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SOCIAL BEHAVIOUR OF THE NEW ZEALAND FUR SEAL ON OPEN BAY ISLANDS, WESTLAND

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SUMMARY

Systematic observations were conducted between August 1970 and June 1971 on a breeding colony of the New Zealand fur seal, Arctocephalus forsteri on Open Bay Islands, in Westland, on the West Coast of the South Island of New Zealand. Some specimens and comparative data were also collected on Kaikoura Peninsula, on the east coast of the South Island.

Ten specimens (6 males, 4 females) were weighed and measured. These included a full-term foetus.

The following aspects of population structure and behaviour are discussed and some are also illustrated by photographs: seasonal changes in population, sex ratio, distribution within the colony, social organisation and behaviour, activity budgets of territorial males, population and mortality of pups.

Activities observed included: "herding", birth, courtship, copulation, aggressive encounters, behaviour of pups and sub-adults.

INTRODUCTION

The objective of the present study was to examine the social behaviour of the New Zealand fur seal, Arctocephalus forsteri (Lesson), with emphasis on the role played by sexual dimorphism, and the relationship of social structure to thermoregulatory requirements and topography. This species, like all otariids, is polygynous and sexually dimorphic in size. It breeds in discrete, established colonies, is ashore in large numbers during the breeding season, and is readily observed. Territorial males fast while ashore, and normally do not leave their stations until defeated by challenging males or until the end of the breeding season. Their social contacts during the reproductive period can therefore be readily monitored. Individually recognizable animals are a requisite for successful field behaviour studies, and it was known from work on other species of otariids that many animals can be individually recognized by natural scars and marks, or can be approached and marked distinctively by a number of methods. Various reports on general biology and characteristics of New Zealand A. forsteri are available, but knowledge of the social system and details of social behaviour have heretofore had to be inferred from published facts concerning other species of fur seals and from general accounts of New Zealand fur seals. In this report, I present information on weights and measures, the annual cycle, population composition, and on general aspects of social organisation and social behaviour.

STUDY AREAS

Time spent in the field was partitioned as follows:

Kaikoura Peninsula (Sugar Loaf Point): 9-17 July 1970; Open Bay Islands (Taumaka): 17-24 August 1970, 27 October 1970 to 13 February 1971, and 26 May to 2 June 1971. Some seals were collected 13-15 October 1970 on the Kaikoura Peninsula and in October and November 1970 on the Open Bay Islands. Total time spent in the field was about 20 weeks.

1. Kaikoura Peninsula

Fur seals haul out on irregular limestone formations on the peninsula itself, and on adjacent reefs, and tend to avoid the available pebble beaches (Plate 1). Weather during the July visit was consistently cool, overcast and rainy and in October warm and clear. The Kaikoura coast is subject to the cool, low salinity water of the Southland Current, (R.A. Heath, pers. comm.). Annual fluctuations in sea water temperature off Kaikoura range about 7°C, but can show wide amplitude within much shorter periods (Heath, 1970).

2. Open Bay Islands

The tops of the two islands, Popotai and Taumaka, are covered with dense vegetation and their leeward limestone shelves are used by fur seals throughout the year. These sloping shelves, stretching from the forest to the sea, are broken up by guts and precipitous drops, but also feature extensive flat areas (Plate 2). Rough, boulder-strewn terrain close to the sea is preferred by fur seals.

The landward side of Taumaka is typified by highcliffs, but a few jagged large rocks are used by occasional resting seals. Off the north end of Taumaka lie some large, exposed reefs which are used by immature females, and by subadult and untenured adult males when the breeding rocks are occupied. One reef was used for breeding and the few territorial males there sometimes had their territories flanked by non-breeders. The other reefs were either awash during stormy weather, or were extremely precipitous with many sharp, jagged edges, and were relatively little-used. At low water, a large area of Hormosira-covered platforms was exposed, and channels running between reefs with associated platforms were heavily used by females with or without pups, subadult males, and in the late summer, lone pups.

Taumaka, where observations were made, is covered with a dense stand of kie-kie (Freycinetia banksii), with an edge of low dense forest consisting chiefly of Hebe elliptica, Schefflera digitata and Fuchsia excorticata. This forest is penetrated by fur seals up to a distance of 50 metres in places (Plate 3). On the north end of Taumaka is an open, grassy plateau used extensively by immature animals during the early summer, by females with pups and immatures in late summer, and by young males, females, and pups with and without females, in May 1971. No strictly defined territories impinged on this plateau, but the areas of influence of some territorial males extended onto the plateau and into the forest behind the breeding rocks.

The side of the island used for breeding is exposed to the prevailing winds, but many parts of the rookery are protected from wind and breaking waves. Only during severe storms is the wind forceful on the level of the rookery. During the summer of 1970-71, maximum and minimum air temperatures were recorded from a location immediately inland of the main study area. Temperatures varied from 6°C to in excess of 35°C, with warmer temperatures predominating after mid-December. Weather varied from clear and calm (especially in the last half of the summer) to windy and rainy. Weather during June 1971 was consistently overcast with frequent wind and rain.

The Open Bay Islands lie in a region of relatively warm water, subject to the influence of the Tasman Current (cf. Brodie, 1960 and Garner, 1961).

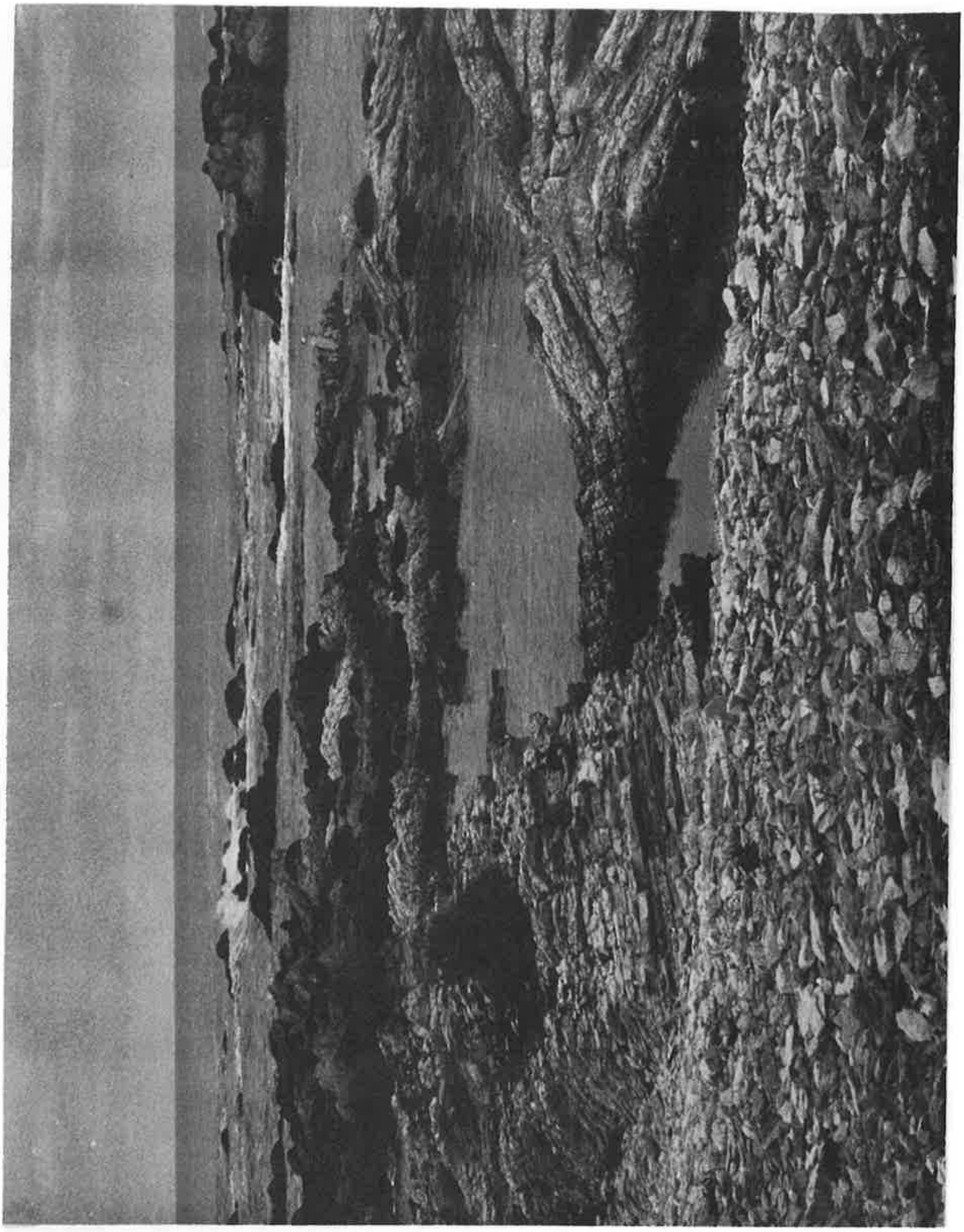


Plate 1 Partial view of Sugar Loaf Point, Kaikoura Peninsula, showing cobble beach (unoccupied foreground) and typical reefs used by resting and playing seals.

