accorded the female he eventually mounted the most attention during the day, and often investigated her perineal area. In two copulations the male investigated the female's perineal area, as well as nuzzled her, before mounting. On one occasion only nuzzling occurred between the male and female before copulation.

A female, presumably not in oestrous, may actively resist being mounted. In one instance, the female continually twisted round to bite the male in the chest while he straddled her; he retaliated by headflicking her when she released her hold. Once or twice he bent down and bit her on the neck either in retaliation or in an attempt to control her. She then reared up, twisted around and bit at him. The male dismounted at least five times in an attempt to change to a better position. On another occasion a male was successful only at the tenth attempt to mount a passive female. This is similar to the situation in *A. forsteri* (Stirling 1971a; Miller 1974) where males mounted females up to nine times before actually copulating (Miller 1974). In *A. tropicalis* a female may try and move away between mounts, but the male always rushes after her to pin her down and mount again. On all occasions the females terminated copulation by rearing up, biting the male in the chest whilst squirming from underneath him, even while he was still copulating. This behaviour of the female to terminate copulation has also been observed in *A. forsteri* (Stirling 1971a; Miller 1974), *A. tropicalis* (Paulian 1964), *A.p. pusillus* (Rand 1955) and *A. gazella* (Bonner 1968).

VOCAL AND VISUAL CONTACT

Adult male:female interactions occasionally amount to no more than a male vocalizing at a female or turning his head in her direction to keep her in view. This can have marked results: for example a female on her way to the territorial boundary will stop in her tracks when the male vocalizes at her or when she becomes aware of him looking at her. Sometimes the female would give an open-mouth submissive display at him and either return to her former position with a submissive head and neck lowered posture, or terminate her attempt to leave. This type of interaction which has a visible effect on the female amounts to 7,4 per cent of all interactions between adult males and females.

ADULT MALE:FEMALE AGGRESSION

A curious feature of adult male:adult female interactions is the limited occurrence of outright aggressive behaviour of female *A. tropicalis* towards the males. This differs appreciably from the situation in other *Arctocephalus* species.

Miller (1974) stated that the dominant quality in male:female encounters in *A. forsteri* is aggression. In *A. tropicalis* this applies more specifically to the male's reaction in a male:female encounter. Female aggression in *A. tropicalis* is only evident in attempted perineal investigations by the male, at the end of copulation and when a male disturbs a female suckling a pup. However, this aggression almost always involve elements of submission by the female. Females are wary of adult males and seem to be careful not to provoke overt antagonism from them; in the case of the female biting the male she may switch back to explicit submissive behaviour when the male's aggression mounts.

In *A. forsteri* 34,4 per cent of male:female encounters involving threats alone were accounted for by female-to-male threats (Miller 1974). Furthermore, female-to-male threats accounted for 27,6 per cent of all male:female social encounters in *A. forsteri*. Moreover, in *A. tropicalis* on Amsterdam Island it was the females that harassed the males (Paulian 1964), and Bonner (1958) described how female *A. gazella* snapped fiercely at a territorial bull when he moved amongst them. Miller (1974) concluded that unprovoked antagonism by females towards males is the rule amongst e.g. otariids (Bonner 1958; Bonner and Laws 1964; Stirling 1971a).

These observations do not hold for *A. tropicalis* on Gough Island. Only 1,5 per cent of all male:female interactions include outright aggressive behaviour by adult females. These involve the female delivering an explicit aggressive open-mouth threat in the form of a guttural challenge at a male vocalizing at, or moving past her. In fact, a male moving towards a specific female and only whickering in the process, may elicit an open-mouth display from another female(s) close by without according them any attention (Fig. 47).

The observation that female *A. tropicalis* in the present study do not show overt aggression towards adult males may be related to the finding that males are much more aggressive towards females than described for other *Arctocephalus* species. In this male *A. tropicalis* is similar to male *C. ursinus* since both may treat their females in a brutal fashion.

Female and pup relations

A. tropicalis pups in the present study are suckled for approximately 10–11 months and weaning is probably forced on them with the mothers' departure prior to the onset of the next breeding season. After parturition the mother makes feeding excursions to sea and up to the time of weaning, periodically returns to the beach to suckle her pup. No births were witnessed but the mother:pup behaviour was recorded shortly thereafter with the mother still experiencing post-partum bleeding and with the pup still attached to the placenta.

SUCKLING

Shortly after birth pups are still inept in finding the nipples in order to suckle. Whilst searching, the pup emits a bleating vocalization. The female usually turns onto her side, exposing the four nipples. The female may also assume a sitting position, only rotating the hindquarters so as to facilitate suckling. Occasionally females assume an almost supine position with all nipples easily accessible to the pup. Older pups may suckle with their front flippers placed on the female's belly, when confronted with such a situation.

A pup close to its mother usually gives a female-attraction call, begs at her or nuzzle at her body, accompanied by pushing motions with its nose against her, if it wants to suckle. If she is already lying in a suckling position it commences suckling straight away, otherwise the female assumes a suckling posture. However, females often resist their own pup's efforts to suckle by lightly biting at them or even pressing with their heads across the pup's back before getting up to move a little way off. A female may also assume a tucked-flipper posture, covering the nipples, or move her hindquarters out of the way under a rock. Sometimes a female may change her mind after initial resistance and assume a suckling posture. For example, a female trying to move a little way off may attract the territorial male's attention who may then herd her to her former position where she settles down for the pup to suckle. Pups always initiate suckling and usually terminates it when they have had their fill. One instance was recorded where a female pushed the pup's head towards her with a flipper when he terminated the suckling bout. This may have been part of the usual flippering action but it appeared as if she encouraged the pup to continue suckling. Especially during prolonged suckling the female sometimes becomes irritated and try to push the pup away with her head, move off or change to a position which conceals the nipples from the pup.

During a suckling bout the female usually flippers her pup with a front flipper, but occasionally also with a hind one. Flippering entails the female placing a flipper on the pup's body and it may be accompanied by a sweeping motion of the flipper over the pup's body, described by Paulian (1964) as "caressing". In some instances this may hinder the pup's suckling since this flipper motion may force the pup's mouth away from the nipple or cover the nipples if the flipper remains in such a position.

A pup suckling frequently alternates between all four nipples and no distinct preference for a particular one is evident. However, with the female lying on her side the topmost row of nipples are probably more often utilized, being more easily accessible. The frequent alternation between nipples is especially evident as the suckling bout progresses and the pup begins to loose interest. Pups often also release a nipple to beg at a female's face before resuming suckling. Pups also interrupt suckling bouts for short rest periods during which they may move around. The nipples are strongly erected during suckling.

The duration of suckling bouts varies substantially according to the duration of a female:pup association between her feeding trips, the time lapse since the last suckle or its early termination resulting from disturbance created by an adult male interacting with the female, interference with the pup by neighbouring females and altercations between females. Moreover, it is often difficult to determine whether the pup is actually suckling whilst in contact with the nipple, since they sometimes push strongly whilst suckling while otherwise they may lie motionless with the nipple clasped in the mouth. However, from the start of a suckling bout to its termination, the on-nipple time amounts to an average of 21,4 ± 20,5 minutes (N = 15) with a range of 1,5 to 52,3 minutes. At the end of a suckling bout a pup may start playing with the female's flippers, or lie back against her before settling down next to her, or move off a little way.

The frequency of suckling bouts was recorded for three female:pup pairs and it shows that the pups suckled, on average, at intervals of 1,2 ± 0,44 hours (N = 7) with a range of 0,5 to 1,8 hours.

FEMALE AGGRESSION TOWARDS STRANGE PUPS

In *A. forsteri* (Stirling 1971b), *A.p. pusillus* (Rand 1955), *A. tropicalis*

(Paulian 1964) and *C. ursinus* (Peterson 1968), females do not suckle strange pups under normal circumstances. This seems to be true for *A. tropicalis* at Gough Island as well since females may be extremely aggressive towards strange pups.

A hungry pup in search of its mother may try and solicit suckling from any female. A strange female usually threatens the pup, bites it in the neck, back or rump or flings the pup away from her. However, occasionally a female may nuzzle a soliciting pup but ignore it afterwards unless the pup persists in its efforts to suckle from her, whereupon she repels the pup. This aggressive behaviour of females also extends to pups not trying to solicit suckling from them and even to pups in the process of being suckled by their own mothers. For example, a female close to a pup being suckled by its mother may stretch forward and bite the pup in the rump up to six times in succession, the fierceness of the bites increasing successively. Whilst at the onset of biting the pup only responds by briefly stopping suckling, towards the end the pup's mother may notice this activity and interact with the offending female. Both females with or without pups in attendance resort to threatening pups in their vicinity in this way.

Sometimes a pup persists in attempts to suckle from a strange female and may threaten her, apparently irritated by her not co-operating. Every time the female threatens or bites at the pup, it may reciprocate by giving an open-mouth threat. This sometimes culminates in the female moving off with the pup in pursuit. Even an aggressive female appears confused when a pup presses her in this manner. Stirling (1970) also observed a frantic *A. forsteri* pup to drive a female back into the sea while she was looking for her own one.

The plight of a hungry pup searching for its mother may be traumatic. For example, a pup searching for its mother twice traversed the width of the beach at Waterfall Cove before settling down. In the process the pup came into contact with strange females on 32 occasions, during most of which the pup tried to suckle. On 11 occasions the females bit him, and he drove two females off with his efforts to suckle from them. Most of the females at least open-mouth threatened him. During these wanderings the pup also tried to suckle from a subadult male, whom on two occasions bit him in the rump, flinging him away. Interesting enough, this pup presumably in an effort to alleviate his pangs of hunger, apparently drank from a small pool of fresh water at the back of the beach. In this study at least two other pups also apparently drank fresh water, both in the absence of their mothers. Bonner (1968) reported *A. gazella* pups to dip their noses into water but they did not suck and therefore the present observations are open to speculation as to whether the pups actually drank the water since no swallowing motions were seen. However, an *A. tropicalis* territorial male definitely drank water as did a non-territorial male *A. gazella* (Bonner 1968). The occasional drinking of water could be a feature, although infrequent, of *A. tropicalis* behaviour.

FEMALE LOCATION, AND RECOGNITION, OF HER PUP

A female *A. tropicalis* hauling onto the beach where her pup is located, gives pup-attraction calls while still near the waterline or when she is moving up the beach. Without fail a number of pups responds some of whom converging on her emitting female-attraction calls. When making contact with a pup, the female nuzzles or sniffs at it before moving on, or else she may threaten it upon finding it not to be her own. When making contact with her own pup, the two nuzzle or sniff at each other. The pup becomes very excited as recognition dawns and they may settle down to suckle, but usually move further up the beach, the female stopping frequently to look if the pup is still following. If the pup cannot surmount an obstacle in its path the female turns back to pick up the pup with her jaws and help him over the obstacle.

Visual recognition by both mother and pup seems to play no role, especially on the pup's part. Pups in good condition are sometimes found with their eyes completely gummed up and even encrusted with feathers from moulting penguins. Pups may respond to any female calling, and indeed, by simulating a pup-attraction call, one can elicit the same response from pups and even lure them up a beach. This is a method successfully employed to determine whether pups are present on a beach apparently devoid of them. As in *A. forsteri* (Stirling 1970) and *A. tropicalis* on Amsterdam Island (Paulian 1964), olfactory stimuli apparently constitute the most important cue by which a female recognizes her pup. Vocalizations serve in the location of a pup in *A. tropicalis,* with olfaction used for final confirmation.

General intraspecific behaviour

INTRASPECIFIC BEHAVIOUR INVOLVING SUBADULTS

Subadult *A. tropicalis* frequent especially east coast sites in large numbers during the breeding season (Table 6). The majority of subadult males, when located on the waterline and especially on exposed areas of the beach at low tide, but not when hauled up the beach, almost incessantly play fight. By contrast subadult females are restricted by the herding activities of adult, as well as large subadult males.

When subadult females are present frontline males as well as males further up the beach, endeavour to gather subadult females into their areas of influence. Since under conditions of e.g. high ambient temperatures these subadult females shuttle between the beach and the waterline, the males have a busy time containing these ever changing groups of females. The males usually try to herd them under larger rocks or rocky ledges which provide a means of easier control over the subadult females. They are however never successful and the number of subadult females in the aggregations fluctuate remarkably. Males on the waterline may also try to actively gather females into their territories and occasionally a male is seen raiding groups of subadult females located in the surf zone and endeavour to haul one towards him by biting her in the rump. This was never successfully performed since the male always abandoned the effort in order to herd the subadults already within his territory.

Sometimes cases of mistaken identity occur and an adult male will herd small sized subadult males in his territory. However, on the discovery of a subadult male in his territory the male would either chase him away or grab him by the rump and fling him away as well as sending him on his way with open-mouth guttural threats. Larger subadult males are, however, wary of their adult counterparts and usually give them a wide berth. Even when a subadult male passes an adult male at a considerable distance it would either glance at him or give an open-mouth submissive display if the latter makes the slightest movement towards him. Territorial male *A. tropicalis,* as in *A. forsteri* (Miller 1975b), are more responsive towards large subadult males than towards small ones. Whilst a large subadult male trespassing is immediately challenged, small subadult males are more or less tolerated in the vicinity of an adult male. However, occasionally he may get irritated with them, especially if they move in amongst subadult females within his territory. Under such circumstances an adult male, from a lying position or sitting up, would whicker at the subadult males, give an open mouth threat or charge them to chase them off. Gentry (1975) stated that male *A. forsteri* rarely gave a boundary display towards subadult males and this holds true for *A. tropicalis* in the present study. A large subadult male that do not move off immediately is chased, usually for a short distance, after which the adult male returns whickering to his former position. However, large subadult males occupying territories vacated by territorial males at the end of the breeding season may put up a token resistance towards an adult arriving or an adult neighbour. However, when hard pressed he flees the newly acquired territory.