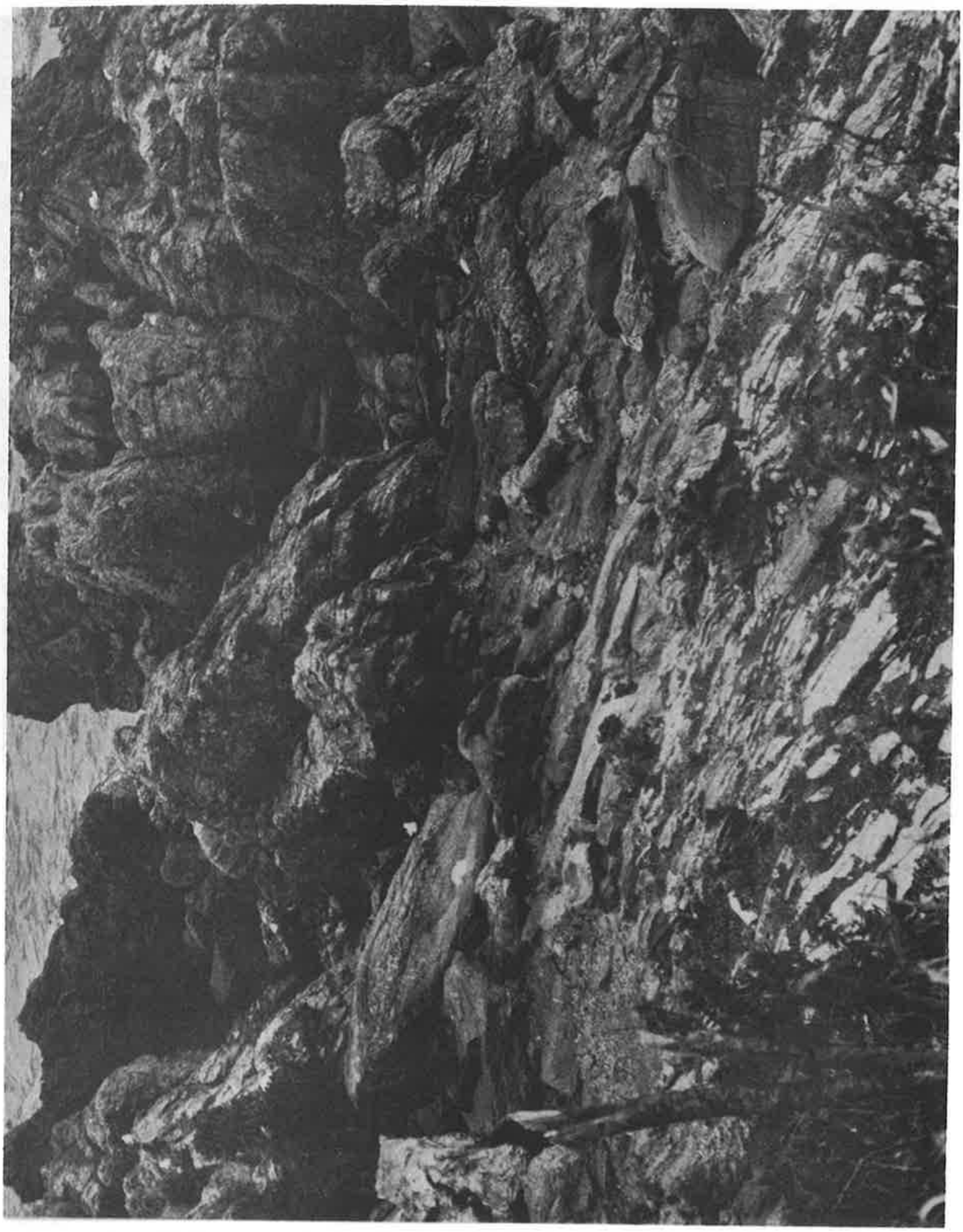


Plate 2 Partial view of breeding area, Open Bay Islands. Note the large boulders and rough terrain typical of *A. forsteri* breeding habitat.

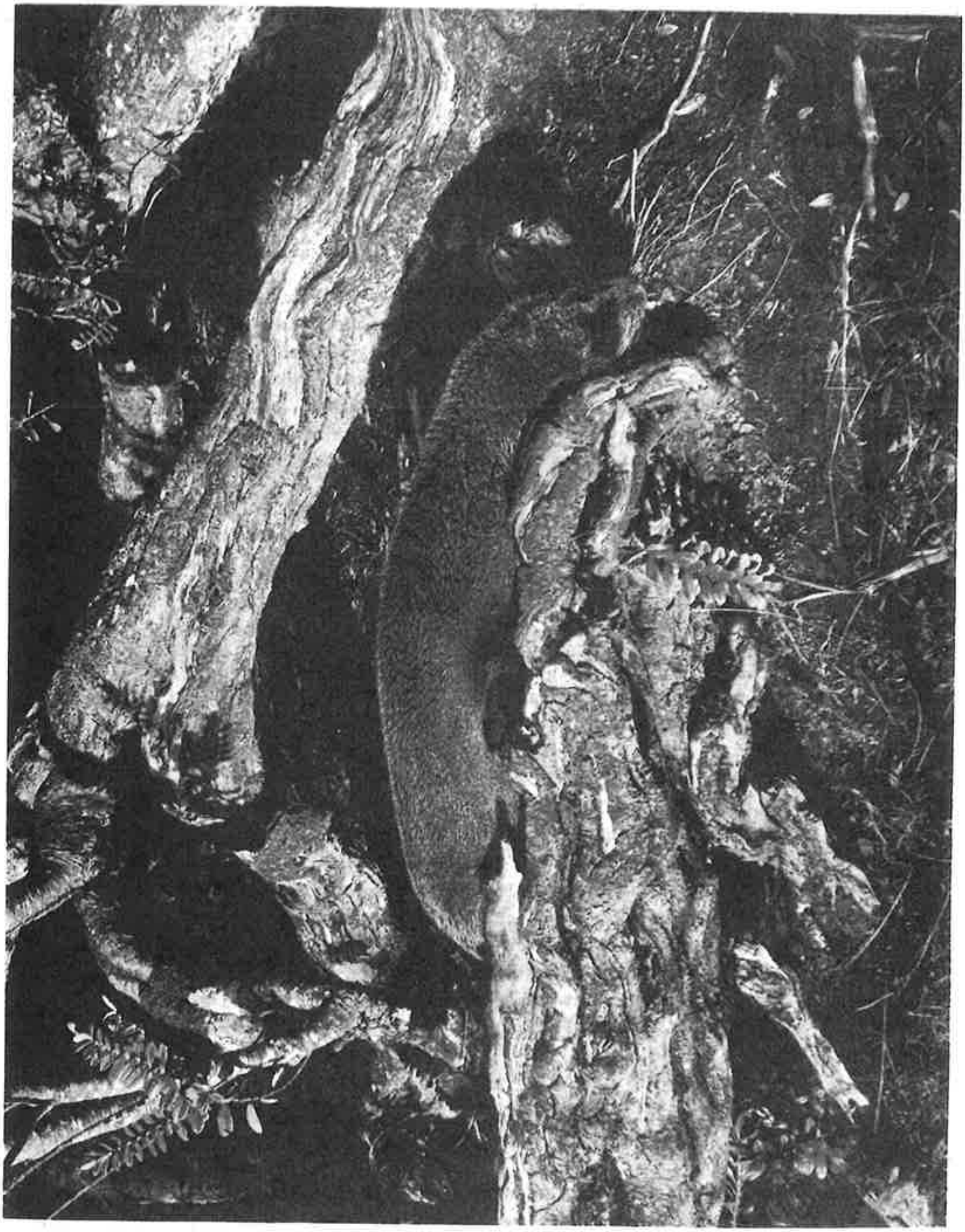


Plate 3 Approximately 6-month old pup sleeping in low forest (on trunk of *Hebe elliptica*), June 1971. Note how smooth the ground is, from seal activity.

METHODS AND MATERIALS

At Kaikoura, data were obtained on activity rhythms, dispersion on shore and reefs as related to body size, general social behaviours, and population size. Specific methods are discussed in appropriate sections.