Subadult males are rarely seen sporting wounds, which accentuates the observation that they are completely submissive to adult males, and therefore they rarely, if ever, stand their ground in conflict with an adult male. However, occasionally subadult males may receive extensive wounds in encounters with adults, where the latter disregard the subadult male's submissive displays. An approximately three year old subadult male succumbed to a bite from an adult male who tore all the skin off around his left front flipper. Only adult males have the strength to inflict such a wound since subadult males in conflict were never observed to inflict damage.

In general, even at nonbreeding sites, the larger subadult males are located higher up the beach and especially on peaty or vegetated areas if available, and they also frequent accessible tussock clad slopes behind beaches. Subadult *A. tropicalis* also tend to follow stream beds inland e.g. at The Glen and Seal beach (Fig. 1) as in subadult *A. gazella* (Bonner 1968). However, on Gough Island such areas are of limited size only, and are usually available only up to the first waterfall. At the back of nonbreeding colony sites, especially if the beach is wide, subadults are interspersed with non-territorial adult males. At breeding colony sites subadults may occur on the lateral fringes, especially if these areas constitute a habitat type not tenable for adult females and their pups.

Subadults often indulge in play-fighting and in all respects thus simulate fights observed between adult males. However, in play-fighting bouts physical contact is the rule and although initially an encounter between two subadults may start off in the form of boundary displays as exhibited by adults, these culminate in a contest of physical strength without the ferocity characterizing adult male contacts (Fig. 52). As concluded by Stirling (1970) for *A. forsteri*, these bouts between subadults must play a role in the gaining of experience that may be used in later years in the procurement and maintenance of territories, and thus breeding success. In *A. tropicalis* herding behaviour to contain females on a territory is also found in subadult males. If the idea of Miller (1974) is accepted, this serves to communicate the characteristics of a male to a female. In this respect it is apparent that subadult males, even the small size category, indulge in herding activities directed at subadult females, and also occasionally at pups whatever their sex may be.

Precocious copulatory play (after Rand 1967) between subadult males are occasionally seen. This involves one of the partners in an encounter between subadults working its way round to the back of the other trying to mount it. This, however, usually happens when e.g. three subadults are interacting and one tries to mount the other while the latter is otherwise engaged.

When subadults have access to pups they may exhibit inquisitive behaviour. For example, a pup that wandered off onto a hauling ground was located there by his mother. However, a large subadult male chased her away, but she returned, picked the pup up and moved him a short distance. The subadult male once more got up, chased the female away and subsequently lifted the pup in his jaws and carried the pup to his (the male's) former position where the male proceeded to play with the pup, nipping at it, and frequently picking the pup up in his jaws. The female, trying to retrieve her pup, was chased away once more. Eventually the pup moved off when the subadult male lost interest in it. On at least two other occasions were subadult males seen to grasp a pup by the back, and in an alert posture, swing it to and fro in the air, putting it down and herding it when the pup wanted to move away.

Subadults do not only interact with pups in idle curiosity, but also presumably in the context of release of aggression or redirection of a particular behaviour pattern. For example, two subadult females may threaten each other, the one biting a neighbouring pup in the rump between threats. Moreover, a subadult male may herd pups after collecting them in the jaws and move them into a position where he can watch them. The fact that on one occasion both pups thus herded proved to be males did not deter the subadult male. Subadults may also bite pups that try and solicit suckling from them, however, persistent pups easily drive them off.

ADULT FEMALE INTERACTIONS

Adult females are normally aggressive towards one another, especially when the numbers of females are high on a rookery. On the two breeding colony study areas this also coincided with the time when the last pups were already born. When female numbers are high on a beach, a female hauling from the sea often have to contend with more interference from adult females on the site than from the herding activities of adult males.

Females also occasionally bite a neighbouring female in the rump when the latter is herded too close to them by the territorial male. As in female *A. forsteri* aggregations (Gentry 1975), female *A. tropicalis* do not permit other females too close and therefore these aggregations of females are spaced out (Fig. 59). This seems to be the case for all *Arctocephalus* species with the exception of *A.p. doriferus* (Stirling and Warneke 1971). In *A.p. pusillus* (Rand 1967) this spacing is prominent after the arrival of the females, but it generally disappears by the time the females settle down to suckle their pups. In *A. tropicalis,* however, a female returning after a short excursion to the sea may find that another female has usurped her place. The owner threatens the encroaching female and without fighting, dislodges her. This is therefore similar to the displacement behaviour of adult males directed at females. Females were never

FIGURE 59 : Adult females spaced out at a breeding colony site through inter-female aggression

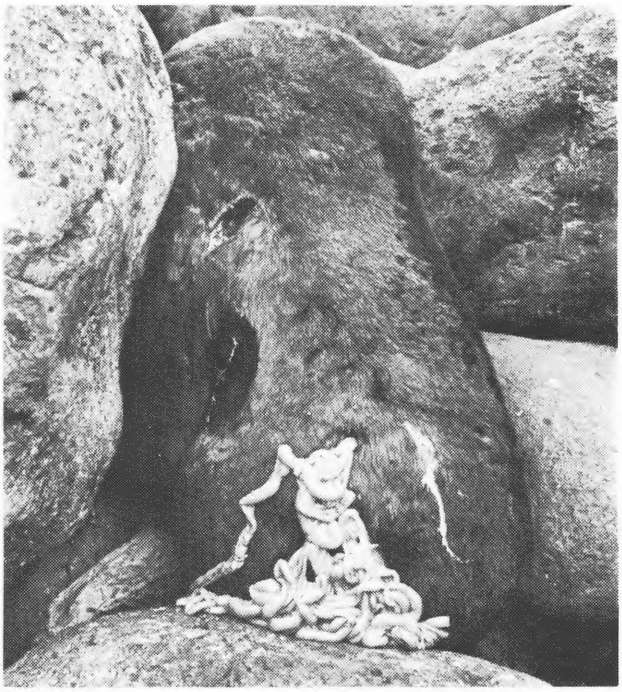

FIGURE 60 : Adult male carcass scavenged by giant petrels, *Macronectes* species, and brown skuas, *S. skua*. Note the wounds around the front flipper and on back, sustained in intrasexual fighting, through which the birds gain access to the soft body tissue beneath the tough pelt

observed to actually fight and disputes are settled by threats alone and at the most include bites at each other.

BEHAVIOUR OF ADULT MALES TOWARDS PUPS

Adult males pay little attention to pups, although pups may scatter at the approach of a male or move out of his path when he chases an adversary. However, occasionally an adult male may also threaten a pup involved in an aggressive interaction with a female or when the pup steps on his injured flipper. On three occasions adult males were observed to pick up a pup after an interaction with another male and this may be related to release of aggression or a displacement activity.

Pups may adopt an aggressive attitude towards a male, e.g. a male chasing a trespasser may come to a standstill in front of a pup not quick enough to move out of the way. In one instance the pup seized the male low down in the chest pulling and worrying at the point of impact. However, the male paid no attention to the pup and went on his way back into his territory.

BEHAVIOUR AMONGST PUPS

Inter-pup behaviour in *A. tropicalis* is similar to that described for other *Arctocephalus* species (Rand 1967, Stirling 1970 and 1971b) and *A. tropicalis* on Amsterdam Island (Paulian 1964). In short it involves the increased association of pups with one another as they grow older and this culminates in the formation of pods at the back of the beach. The expression of aggressive behaviour and play-fighting with associated postures also increase with age. An account of pup behaviour has already been given (see annual cycle).

Interspecific relationships

A. tropicalis shares its island habitat with only one other pinniped, the southern elephant seal, *M. leonina.* However, there is a distinct temporal and spatial separation between the two species as discussed above and the influence of *M. leonina* on *A. tropicalis* on the island is minimal.

Rockhopper penguins, *Eudyptes chrysocome*, breed in large numbers on the island but their nesting sites are mostly well set back from the parts of the beaches utilized by the fur seals. These nesting sites occur on the steep tussock clad slopes as well as peaty areas raised above the general level of the beach. Some disturbance to the birds are caused by especially subadult *A. tropicalis* wandering into the fringes of such nesting colonies, although the aggressive behaviour of the penguins keep the seals out of their nesting sites. On the other hand a steady stream of *E. chrysocome* move through seal colonies on their way to and from the sea. However, they cause little disturbance to *A. tropicalis*, in fact, the seals almost completely ignore them. It can often be observed that penguins dam up next to an adult male blocking their path. They then proceed to jump onto him, one after the other, and off on the other side without being molested by him. A penguin may even jump onto an adult male and almost walk his complete length before jumping off. The male may look up or whicker at the offender, but more often than not no response is elicited from him. Rarely would a subadult sniff at a penguin and sometimes they would bite at the bird without causing any damage. However wounded penguins are sometimes found, probably as a result of the seals biting them. Swales (1965) e.g. saw a male *A. tropicalis* catch and kill a rockhopper penguin at Gough Island, but he did not eat it. Neither do *A. tropicalis* on Marion Island eat penguins (Rand 1956), although their counterparts on Amsterdam Island exhibit this behaviour (Paulian 1964).

Giant petrels, *Macronectes* species, and brown skuas, *Stercorarius skua*, frequent the beaches to feed on fur seal carcasses (Fig. 60). Only *S. skua* were observed to scavenge placentas and feed on dead pups. Being more mobile than *Macronectes*, skuas are often observed scavenging at jumbled rocky beaches of breeding colonies, whilst giant petrels were only seen on open boulder beaches. *A. tropicalis* pay little attention to these birds and only occasionally would an adult female threaten a skua that ventures too close.

The introduced house mouse, *Mus musculus*, are also found on the beaches and may feed on dead seals since they were noticed amongst the boulders on which a dead seal lay.

None of the animals associated with *A. tropicalis* parasitize the fur seals and function only as scavengers or use the beaches as a through fare *(E. chrysocome)*.

Whereas interspecific relationships between *A. tropicalis* and other animal species they come into contact with on land are one of indifference, human interference results in major disturbances on especially nonbreeding colony sites (stampedes). During the rut adult males at rookeries, however, defy human presence. Disturbance created by human intruders is an occasional occurrence and chiefly limited to the few beaches around the meteorological station (Fig. 1).

CONCLUSIONS

The Gough Island fur seal population has recovered markedly since 1829 when sealers reported that the island, which used to abound with seals, was abandoned by them (Swales 1956). At present the entire stock of *A. tropicalis* at Gough Island could comprise 100 000 animals and this represents the largest single population of this species. This remarkable increase in the fur seal population is probably the direct result of the absence of commercial exploitation.

There is a marked segregation of the different age and sex classes into breeding and nonbreeding colonies, although all available beaches are occupied by the fur seals during the austral summer and autumn. These colonies also show a different distribution pattern, with breeding colonies predominating on westerly beaches whilst nonbreeding colonies are found on beaches in the eastern sector. This distribution pattern results from the topography and physical nature of the beaches on the south-west coast being less restrictive to breeding seals. The only requirements are ease of access from the sea, sufficient protection from high seas as offered by a wide beach, a seaward fringe of larger rocks, possibilities to move onto adjacent higher ground or to the back of the beach, the protection of headlands or combinations of the above. On the east coast, however, the habitat types as such are a limiting factor and only those which provide shelter also from high ambient temperatures and solar radiation are used by breeding seals. On the south-west coast this is not a prerequisite since the spray-laden predominantly westerly winds aid in alleviating heat stress of land-bound fur seals. The present local distribution of *A. tropicalis* breeding colonies is therefore considered to be a behavioural characteristic of the fur seal in the absence of an effective physiological response to heat loading (exogenous and endogenous). The presence of the southern elephant seal *M. leonina,* because of their low numbers and different beaches occupied, does not influence the local distribution of *A. tropicalis.* Neither does human interference at present, although this may have been the case initially after exploitation ceased.

Since 1955/56 an increase in the number of breeding sites has taken place, presumably as a result of the marked population increase. The increase in population size has also resulted in small isolated breeding colonies being established on the east coast where they are located on parts of the coastline favourable as far as topography, physiognomical characteristics and also prevailing weather conditions are concerned. This process of breeding site expansion is by no means complete.

A. tropicalis numbers ashore increase dramatically during early summer, and high numbers of seals are present for the duration of the summer and autumn. However, the majority of fur seals are absent from the island during winter. The reason for this movement away from colony sites during winter is obscure although it is documented for other pinniped species as well. Miller (1974) postulated that the summer's rigid territorial social system, the extreme sexual dimorphism in size and the high levels of intra-male aggression could be incompatable with year-round residence at colony sites of adults of both sexes. Carrick *et al.* (1962) and Peterson (1968) considered it likely that environmental conditions e.g. food supply and weather conditions influence the annual cycle of pinnipeds and that the regular seasonal variation in day length might provide the cue that permits synchrony (Peterson 1968). Any one or all of the above may determine the annual cycle of *A. tropicalis* at Gough Island.