During the 1970-71 summer on the Open Bay Islands, two study areas were chosen. A grid of squares (each of area 10 m^2) was painted on the main study area with durable bright orange house paint. This grid did not apparently alter the seals' behaviour. Using this grid plus topographical reference points, maps were prepared on which were entered census data, agonistic encounters involving territorial adult males, non-territorial adult males, and sub-adult males, arrivals on shore of males, copulations, births, "herding" efforts, and movements of individually recognizable seals.

All territorial males and many sub-adult males could be identified by behavioural and anatomical characters. Some yearlings had been previously tagged, or wounded, and were also easily distinguished. Fifteen pups were lightly marked with a bleach. Females, due to their shyness, were necessarily left unmarked, but some were distinguishable by anatomical characteristics. When an unknown and recognizable seal was seen, a written and graphic record was entered on a 12.5 by 20 cm file card, and the date, time, and location of observations entered on the other side. Subsequent sightings were made on the card and on maps of the study area.

During the winter field work on the Open Bay Islands, emphasis was given to determining the sex ration of seals present. Censuses of some areas were made, and habitat preferences were documented.

BODY SIZE

Ten specimens were weighed and measured (Table 1). There are few published records of weights of this species in New Zealand. Hector (1871) provided figures of 117 kg and 123 kg for two males, and 94 kg for a female. Thomson (1921) reported males exceeding 118 kg, and females ranging from about 90 to 100 kg. Weights for males of 117 and 123 kg were given by Clarke (1875); Clark's and Thomson's figures may have come from Hector's earlier published weights. In this study, the largest male (Kl) weighed 134.5 kg, and was rather small compared to territorial males observed during the subsequent breeding season. Adult males are heaviest in the early summer (Howell, 1930; Schusterman and Gentry, 1971), and male <u>A. forsteri</u> probably surpass 180 kg or so, at that time. The female weights reported by Hector and Thomson are suspiciously heavy. K2, an old female, weighed only 37.3 kg; young pregnant female OBI-3 weighed 34.8 kg without her foetus. Both specimens were of average size, and I seriously doubt that adult females commonly exceed about 50 kg in weight. By these estimates, a breeding adult male : adult female ratio of body weight for this species is about 3 or 4 to 1.

SEASONAL CHANGES IN NUMBERS AND POPULATION COMPOSITION

1. Kaikoura

Counts of seals on Sugar Loaf Point were greatest in mid-winter and lowest in mid-summer (Table 2). This trend agrees with that noted by Stonehouse (1965, 1969). There appeared to be a greater fraction of small males present in July than in October, but this is not substantiated.

Females haul out occasionally at Kaikoura. Non-pregnant female K2 was collected there in October 1970, and a still born pup was found on Sugar Loaf Point in September 1968 (G.C.B. Poore, pers. comm.).

Table 1. WEIGHTS AND MEASUREMENTS

Date of Collection	Locality of Collection	Code reference	Sex	CL[1]	CHG[1]	NG[2]	AFL[1]	AFD[2]	PFL[1]	CHB[1]	ABB[2]	Intestine length[3]	weight[4]	Weight skin plus blubber[4]	Comments
13 Oct/70	Kaikoura	K1	M	195	140	47	53	20	35	56	45	1950	134.5	45.5 (33.85)	Kidneys 400 g, 460 g
14 Oct/70	Kaikoura	K2	F	136	87	89	38	12	26	11	-	2005	37.3	6.4 (17.15)	
14 Oct/70	Kaikoura	K3	M	107	68	73	29	12	22	19	16	1260	19.5	4.5 (23.25)	
15 Oct/70	Kaikoura	K4	M	140	81	86	38.5	14	28.5	19	18	1459	35.9	6.8 (19.05)	Testes plus epididymes total weight 5 g; 21 x 45 mm and 19 x 50 mm
15 Oct/70	Kaikoura	K5	M	117	63	71	30	12	22	17	19	1164	17.3	4.1 (23.75)	Testes 10 x 20 mm and 10 x 20 mm
15 Oct/70	Kaikoura	K6	M	105	71	76	31	12	21	25	33	1319	19.1	3.6 (19.15)	Testes 18 x 22 mm and 18 x 23 mm
16 Nov/70	Open Bay I	OBI-1	F	97	57	62	26	8	19	12	10	-	32.0	7.0 (21.95)	Kidneys 73 g, 77 g, heart 124 g.
21 Nov/70	Open Bay I	OBI-2	M	90	52	54	24	9	19	13	15	-	20.5	7.5 (36.65)	Kidneys 75 g, 70 g, heart 52 g.
30 Nov/70	Open Bay I	OBI-3	F	124	83	88	34	12	23	20	-	1590	34.86	8.9[6] (25.55)	Kidneys total 250 g, heart 215 g.
30 Nov/70	Open Bay I	OBI-4	F[7]	62	33	34	18	7	13	1	3	-	4.3	-	

Table 1. continued

[1] CL = curvilinear length; CHG = chest girth; AFL = Length anterior flipper; PFL = length posterior flipper. Measurements correspond to recommendations by American Society of Mammalogists, Committee on Marine Mammals (1967). All lengths in cm.

[2] NG = neck girth, just anteriad the foreflippers; AFD = maximum antero-posterior measurement of foreflipper; ABB = thickness of abdominal blubber, measured as for CHB (see [1]). All lengths in cm.

[3] In cm.

[4] In kg.

[5] As % total weight.

[6] Weights with foetus removed.

[7] Foetus (full-term) of OBI-3.

TABLE 2. SUMMARY OF CENSUSES AT SUGAR LOAF POINT, KAIKOURA PENINSULA, 1970-71

DATE	TIME OF CENSUS	MAXIMUM CENSUS
10 July, 1970	1200	282
11 July, 1970	1550	357
12 July, 1970	0900	375
13 July, 1970	1110	307
14 July, 1970	1200	323
15 July, 1970	1200	301
16 July, 1970	1200	268
17 July, 1970	1000	284
13 October, 1970	1525	94
14 October, 1970	0830	160
15 October, 1970	0940	125
19 December, 1970[1]	-	7
8 March, 1971	1230	170
6 July, 1971[2]	-	550-580[3]
27 August, 1971	1000	156[3]

[1] Censused by M. Skeel.

[2] Censused by B. Hicks.

[3] Only censuses of day.

2. Open Bay Islands

(a) Breeding season

Early morning census figures for females, yearlings, and territorial males for the two study areas are plotted in Figure 1. Early morning censuses were preferred to evening censuses, because the former were consistently higher and less affected by the weather of the day.

Some territory-holding males were present on the islands in late October, and their numbers increased slowly until mid-December.

Yearlings, some still nursing, were seen on most days until 9 December. There was a number of gaunt starvelings present, but most yearlings appeared to be well-fed. The low number of females ashore during the last half of November may be due to a tendency for pregnant females to feed heavily in the weeks before giving birth. Rand (1967) noted that females of Africian A. pusillus spent increasingly longer periods of time at sea before giving birth. Many pregnant females arrived on the Open Bay Islands in Late November, a few days prior to giving birth. This accounts for the sudden increase in the female census figures after 23 November. Numerous females were present throughout December, for two reasons. First, the period which a female spends on shore with her newborn pup is probably the longest continuous association they ever have together on land. Since births occurred in a brief period, many females were in the post-partum association with their pup simultaneously. Second, pregnant females continued to arrive ashore throughout December. The decline in the numbers of females in late December was due to the lower rate of recruitment of pregnant females, the increased amount of time which mothers were spending away from the rookery feeding, and probably the tendency of females who had lost their pups to stay away.

Sub-adult males on and adjacent to the trail to the blind (through the kie-kie and low forest) on the grassy plateau on the north end of the island, and on the northerly reefs, were counted each day between 0400 and 0700 hours (Fig. 2A).

Males encountered on the trial and plateau could be unequivocally classed as sub-adult or adult, but it was difficult to distinguish between these classes on the outlying reefs. A few territory-holding males were present on the reefs, and their occasional inclusion as sub-adults accounts for part of the difference between the curves for 'total males' and 'total SAMs' in Figure 2A. The similarity in the two curves suggests that errors in distinguishing the classes were minor.

The number of sub-adult males fluctuated at a high level until day-block 10, then decreased steadily (see Appendix B). The curve in the bottom left of Figure 2A indicates that the number of sub-adult males present on the main study area (and by extension, on the breeding rocks) was high until day-block 7. Thus, the trends for the sub-adult male population, based on censuses made on non-breeding areas of the island, are obscured until about day-block 8 due to the use of breeding rocks by members of this class. The decline apparent after day-block 10 may simply be a continuation of a decline present throughout the summer, which was obscured by changes in the patterns of space-use by sub-adult males.