The summer haulout in *A. tropicalis* is characterized by two peaks in numbers ashore with the first peak during December, i.e. the breeding season and with the second peak during March/April which represents the maximal haulout for the moult. Pupping and mating occur during the breeding season although the mating season extends over a longer period of time than the pupping season. Furthermore adult female numbers ashore peak after the last pups are born, showing that at least some of them are nonpregnant. This is especially true for east coast breeding colonies where subadult females, representing the presumably nulliparous receptive female class, also locate themselves. The reason for this is obscure but this may represent a movement away from crowded breeding colony sites elsewhere on the island. These females may represent ones impregnated elsewhere during the current breeding season, or females that have lost their pups at established breeding colony sites. Data are needed from the latter colony sites to validate the trend in late breeding season haulout of nonmothers.

Adult male, adult female and the smaller size category of subadults show the same trend in numbers ashore during the breeding season whereas the older subadult male numbers decrease during the time of peak attendance of the other age and sex classes. This results from the exclusion of these subadult males from the territories of territorial males, as well as from the immediate vicinity of non-territorial males. Furthermore, the animosity of territorial males results in the exclusion of all other males inferior to them and which could represent a threat to their territorial status. As a result these subadult males are located away from breeding colony sites or on the fringes of rookeries during the breeding season. Since mate choice by female otariids is to some extent precluded by the intensity of competition amongst adult males (Miller 1975b) and which results in low genetic variance amongst them, the exclusion of males incapable of holding territories during the breeding season would result in the dominant territorial *A. tropicalis* males contributing largely to the gene pool. This may promote mating success and may also favour seasonal synchrony in pupping and copulation by females (Miller 1975a) and could therefore be a determining factor in the annual cycle.

Yearlings are absent from the island for the duration of the breeding season, after being weaned just prior to the onset of it. Their departure is presumably related to a feeding trip before returning for the moult haulout.

The moulting peak in numbers ashore suggests that the fur seals haul out to moult on land although this is no prerequisite since the moult is a gradual one without the pelage losing its insulative capacity. Also moulting postparturient females return periodically to sea to feed to enable them to sustain their pups. Furthermore, Ling (1970) considered the pelage cycle to be closely related to the annual cycle in mammals with respect to "seasonal requirements dictated by the environment, such as climate, and life processes, particularly reproduction". Although hair growth and moulting are established before sexual maturity they are, nevertheless, co-ordinated with respect to season and may, furthermore, be influenced by nutritional status, temperature, and behaviour. In this study the above requirements are met during the period February to April/May as shown by the increase in seal numbers ashore.

The present study showed that the influence of weather modifies the effect time of day may have on the number of seals ashore. Furthermore the state of the tide, sea conditions, the status of a colony (breeding or nonbreeding), time of season, etc. may all influence the diurnal pattern of *A. tropicalis.* However, the attainment of maximum or near maximum numbers ashore during the afternoon, in conjunction with the increased hauling rate during the morning, suggests that *A. tropicalis* haul out during the day to rest and that feeding is done at night similar to *A. forsteri* (Street 1964; Stirling 1968) and some other species of pinnipeds (Mathisen and Lopp 1963; Smith 1965) but different to *A.p. pusillus* which feed during the day (Rand 1959).

Although much more data are needed before correction factors can be applied to daily censuses, the following may be provisionally followed: on warm clear days, mid-afternoon counts must be adjusted to allow for an eight per cent undercount, but during mid-day this value increases to 34 per cent. Afternoon counts on cool cloudy days can be accepted at face value whilst morning censuses under similar conditions must be adjusted to allow for a maximum undercount of 20 per cent. These correction factors apply specifically to nonbreeding colonies of *A. tropicalis* in the present study.

Under natural conditions the single most important threat to a seal's ability to remain hauled out on a beach is undoubtedly excessive heat input and endogenous heat production through activity in the absence of water for cooling. It appears that *A. tropicalis* at Gough Island cannot thermoregulate effectively without making use of postural and behavioural adjustments to either escape heat loading or to facilitate its dissipation to the environment. For this reason inactivity, an obscure behavioural adjustment considering thermoregulation, may be important in the ability of especially a male with territorial obligations and without access to water for cooling, to maintain his position on the beach by reducing the endogenous heat production. These are the reasons why all age and sex classes of *A. tropicalis* spend, on average, between 76 per cent and 96 per cent of their time in an inactive state with activity depressed at high ambient temperatures. Furthermore, a high activity rate is associated with seals in the surf zone or close to free water.

Activity levels as determined for breeding and nonbreeding colonies alike vary between different age groups with adult males, presumably less heat tolerant than the subadults, showing the highest inactivity rate whatever their status (6,65; 4,60 and 6,65 per cent of time spent active for territorial males, males at nonbreeding colony sites, and idle males respectively). The subadult class, especially the younger age category, is the most active and since they do not participate in breeding and have no territorial obligations, can readily move to the surf zone and sea when experiencing excessive heat loading.

The activity level may also vary with the time of season since in *A. forsteri* frequency of encounters between territorial males was greatest during the time of territory establishment than the period thereafter (Stirling 1971a). The activity level varies with the population size (density) on a particular site; is correlated with the hauling-out and departure pattern of seals when frequent contact is made between seals traversing the colony site, and therefore also related to time of day. Furthermore, the level of activity in individual seals may vary with their location on a site with e.g. those on the waterline coming into contact with more individuals hauling onto or departing from the site. The level of activity within a colony may also vary with the age/sex composition of the colony and environmental conditions, notably rain, solar radiation and prevailing ambient temperatures also modify the activity level of a seal colony. Disturbance within the colony resulting from single important events at least temporarily increases the activity level through chain interactions within the colony.

Considering all the abovementioned modifying factors, it can be concluded that the activity level of the fur seal *A. tropicalis*, is an ever changing phenomenon which mask any constant rhythm which may be an innate aspect of a seal colony's behaviour. Also contrary to the first impressions gained of the seemingly perpetual activity in the *A. tropicalis* colonies, a high level of individual inactivity prevails.

Territoriality in male *A. tropicalis* shows a change in degree of intensity during the austral summer with territorial behaviour not intense during the early breeding season. Rigid territoriality becomes evident when adult females start arriving and their presence is therefore the stimulus for this behaviour which is maintained throughout the peak period of adult female attendance. A decrease in intensity of territorial behaviour occurs presumably when the number of oestrous females decline since some males relinquish their territories even before the peak in adult female numbers is reached. However, territory maintenance behaviour may tax an adult male's energy reserves since territorial males do not feed during the period of their territory tenure, and may force them to return to the sea to feed. The above therefore results in a territory tenure of approximately six to seven weeks.