When seals could not be sexed, they were listed as "neuters". A general increase in the number of "neuters" occurred over the summer (Figure 2B). That this class was comprised largely of females is suggested by the following evidence. When the outlying reefs were visited and censused, most individuals were females. For example, on 31 October two females were seen there, none on 2 or 3 November, 18 on 20 December, 17 on 13 January, 20 on 4 February and 27 on 5 February. Only two pups were known to have been born on the reef, so the females present can not be accounted for in terms of births. Second, the population of sub-adult males decreased over the summer (Figure 2A), and it can be inferred that the population of male "neuters" also declined. Finally, female BT, who gave birth on the main study area, and whose pup died, was observed on the outlying reefs twice in the weeks following the death of her

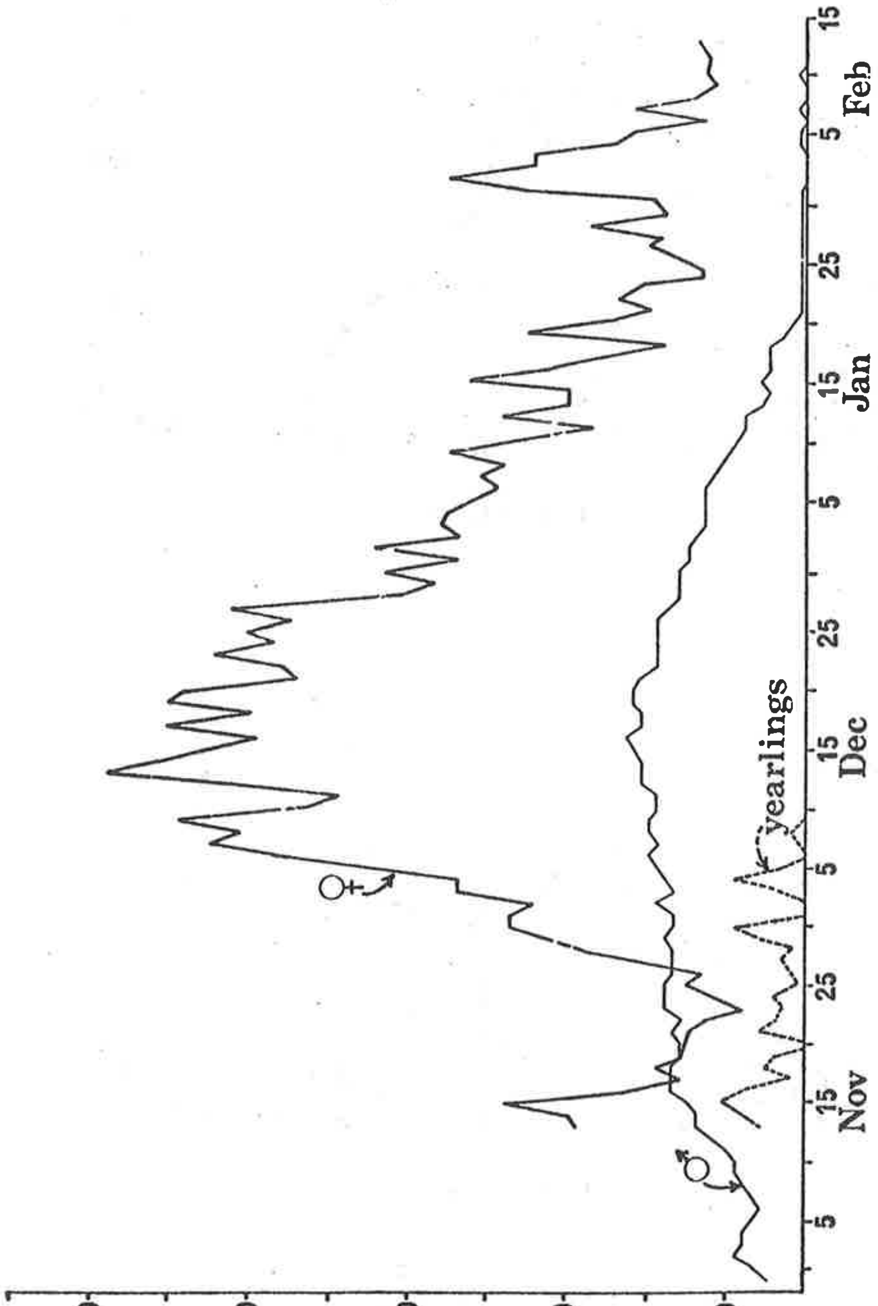
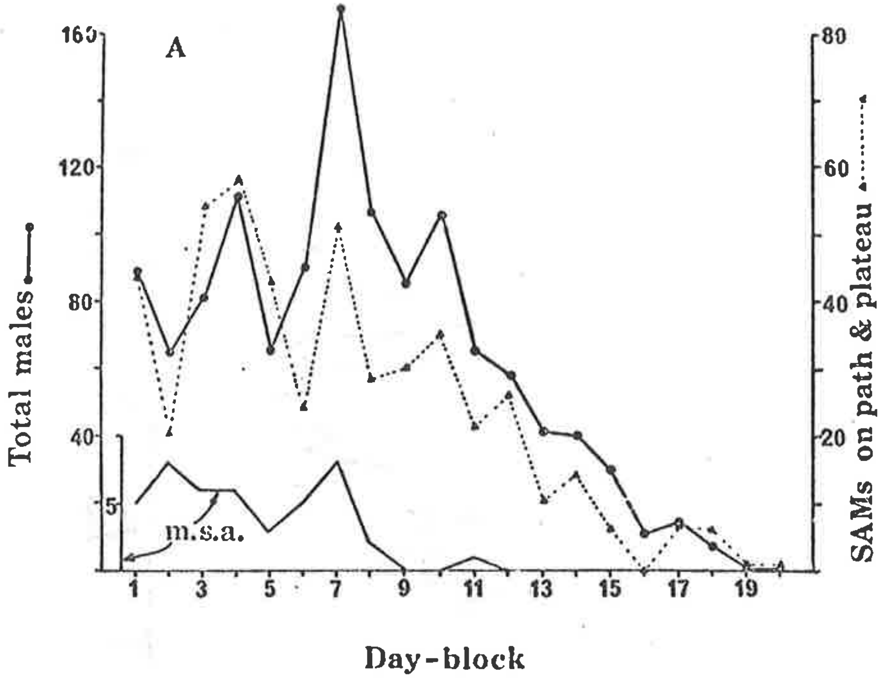


Figure 1 Seasonal trends in population composition and numbers, figures for both study areas combined.



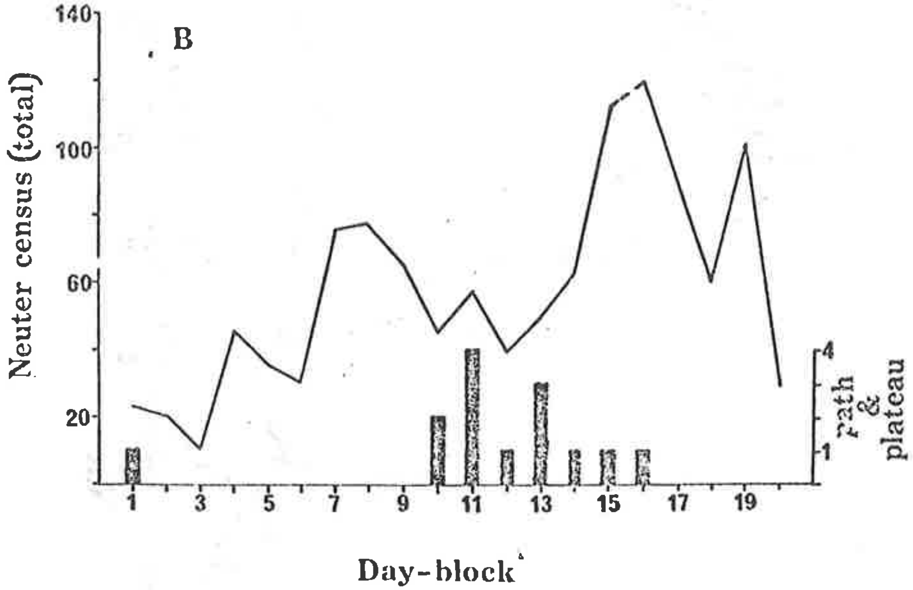


Figure 2A Seasonal trends in the numbers of adult plus sub-adult males ("Total males") censused on the reefs, path, and plateau, and in the numbers of positively identified sub-adult males (SAMs) on the path and plateau and main study area (m.s.a.)

2B Seasonal trends in the numbers of seals unable to be sexed ("Neuters") on the path, plateau, and reefs ("Neuter census (total)"), and on the path and plateau.

pup. Hence females that lost their pups may have formed a proportion of the "neuter" class on the outlaying reefs.

A stillbirth occurred on 31 October, and live births occurred for a 42 day period, from 18 November to 29 December. The mean date of pupping was 9 December, with more than three-fourths of the births (76.9%) falling between 29 November and 19 December (inclusive). The frequency distribution of births over the summer approximated a normal distribution.

(b) May-June 1971

Numerous sub-adult males were present from 26 May to 2 June (Table 3). Most of these were very small, and some very small females were also sighted.

Table 3. SUMMARY OF CENSUS DATA, 26 MAY-2 JUNE 1971, OPEN BAY ISLANDS (SELECTED AREAS ONLY)

	N	%
Adult males	6	1.0
Sub-adult males	112	19.0
Females	173	29.3
Pups	299	50.7
Total:	590	100.0

ADULT SEX RATIO ON THE ROOKERY DURING BREEDING

It is well established that nursing female otariids feed at sea, and regularly return to shore to suckle their pups. Because of these feeding periods, there are fewer females than pups present on the rookery at any one time. As a result, sex ratios recorded during the breeding season based on censuses are highly inaccurate. To determine the sex ratios of adult seals on the rookery, the following data are needed: the number of pups born; the proportion of females bearing pups, that copulate; the number of females not bearing pups, that copulate; and the number of territory-holders. For the present purposes it will be assumed that all females bearing pups copulated with territorial males. This is probably not true, but the error should be reduced because of the exclusion of virginal and non-parturient females from consideration.

Females came into oestrus about 8 days after giving birth. For the period in which oestrus females were assumed to be present (birth frequency distribution over the summer, plus 8 days), a sex ratio was computed as: (total number of births/mean number of territorial males censused per day). Resulting figures were: main study area - 7.9; overall - 6.1. These figures are higher than those computed on the basis of daily censuses, and support the suggestion that sex ratios derived from census data are inaccurate. Furthermore, the goodness of fit of sex ratio based on census figures, and sex ratio calculated as above, varied seasonally and between study areas.

DISPERSION

At Kaikoura, there was a striking segregation of large and small males. Large males predominated on the mainland, whereas smaller males were far commoner on and about the outlying reefs. Large males preferred broad ledges or flat areas, where wave action and disturbance by active and playing seals were minimal. Small males gravitated to areas too rugged and angular for use by large males, and to areas with ready access to the sea. The former tendency probably reflects the dominance relations between large and small males in favour of the larger; the latter is indicative of the greater activity levels of small males than large ones.

As the breeding season progressed on the Open Bay Islands, sub-adult males became increasingly uncommon on the main rocks of Taumaka, and concentrated on outlying reefs and non-breeding areas of Taumaka (forest, trail, plateau). In comparison with other populations of otariids, there was a very small number of sub-adult males using the islands in the summer. As discussed, non-breeding females also appeared to use areas favoured by sub-adult males (cf. Fig. 2). Few females hauled out in the forest, though it was used commonly in certain places on hot days. As pups matured, they followed regular routes through the low forest between the two study areas. In the winter months, there were no social factors operating strongly enough to segregate any age or sex classes on Taumaka. The fraction of seals resting in the forest (vs resting on the breeding rocks) was computed (Table 4). Small males were greatly in the majority among the male population ashore, and the proportion of males in the forest varied inversely with the size of the males. No comparable figures are available for the summer, but there seemed to be many more pups in the forest during winter observations (101/299 = 33.8%) than during the summer.

SOCIAL ORGANIZATION

1. Kaikoura

(a) Winter

Different areas of Sugar Loaf Point were favoured by males of different sizes. Generally, low-lying and smooth reefs were favoured by small males, and were areas where a great deal of chasing and mock-fighting was observed. Some regions were used mainly by resting seals, and in these areas a seal's body size appeared to be the major determinant of his ability to rest where he desired. As a result, segregation by size was also apparent on areas used for resting.

The higher activity levels of small males contributed to their greater involvement in social encounters. Small males engaged in 644 of 876 recorded encounters (73.5%), but comprised only 57.4% of 5,436 seals classified for size in the same period (based on repeated censuses during the week). These social encounters were most commonly prolonged mock fights and chasing over shallow reefs and in adjacent shallow water. Large males engaged in social encounters most often in vying for resting space, and such interactions tended to be brief and to the point.

2. Open Bay Islands

(a) Winter

Few adult males were seen on the islands in May and June. Those present showed little interest in females or other males, and slept most of the time. They engaged in no activities reminiscent of breeding activities, such as "herding" or territoriality.

Table 4. HABITAT PREFERENCES OF DIFFERENT CLASSES, OPEN BAY ISLANDS, MAY-JUNE 1971

	ON BREEDING ROCKS	IN FOREST	TOTAL
Adult males	6	0	6
Large sub-adult males	20	0	20
Medium-large sub-adult males	32	2	34
Medium-small sub-adult males	38	15	53
Females	156	17	173
Pups	198	101	299
Pups: Lone (%*)	103 (50.5)	59 (63.4)	162
Pups: Groups (%)	53 (25.9)	30 (32.3)	83
Pups: With females (%)	48 (23.5)	4 (4.3)	52

* % of pups in social association indicated, in specified habitat type.

There were numerous sub-adult males present on the Open Bay Islands in May and June 1971. Some large sub-adult males were present on the main study area for 3 days consecutively, during which time they engaged in crude boundary displays with one another across topographically distinct territorial "borders", mildly chased away smaller sub-adult males, and "herded" females. Small sub-adult males were scattered, and did not seem to defend fixed points in space. Sub-adult males of various sizes engaged in mock battles in shallow water.

Although elements of serious territorial behaviour pervaded the actions of the three large sub-adult males present continuously on the main study area, their behaviours were in some ways playful. Their herding of females and chasing of small sub-adult males were erratic, and varied in intensity. Sometimes a large sub-adult male rushed towards a smaller one as if to attack, only to engage in a naso-nasal greeting. The boundary displays were similar to true boundary displays in the stimuli evoking them, the spatial relationships of the interactants, and the postures and movements. Postures were not held rigidly, and the interactants easily became inattentive to the interaction, or started yawning and turning away. Whimpering and trumpeted roaring vocalizations, most commonly given by adult territorial males during the breeding season, tended to occur in the latter stages of the display, and tongue-flicking often accompanied or followed facing-away at the end of the encounter.

Interactions between sub-adult males and pups, and sub-adult males and females, were similar to those seen during the summer although more prolonged play encounters were seen between pups and small sub-adult males than during the summer.

Females and their pups showed site specificity, as was apparent during the proceding summer, but they wandered more widely. One distinctively marked female nursing a pup was seen in low forest near the plateau, in a location she had been seen the previous August with her previous season's pup (C. Horning, pers. comm.). Females showed no interest in sexual activity, and threatened the omnipresent sub-adult males whenever the latter approached to olfactorily investigate them.

(b) Summer

The middle of the breeding season was characterized by rigid and mutually exclusive territoriality among breeding males, and early and late summer were typified by a gradual change from the winter conditions. In late October and early November, large sub-adult and near-adult males showed site tenacity, but territorial boundaries were loosely-defined and sporadically defended. At this time, there were as yet no females hauled out just prior to their giving birth, but non-pregnant females and females with yearlings were common near shoreline. Gradually, the number of large adult males holding territories increased, concomitant of increased fighting, more frequent visual and vocal displays of threat, and lessened tolerance of the presence of sub-adult males on the breeding rocks. The rate of growth of the population of territorial males slowed before the influx of pregnant females commenced (cf Fig. 1). These females showed a more scattered dispersion than did females present earlier, and they concentrated less near shoreline. Territorial males assiduously "herded" females (see next section) but were generally ineffective in influencing their movements. Female dispersion was determined by the females themselves.

During the period in which births occurred, peri-parturient females remained ashore within a small area. Recently parturient females were very aggressive, and threatened any females, pups, or males that approached.

As the breeding season drew to a close, adult males deserted their territories, usually for good, but a few males returned after brief absences, only to leave again. Small adults and sub-adult males again were seen on the rookery, and were tolerated increasingly by the lingering territorial adults.