A. tropicalis males occupy five different types of territories that differ in their location on rookeries and other colony sites, differ in seasonal timing of formation as well as in their permanence and success in attracting females. Frontline territories are first established probably because they are situated close to the waterline with its favourable micro-climate. Since males of territorial status show good timing in arrival to claim territories (± a week before the arrival of the first females) and females are intercepted here when they haul onto the beach, it may also influence the males in selecting these territories. Inland territories are usually formed subsequent to frontline territories, are also formed before the arrival of the adult females, and result from lack of undefended space remaining on the waterline. Back fringe territories are found at the furthest points from the sea, and are formed upon the arrival of females there. Depending on circumstances they may have more females located on them later in the breeding season, than all other types. Seaward and inter-tidal territories are established in the mid-breeding season as a result of the lack of unclaimed beach space but also probably as an urge to be close to the sea although these generally are unsuccessful in attracting females. These territories are of a temporary nature as well as ill-defined since the rise and fall of the tide determines its size and it may be non-existant during storms. The occasional frontline territories observed on hauling grounds are formed when usually single females haul out away from pupping colonies. These are normally shortlived since they occur on a habitat type not preferred by adult females and furthermore females are attracted to sites where other females are present.

Male *A. tropicalis* as a rule clearly delineate their territories but this is subject to topographical definition. Furthermore, territories may vary in size and shape according to the topography of a beach, its location on the beach as related to the waterline, as well as time of season and the status of a colony within which they are established. The effective space available for territorial demarcation vary with the topography of a beach and this influences the number of territories that can become established. As in *A. gazella* (Bonner 1968), visual clues in the demarcation of territory boundaries seem to play an important part in adult male *A. tropicalis*. Pathways of least resistance are recognized and utilized in an effort to avoid territorial male aggression when a back fringe male hauls or departs from the colony sites The limited number of males which may use these, depending on opportunity, deviates from the norm.

True fighting is correlated with the initial procurement of a territory. Boundary threat displays suffices thereafter to maintain an established territory as well as to advertise a resident male's territorial status and the extent of his controlled area. Overall physical contact involving biting is infrequent and in interactions across territorial boundaries it occurs more often when females are involved than otherwise. On the other hand most interactions result from the departure and hauling-out of adult males emphasizing the need of an adult male to exercise his territorial rights, and would even forfeit a female in favour of defence of his territory. This presumably indicates that the possession of a territory signifies access to females and seems to be the primary aim in territory procurement and maintenance. Comparatively few encounters result in a territory changing owners, considering the total number of interactions occurring on a colony site where territories are staked out. Boundary interactions in the present study always result in stalemate being reached confirming that this type of interaction is no dispute but rather a means of communication between neighbouring territorial males. Furthermore, the development of threat vocalizations and displays culminate in the minority of intrasexual encounters being resolved without physical contact and may be directed at the conservation of stored energy as pointed out by Stirling (1971a) for *A. forsteri.*

Fighting is ritualized, especially as a fight progresses and is directed at the physical displacement of the opponent out of a territory with biting an ancillary contribution. The outcome of a fight hinges on size and physical strength, and expertise in inflicting a painful wound. It is evident that the less protected areas of an adult male's body are prone to extensive damage. This in particular applies to the face, flipper areas and the back and rump. Common wounds here involves eye loss, deep gashes around the flippers and even areas of skin and underlying tissue being torn off the rump. The flipper areas are most sought after to inflict damage and a holdfast gained here gives a male considerable advantage and can be the direct result of the termination of a fight. Furthermore, the advantage thus gained weighs heavier than the neck being undefended at such a time. The posterior location of wounds, especially those on the rump, is not directly related to fighting since this area is usually out of reach of an opponent in the face to face oriented contests. These wounds are associated with subdominant males temporarily trespassing on territories as well as those defeated in a fight. As observed, such males are often bitten in the rump when fleeing or when passing a territorial male.

Boundary displays follow a predictable pattern and are not normally intended to inflict damage, and are therefore used in a different context as discussed elsewhere. Group aggression is a common occurrence but do not culminate in even temporarily ignoring territory boundaries by neighbouring territorial males. Submissive behaviour commonly exhibited by temporary trespassers, serves as an appeasement but do not safeguard them against injury. Territorial males never exhibit this behaviour when on site of their established territory, unless defeated in a fight.

Adult male:female interactions are characterized by the high incidence of herding and crowding responses, with by far the most numerous interactions directed at olfactory investigation of the female by the male. Herding responses are directed at the containment of a female(s) within a male's territory, whilst crowding of the female has an obscure value, probably related to a communicative function whereby the male advertises himself to the female. Olfactory investigation relates to the male's assessment of the female's reproductive condition and therefore occurs more often than any other male:female contacts. As the austral summer progresses males often show only passing interest in some females whilst others are frequently the object of a male's attention, presumably since they are approaching the oestrous phase. Since female *A. forsteri* were sexually receptive only for a brief period of oestrous which lasted up to approximately 24 h (Miller 1974), and this presumably also applies to female *A. tropicalis*, the high incidence of assessment of a female's reproductive condition by the male must play an important part in the successful fertilization of a female.

Displacement and peacekeeping behaviour form a very low percentage of male:female encounters, are essentially the same as described for other Otariidae, and relate to the seeking of a preferred location on the territory by a male, as well as a response to heightened activity. Vocal and visual contact are related to non-physical herding responses which may culminate in herding if the female does not positively react to it.

Copulation represents the lowest percentage of the total number of male: female interactions recorded although this is the ultimate aim of a territorial male in intersexual relationships.

The behaviour expressed in male:female interaction is stereotyped in the sense that especially overt aggression from the male is usually reciprocated by submissive behaviour from the female. Females rarely exhibit explicit antagonism towards the male and female aggression towards the male usually has undertones of submissiveness. Unprovoked female antagonism towards territorial males is rare. This contrasts markedly with other *Arctocephalus* species and is probably related to the uncommonly brutal way in which an *A. tropicalis* male may deal with a female e.g. when persistent in leaving his territory.

Female aggression towards one another as well as towards strange pups is the rule, resulting in at least discreet distances being kept between females and probably precludes forster suckling. The latter will have survival value for a pup when his mother is in attendance since it is unlikely that a female could nourish two pups until weaning. A pup could, therefore, derive maximum benefit from his mother's milk supply whilst she is present on the rookery.

Female recognition of her pup is ultimately determined by olfactory means and all other pups presumably rejected, often violently. Female:pup behaviour in general follows the pattern found in other *Arctocephalus* species (Rand 1955; Paulian 1964; Bonner 1968; Stirling 1970) with the violence elicited from females by strange pups a pronounced feature in *A. tropicalis* at Gough Island.