The above description suffices to show that social "structure" is essentially lacking except during the period of pupping and copulations, and then the territoriality and aggressiveness of males, plus site specificity and defence by (especially) recently parturient females, give the society its clearest form. Pups played little role in moulding social structure. They, like their mothers, localized after birth, but wandered more widely as they matured. When pups were older, and when their mothers were absent on feeding trips, pups commonly concentrated in pods inlant, where they were buffered from the activities of adult males and attacks from females.

Adult males held territories for periods varying from a few hours to 9 weeks, during which they were (with few exceptions) in continuous attendance on the breeding rocks. Long periods of tenure sometimes terminated with a male leaving spontaneously, but most males left after being deposed through fights. This was especially true for males present for brief periods.

The amount of time females spend on land around birth, and subsequently, determines the number of females on shore at any time. It was difficult to collect complete records on individual females because of their shyness, uniform appearance, and the rugged nature of the terrain.

Females localized in their movements before birth, and may even have done so before the last feeding excursion prior to giving birth. For example, female ACE was first identified in HL's territory on 3 December. She remained until 5 December, then disappeared until 15 December, when she reappeared on the same rest rock. She gave birth the following day. For nine females, the mean time ashore prior to parturition was 2.1 days (range 1-5 days). Females copulated on average of 7.9 days after birth (range 6-12 N = 10 - see Table 5), and left the rookery 0.9 days later (Y = 8.8 days after birth, range 6-12, N = 21). Female CR copulated twice within 14 hours. If other females remained sexually receptive as long as 14 hours, this may explain why they remained ashore for about a day after the first copulation.

Data collected on subsequent returns to the rookery and time on shore around birth are summarized in Table 6. Except for female BT, whose pup weakened and died, the first absence of females from land varied from 3 to 5 days, with no obvious correlation with the time on shore around birth. The first return to shore to nurse the pup varied from 2 to 4 days, and the figures thereafter varied more widely. Nursing periods were consistently shorter than the adjacent periods at sea.

In summary, females sometimes appeared on the rookery weeks before giving birth. Near the time of birth, females localized at the future pupping site from less than 1 to 5 days before birth. They remained on land about 10 more days, and left for their first feeding trip after about 13 days ashore. The first feeding bout normally lasted 3 to 5 days, and was followed by a 2 to 4 day period of nursing. Subsequent feeding and nursing periods were difficult to document.

SOCIAL BEHAVIOUR

Though gregarious, New Zealand fur seals are generally intererant of body contact with conspecifics (Plate 4), and many of the agonistic encounters observed resulted from the too close approach of one animal by another. Social encounters between two individuals were generally brief and unstereotyped. They involved open-mouthed threats, infrequent nips, feints of the head and neck, and sometimes chest-to-chest pushing. This was true, at least, of young males, pups, yearlings, and females. Territorial adult males evinced more stereotyped threat behaviour, which was usually in the form of mutual threat between adjacently-situated territory-holders (Plate 5). These "boundary displays" recurred at particular

Table 5. SUMMARY OF INTERVALS BETWEEN BIRTH AND COPULATION FOR KNOWN FEMALES

FEMALE	DATE OF PARTURITION	DATE OF COPULATION	ROUNDED INTERVAL (DAYS)	EXACT INTERVAL
CL	20 November	26 November	6	5 days 17 hrs 40 minutes
14	30 November	7 December	7	-
41	6 December	13 December	8	7 days 17 hrs 10 minutes
38	6 December	13 December	7	7 days 0 hrs 67 minutes
F2	9 December	17 December	7	7 days 5 hrs 29 minutes
WV	17 December	23 December	7	7 days 5 hrs 29 minutes
74	13 December	24 December	11	-
PB	17 December	24 December	7	6 days 23 hrs 37 minutes
CR	17 December	24/25 December	7, 8	7 days 10 hrs 11 minutes 8 days 0 hrs 21 minutes
65	14 December	26 December	12	12 days 5 hrs 25 minutes

$\bar{Y} = 7.9$ days

Table 6. SUMMARY OF TIME ON LAND FOR KNOWN FEMALES

	DAYS ON LAND AROUND BIRTH			SUBSEQUENT RECORDS				
FEMALE	Before	After	Total	Feed 1	Nurse	Feed 2	Nurse	Feed 3
A	–	–	–	5	–	–	–	–
ACE	1	8	0	4	3	8 (?)	2 (?)	–
AR	3	9	12	3	–	–	–	–
BBC	–	10	10+	5	–	–	–	–
BT[1]	–	10	10+	8	3	8	7	9
CL	3	9	12	4	2	–	–	–
CR	1	9	10	4	2	4	–	–
MC	2.5	–	–	3	4	4	–	–
PB	–	9	9+	3	–	–	–	–
UM	1	11	12	5	3	7	2	–
Y				4.4	2.8			
S.E.				0.45	0.28			
N				10	6			

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[1] Pup died.

locations, and were engaged in more frequently by certain males and certain male-pairs than by others. They served to delimit and redefine territorial boundaries between territories, and were clearly separate from true fights. Fighting was a high intensity manifestation of aggression, and occurred only when males defended or obtained territories from other males; fights occurred far less commonly than did boundary displays.

"Herding" was a frequently observed kind of social encounter, occurring between males and females. Males intervened between territorial boundaries and females trying to leave territories via those boundaries, and appeared to try to contain the females within the territories about to be left (Plate 6). As mentioned, such apparent attempts always failed, for the females persisted until successful, or left by another route. Males showed no clear-cut tendency to preferentially herd pre-oestrus rather than post-oestrus females, but energetically herded oestrus females.

Copulations formed the sole class of social encounters between adult females and territorial males in which bodily contact was sought and tolerated by both partners. Since most females copulated but once (Table 5), less than a hundred copulations occurred forthe 80+ females giving birth on the main study area, and they formed a numerically unimportant class of social encounters. Notes were made on 54 copulations, two involving sub-adult males and 52 involving territory-holders. The mean date of observed copulations was 16 December.

There were departures from predicted values of copulation frequencies in early and late summer. The four observed copulations prior to day-block 6 involved very small females with distinctive light brown pelage. This pelage is characteristic of 2-year old African A. pusillus (Rand, 1956), and it is assumed that the observed females were virgins. This is supported by the sighting of a member of this distinctively coloured class bearing a tag put on 2 to 3 years previously, by Dr I. Stirling. The single copulations observed on 13 and 18 January are more difficult to explain. One (18 January) was with a female with a pup, perhaps a late undocumented birth, and the other involved a lone female.

Copulation frequency declined in the hot early afternoon. Females moved more often, and males holding land-locked territories (hence without access to the cool sea water) responded less to female movements at air temperatures above 17.0°C. However, male-female encounter frequencies did not vary significantly with temperature. Therefore the dip in the rate of copulation in the early afternoon was not due to a drop in encounter frequency.

The sedentariness of females after birth usually resulted in females copulating with the males in whose territories they gave birth. However, of nine females, two (22.2%) copulated with territory-holders other than the one in whose territory they pupped. Of six other females who were not observed to copulate, only one moved to a different territory within 8 days of birth. Combining these data, three of 18 (16.7%) of the females under observation copulated with males in other territories. One of the reasons for this may be the suddenness with which females became sexually attractive to males, and the inability of territory-holders to always be present and willing when females became sexually receptive. For example, on 6 December, female 14 was soliciting MrX, who smelled the rock she was on, but made no attempt to herd or copulate with her. They copulated 17 hours later. On 24 December, LH investigated female PB who mildly resisted. LH smelled the ground, but did not pursue the matter. One hour and 57 minutes later, PB copulated with an adjacent male.

Olfactory investigation of females and rocks used by females was a characteristic activity of tenured males. It enabled them to monitor the sexual state of the females on their territories. Distinguishing features of sexually receptive females were their playfulness and low aggressiveness toward males. Oestrus females often moved in a strange, jerky manner, for example by running a short distance, then suddenly assuming a rigid nose-up posture, or stopping quickly and lying on the ground with flippers tucked beneath the body. If a female did not react aggressively to an investigating male, she inevitably proved to be in a sexually receptive state. Females who actively solicited males approached them silently with mouths slightly ajar and eyes glazed, gently grasped the bull's neck skin or flank,

Plate 4 Typical resting dispersion in *A. forsteri*. Wintering males at Sugar Loaf Point are shown. Note the regular distances between the animals, and how none are in bodily contact.