Adult males generally ignore pups and never treat them with overt aggression. Whilst adult males involves themselves with pups probably as a re-direction of a specific behaviour pattern, subadult attitudes towards pups are usually ones of curiosity, but may include herding responses which is a characteristic behaviour pattern even in young males directed at especially young females. This herding behaviour and playfighting bouts between subadults apparently play an important role in the maturation of their behaviour patterns and experience gained may be used to good effect in adult years. This also applies to play-fighting amongst pups which exhibit behaviour similar to that described for pups of other *Arctocephalus* species.

Interspecific relationships on land are of little importance with the threat of human interference of no consequence owing to the paucity of it at present.

SUMMARY

This study on the Amsterdam Island fur seal *A. tropicalis* at Gough Island (40°20'S, 9°54'W) was undertaken during the austral summers of 1974/75 and 1975/76 to acquire basic knowledge of this little known species.

The study population was classified into different age and sex groups. A description of external characteristics is provided for future use in field identification. Beaches were classified according to their topography and structure, and the study population into colony types according to their age and sex specific composition during the breeding season.

A census of part of the coastline showed that all beaches were occupied by *A. tropicalis* during the austral summer and autumn, and that the present day population numbers an estimated 100 000 animals. The characteristic feature of their local distribution is the presence of predominantly nonbreeding colonies on the east coast and breeding colonies on the west coast. An expansion of breeding colony sites and a vast increase in fur seal numbers are evident from comparison with a previous study done by the Gough Island Scientific Survey in 1955/56 (Swales 1956).

Factors influencing the local distribution of *A. tropicalis,* in particular the distribution of breeding and nonbreeding seals, are the topography and physical nature of the beaches, ambient temperatures and solar radiation, sea conditions, and exposure to wind and sea spray.

The annual cycle of *A. tropicalis* shows a rapid increase in numbers for the austral summer and autumn, with only a fraction of these present during winter. The outstanding feature of the summer and autumn haulout is the presence of a breeding season peak ashore during December, as well as a moulting season peak during March/April. The latter is a hitherto undescribed feature of *Arctocephalinae* seasonal haulout and departure behaviour.

Adult males and females, and subadults excluding the larger sized subadult male group (SAM), show similar trends in their haulout and departure during the breeding season. Subadult male (SAM) numbers are inversely related to adult male numbers. Pupping is synchronized, the majority of pups being born during mid-December for both breeding seasons studied. Adult female numbers peak later than adult male numbers and after the pupping season, showing that non-pregnant females contribute to this phenomenon.

The diurnal haulout pattern of *A. tropicalis* at nonbreeding colonies results in maximum (or near maximum) numbers being hauled out during the afternoon, and suggests that feeding is done at night. Climatological factors have a pronounced effect on the hauling-out and departure pattern, and correction factors for adjusting seal counts with respect to time and circumstances of counting are provided.

Activity patterns in *A. tropicalis* colonies during the breeding season vary substantially between the different age and sex groups. Adult males show very low activity which can be related to a need to conserve energy as well as minimizing the possibilities of heat overloading. Subadults are the most active whilst seals in the surf zone or near the waterline where heat dissipation possibilities are favourable, are more active than seals on the dry zone of the beach. High ambient temperatures and solar radiation depress activity in a seal colony but increase the movement to and from the surf zone and sea. Prevailing weather and sea conditions, as well as single important events may also modify the level of activity of a colony of fur seals.

Behavioural and postural adjustments are utilized to supplement physiological means of thermoregulation, which alone are inadequate under extreme local temperatures.

A. tropicalis utilizes a variety of postures and vocalizations as a means of communication in inter- and intrasexual encounters, and these are developed at an early stage.

Adult males show a seasonal change in territorial expression with rigid territoriality exhibited during the breeding season at rookeries. Territorial males stay on average for 45 days (mean 45,4 ± 6,7, N = 15) on their territories.

Five types of territories exist which differ in their location on the beach, time of formation, duration of maintenance, and success in attracting females. Territories differ in size depending on their location on the beach, colony type within which they are maintained, and their topographical definition.

Fighting between males is ritualized, especially as a fight progresses, and only occurs when attempting to defend or procure a territory. Boundary displays on the other hand involve little physical contact and serve to advertise territorial status and fix territory boundaries. A variety of stimuli may initiate boundary disputes. These include e.g. intersexual activity, and temporary trespassing by males hauling and departing from the rookery.

Fighting is directed at physical displacement of the opponent and size, strength and expertise in inflicting a wound or obtaining a holdfast on the opponent are the important determinants in the outcome of a fight.

Adult male interactions with adult females mainly concern containment of females within the males' territories as well as assessing the females' reproductive condition. Crowding behaviour by the male presumably has a communicative function in advertising his characteristics to the female(s).

Female aggression towards the male usually has undertones of submissiveness, since territorial males may treat females in a brutal fashion when they have to contend with pronounced resistance from the females.

Females are good mothers, but react aggressively towards strange pups. Females employ olfactory means in final recognition of their pups.

General intraspecific behaviour is characterized by adult males ignoring pups except in the redirection of a specific behavioural response, curiosity shown by subadults when making contact with pups, inter-female aggression, play-fighting between subadults, and the herding behaviour of even subadult males directed at females.

On land, interspecific relations have little impact on *A. tropicalis.* The fur seals are temporally and spatially removed from *M. leonina* during the breeding season and the birds they come into contact with [illegible] act as scavengers.

OPSOMMING

Hierdie studie van die Amsterdameiland pelsrob *A. tropicalis* te Gougheiland (40°20′S, 9°54′W) is gedurende die suidelike somers van 1974/75 en 1975/76 onderneem om grondige inligting betreffende hierdie onbekende spesies in te win.

Die robbevolking bestudeer is in verskillende ouderdoms- en geslagsgroepe ingedeel. 'n Beskrywing van uitwendige eienskappe vir toekomstige toepassing in veldidentifikasie word voorsien. Strande is ingedeel na gelang van hulle topografie en struktuur, en die bevolking bestudeer is ingedeel in soorte kolonies op grond van hulle ouderdoms- en geslagspesifieke samestelling gedurende die teelseisoen.

'n Telling van die pelsrobbe op 'n gedeelte van die kuslyn het getoon dat alle strande beset was deur *A. tropicalis* gedurende die suidelike somer en herfs, en dat die huidige bevolking na beraming 100 000 diere behels. 'n Kenmerkende eienskap van hulle verspreiding ter plaatse is die teenwoordigheid van oorwegend nie-teelkolonies op die ooskus en teelkolonies op die weskus. 'n Uitbreiding van teelkolonies sedert 'n studie uitgevoer deur die "Gough Island Scientific Survey" van 1955/56 (Swales 1956), asook 'n veelomvattende toename in pelsrobgetalle sedertdien, is opmerklik.