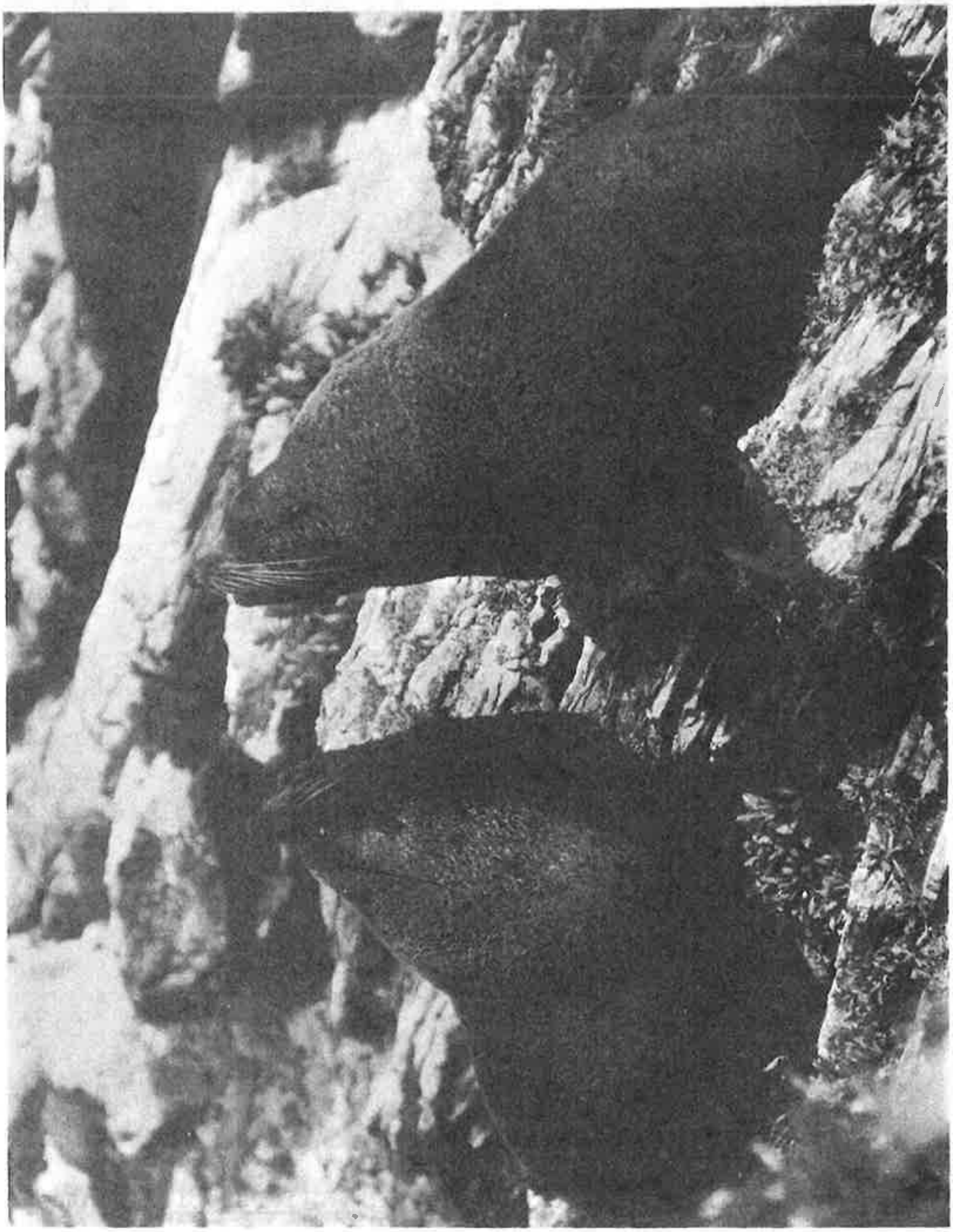

Plate 5 Part of a mutual threat display ("boundary display") between two territorial adult males during the breeding season.

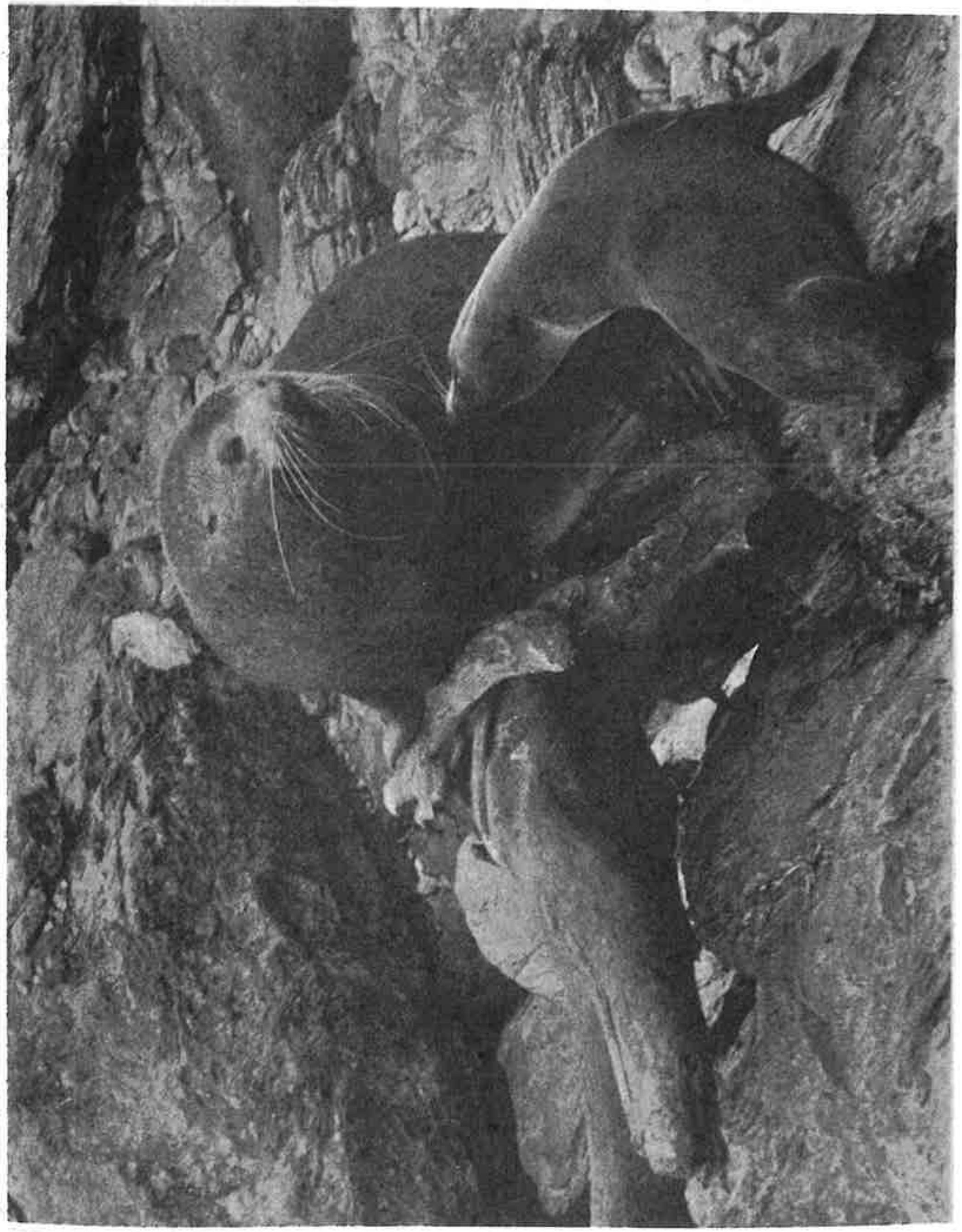

Plate 6 "Herding" effort by male, forcing, by his lateral movements in the direction of the female, the female to move back within his territory. The female had been walking toward the male's territorial boundary, just to the left of the photograph.

and slowly and gently shook their heads from side to side while maintaining a grip. One female bounced playfully, with her mouth ajar, toward a male, and silently made some slow feint swings at him. If males failed to respond positively toward them, oestrus females lay down, or moved off in the jerky manner described.

No true courtship preceded copulations. Occasionally, males excitedly investigated females for as long as 15 minutes prior to mounting. In contrast, many males mounted almost immediately upon determining that a female was sexually receptive. A male's initial reaction to an oestrus female was to whimper in a high-pitched tone, and to seek body contact by rubbing, mounting, or softly biting, or to repeatedly investigate the perineal region. Only one (attempted) copulation was seen in which a male forcefully held a female. The female was a probable virgin, and the male grasped her with his teeth to prevent her leaving. The copulation was unsuccessful; when the male mounted the female, she was completely covered by his body, yet the male's extruded penis was 20-30 cm short of the female's hind end.

Mounting was almost always done dorsally (Plate 7). A single mount of a female lying on her back was seen, but the female squealed, turned over, and the copulation proceeded normally. It was usual for males to mount more than once (67.8% of observed copulations). Initial mounts were of varying duration, and the last mount was usually the most protracted.