Agente wat die plaaslike verspreiding van *A. tropicalis*, in besonder telende en nie-telende robbe, beïnvloed, behels die topografie en fisiese eienskappe van die strande, omgewingstemperature en sonstraling, seetoestande, en blootstelling aan wind en seesproei.

Die jaarlikse kringloop van *A. tropicalis* vertoon 'n snelle toename in getalle vir die suidelike somer and herfs, met slegs 'n breuk hiervan teenwoordig gedurende die winter. Die uitstaande kenmerk van die teenwoordigheid van die robbe gedurende die somer en herfs is die teelseisoen piek in getalle gedurende Desember, asook 'n verharingseisoen piek gedurende Maart/April. Laasgenoemde is tot dusver nie beskryf vir die seisoenale aankoms- en vertrekgedrag van die *Arctocephalinae* nie.

Volwasse mannetjies en wyfies, en onvolwassenes met die groter onvolwasse mannetjies uitgeslote, vertoon ooreenstemmende neigings in hul aankomste en vertrekke gedurende die teelseisoen. Getalle van onvolwasse mannetjies daarenteen is omgekeerd eweredig aan getalle van volwasse mannetjies. Geboortes is gereguleerd met die meeste van die welpies gebore gedurende middel Desember tydens beide teelseisoene wat bestudeer is. Getalle van volwasse wyfies bereik 'n hoogtepunt later as volwasse mannetjiegetalle asook nadat die laaste welpies gebore is. Dit dui aan dat nie-dragtige wyfies bydra tot hierdie verskynsel.

Die daaglikse aankomspatroon van nie-telende *A. tropicalis* het die gevolg dat die meeste (of byna die meeste) getalle gedurende die namiddag op land aangetref word. Dit wil dus voorkom asof die robbe gedurende die nag voed. Klimaatsfaktore het 'n besliste uitwerking op die aankoms- en vertrekpatroon, en korreksiefaktore vir die aanpassing van robtellings na gelang van die tyd en omstandighede van tellings, word voorsien.

Patrone in die bedrywigheid van *A. tropicalis*-kolonies verander aanmerklik tussen die verskillende ouderdoms- en geslagsgroepe gedurende die teelseisoen. Volwasse mannetjies vertoon 'n baie lae vlak van bedrywigheid wat in verband staan met 'n behoefte om energie te bespaar sowel as die vermindering van oorverhittingsmoontlikhede. Onvolwassenes is die meeste bedrywig terwyl robbe in die brandingsgebied of naby die water meer bedrywig is as robbe op die droë strand as gevolg van die groter moontlikhede van hitteverstrooiing. Hoë omgewingstemperature en sonstraling verlaag bedrywigheid in 'n robkolonie maar verhoog die beweging van robbe na en van die brandingsgebied en see. Heersende weers- en seetoestande, sowel as enkele belangrike gebeurtenisse, mag ook die bedrywigheidsvlak van 'n pelsrobkolonie wysig.

Aanpassings in gedrag en liggaamshoudings word gebruik as aanvulling tot fisiologiese hitteregulering wat op sigself onvoldoende is onder uiterste temperature ter plaatse.

A. tropicalis maak gebruik van 'n verskeidenheid van houdings en stemklanke as mededeling in tussen- en binnegeslagtelike ontmoetings, en dit is reeds op 'n vroeë ouderdom ontwikkel.

Volwasse mannetjies vertoon 'n seisoensverandering in mate van gebiedsafbakening en vertoon strenge gebiedswering gedurende die teelseisoen op teelkoloniestrande. Gebiedswerende mannetjies bly in hulle gebiede vir 'n gemiddelde tydsduur van 45 dae (gemiddeld 45,4 ± 6,7, N = 15).

Vyf soorte gebiede, verskillend in hulle ligging op die strand, tydstip van afbakening, tydsduur van instandhouding, en mate van sukses in aanlokking van wyfies, bestaan. Gebiede verskil in grootte afhangende van hul ligging op die strand, die soort kolonie waarbinne hulle in stand gehou word asook hul topografiese omlyning.

Gevegte tussen mannetjies, veral met die vordering van 'n geveg, volg 'n ritueel en geskied slegs in 'n poging om 'n gebied te verkry of te verdedig. Grensvertonings egter behels min liggaamlike aanraking en dien in bekendstelling van gebiedsweerbaarheid en die vaslegging van gebiedsgrense. 'n Verskeidenheid van prikkels mag grensvertonings inlei. Hierdie prikkels sluit byvoorbeeld aktiwiteit tussen geslagte in, asook tydelike oortredings deur mannetjies wat by 'n teelkolonie aankom of dit verlaat.

Gevegte is daarop gerig om deur liggaamlike aanraking 'n teenstander te verplaas, en liggaamsgrootte, krag en vaardigheid in die toediening van 'n wond of die verkryging van 'n houvas op die teenstander, is belangrike bepalende faktore in die uitslag van 'n geveg.

Wisselwerking tussen volwasse mannetjies en volwasse wyfies is hoofsaaklik ondernemings deur die mannetjies om die wyfies binne hulle gebiede te behou, asook om die wyfies se voortplantingstoestande te bepaal. Opdringingsgedrag deur die mannetjie het vermoedelik 'n mededelingsdoel om sy eienskappe aan die wyfie(s) te vertoon.

Aggressie jeens mannetjies deur wyfies het gewoonlik gedempte eienskappe van ondergeskiktheid aangesien gebiedswerende mannetjies hulle ru mag behandel wanneer hulle bestry word deur besliste weerstand vanaf wyfies.

Wyfies is goeie moeders maar reageer kwaadaardig teenoor vreemde welpies. Wyfies maak gebruik van hul reuksintuig om hul welpies beslissend te eien.

Algemene gedrag binne die spesies word gekenmerk deur die verontagsaming van welpies deur volwasse mannetjies behalwe wanneer laasgenoemde 'n bepaalde gedragsreaksie herrig, nuuskierigheid vertoon deur onvolwassenes wanneer hulle in aanraking kom met welpies, aggressie van wyfies jeens mekaar, speelgevegte tussen onvolwassenes, en saamhokkingsgedrag van selfs onvolwasse mannetjies teenoor wyfies.

Die verhoudings tussen *A. tropicalis* en ander diersoorte waarmee hulle op land in aanraking mee kom, het min invloed. Die pelsrobbe is gedurende die teelseisoen tydelik en ruimtelik verwyder van *M. leonina,* en die voëls waarmee hulle in aanraking kom, speel die rol van aasvreters.

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