The durations of copulations were estimated beginning from the initial mount, and terminating with the final dismount. The briefest copulation was 5 mins 25 secs. (single mount) and the longest was 38 mins. Some copulations were prolonged, with series of brief mounts and intermittent periods of distinterest by the male. For example, male XR mounted a female twice within 5 mins, and excitedly investigated her. The female ran away a few metres toward her pup, and lay down restlessly rubbing herself with a foreflipper. XR followed whimpering, but stopped en route to investigate another female. The oestrus female solicited XR again 21 minutes after the initial encounter, by XR showed no interest. When observations terminated, 3 hours 15 minutes leter, the copulation had not been completed.

ACTIVITY BUDGETS OF TERRITORIAL MALES

Despite the fundamental importance to animals of the partitioning of time into different activities, very few studies have included a measure of time budgets. Such studies have been mainly concerned with birds (see Schartz and Zimmerman, 1971, and references therein) although Smith (1968) did this with squirrels (Tamiasciurus) and Stirling (1971) sampled time budgets of territorial male *A. forsteri* in Australia. Territory-holding otariids are excellent models for time budget studies, since they are not involved in care of the young or feeding, and channel all their time into other personal or social activity.

Between 15 and 45 minutes each day were spent recording the activities of territorial males. Males were classified as: prone inactive silent (PIS), prone threat vocalization (PV), prone comfort activity (PC), upright inactive silent (UIS), upright threat vocalization (UV), upright comfort activity (e.g. grooming) (UC), interact with sub-adult male (SAM), interact with female (F) or with territorial male (M). The activity of each male was noted at 10 second intervals during the sample period. Activity was sampled between 0500 and 0700 hours, and between 1900 and 2100 hours. These times were chosen because males were least active in mid-day, and the sampling time was so small as to necessitate a bias in sampling. It was assumed that seasonal changes in activity budgets would be reflected under any consistent methods of sampling.

Plate 7 Typical copulatory postures.

Until day-block 7, only once were activity levels above 5%, whereas they were never less than 5% in subsequent day-blocks. Trends varied, but a consistently high proportion of the males' time was spent in upright postures from day-block 6 to 10. This suggests a preferential use of the upright rest posture during that period. Whether fortuitious or not, males spent the largest proportion of this time in the upright posture during the period of most intense reproductive activity. The proportion of a male's time spent interacting with males and females varied in a similar manner.

Males spent the most time in social encounters when many oestrus females were present (day-blocks 8, 9, 10), with fairly high levels in day-blocks 7 and 11-13 (table 7). Similar trends have been noted for Australian A. forsteri (Stirling,1971). Stirling's and my data contrast with reports for other otariids, such as A. tropicalis: "until the break up of the harems the males know no longer of rest...." (Paulian, 1964). Such differences in activity are probably strongly influenced by breeding density.

Males locate at rookeries to have access to females. Inter-male strife, and the inter-male interactions concomitant of holding a territory impose a certain social regime on the territory-holders. But what of the involvement of males with other classes ashore? The importance of such involvements varies with the proportions of the classes ashore, in part. During daily 1 to 2 hour sampling periods between 6 December and 9 January (inclusive) the following data were collected:

Percentage of interactions between territory-holder and:

	Territorial male	Sub-adult male	Female	Pup	Total
%	9.6	1.8	87.0	1.6	100.0
(N)	(114)	(22)	(1038)	(19)	(1193)

Males interacted with females much more frequently than with other classes. Interactions with pups were few, even though pups formed the numerically dominant class during the sample period. This reflects the fact that males tended to ignore pups.

Male otariids fast during their periods of tenure, and some workers feel that their activity budgets during this period may have an important effect on their ability to copulate with females, and successfully defend their territories. For New Zealand A. forsteri, I think this unlikely (cf Miller, 1973).

PUP POPULATION AND MORTALITY

Fifteen pups were dye-marked on the main study area, and repeated counts of marked and unmarked pups were made daily from 10 January to 13 February. The records for each day-block were lumped (Table 8).

Population estimates varied from 55.1 to 115.0 ($\bar{Y}$ = 69.3). Using the mean estimate,pup mortality can be estimated as (81-69.3)/81, or 14.4% (where 81 = number of births on the main study area) up until 27 January (the middle of the sampling period). The mean date of pupping on the main study area was 8 December, so the estimated mortality rate applies to the first 50 days of life.

Table 7. SEASONAL TRENDS IN THE PERCENTAGE OF TIME SPENT BY TERRITORIAL MALES IN SOCIAL ACTIVITY[1]

DAY-BLOCK	% TIME	N
1	3.0	1211
2	1.0	494
3	3.1	5198
4	0.5	5655
5	0.6	4620
6	1.0	5407
7	4.1	5861
8	5.8	4534
9	6.3	4680
10	5.0	4827
11	3.1	4145
12	2.4	4547
13	4.0	4133

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[1] Includes: aggressive vocalizations (whether directed or undirected), interactions with males, females, yearlings, and pups.

Two other points arise from the data in Table 8. The first is that the mean pup census figures declined steadily. This was probably due in large part to extensive use of shoreline by pups. During day-blocks 20 and 21, population estimates deviated markedly from the mean, probably because of an interchange of pups between the main and subsidiary study areas, and the small sample sizes. The second point is that during late summer, particularly, pup census data never provided reliable estimates of the numbers of pups on shore. To determine whether the accuracy of the pup censuses was affected by changes in the behaviour of the pups, the following calculations were carried out: assume that the estimated mortality rate of 14.4%/50 days remained constant through the sample period. Then day-blocks 17 and 19 would hold, respectively, (69.3 + (0.144) (69.3)) and (69.3 - (0.144) (69.3)) pups, and so on for the other day-blocks. When the mean pup census data are taken as percentages of these projected population estimates, the picture in the last column of Table 8 emerges. Judging from the table, the behaviour of the pups strongly affected the accuracy of the census, and censuses in late summer provided less accurate estimates than earlier. Even so, the percentage of the estimated pup population which was sampled never exceeded 52.7%.

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Table 8. ESTIMATES OF THE PUP POPULATION ON THE MAIN STUDY AREA

DAY-BLOCK	(a) PUPS MARKED[1]	(b) PUPS UNMARKED	(c) MEAN AM CENSUS[2]	(d) MEAN PM CENSUS[2]	(e) MEAN CENSUS	(f) POPULATION ESTIMATE[3]	(e/f) %
15	38	163	35.0	32.8	33.9	64.3	52.7
16	103	522	34.8	38.0	36.4	76.0	47.9
17	113	600	31.4	31.8	31.6	79.6	39.7
18	191	701	25.0	33.0	28.4	55.1	51.5
19	171	650	26.0	22.0	24.0	57.0	42.1
20	96	555	25.8	27.8	26.8	86.7	30.9
21	33	253	14.5	10.5	12.5	115.0	10.9
	745	3444			27.6	69.3	39.8

[1] Based on repeated counts in the day-blocks indicated.

[2] AM = early morning; PM = late evening.

[3] Marked pups: 15 at start of sampling period ∴ Population = (15b/a).

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Appendix A. Classification by sex and age

Despite the size dimorphism between the sexes, it can be difficult to determine the sex of immature animals without inspection of the genitalia. On the average, males, even as yearlings, have thicker and more robust heads and necks than do yearling females. During growth, immature males have disproportionately large faces, necks, and foreflippers (Plates 8, 9). Immature males, as young as a few weeks in age, appear more aggressive than do females, and past one year of age. clearly become interested in females to some extent, as shown by attempted olfactory investigations, and abortive and crude "herding" behaviour. During sexing of small seals in winter 1971, it proved imperative to capture individuals to assess the accuracy of sexing by visual examination of the face and head. Although all seals so checked had been correctly sexed, it should be cautioned that this was possible only after nearly 5 months of previous observations, and is undoubtedly an unreliable technique except for those workers thoroughly familiar with adult females and immatures of both sexes, in different contexts. Throughout the report, "female" refers to adult female except where otherwise specified; "sub-adult males" refers to all males greater than a year of age, and of smaller size than males holding territories during the breeding season.

Appendix B. Date index to day-blocks

Day Block	Corresponding dates
1	1-5 November
2	6-10 "
3	11-15 "
4	16-20 "
5	21-25 "
6	26-30 "
7	1-5 December
8	6-10 "
9	11-15 "
10	16-20 "
11	21-25 "
12	26-30 "
13	31 December-4 January
14	5-9 January
15	10-14 "
16	15-19 "
17	20-24 "
18	25-29 "
19	20 January-3 February
20	4-8 February
21	9-13 "

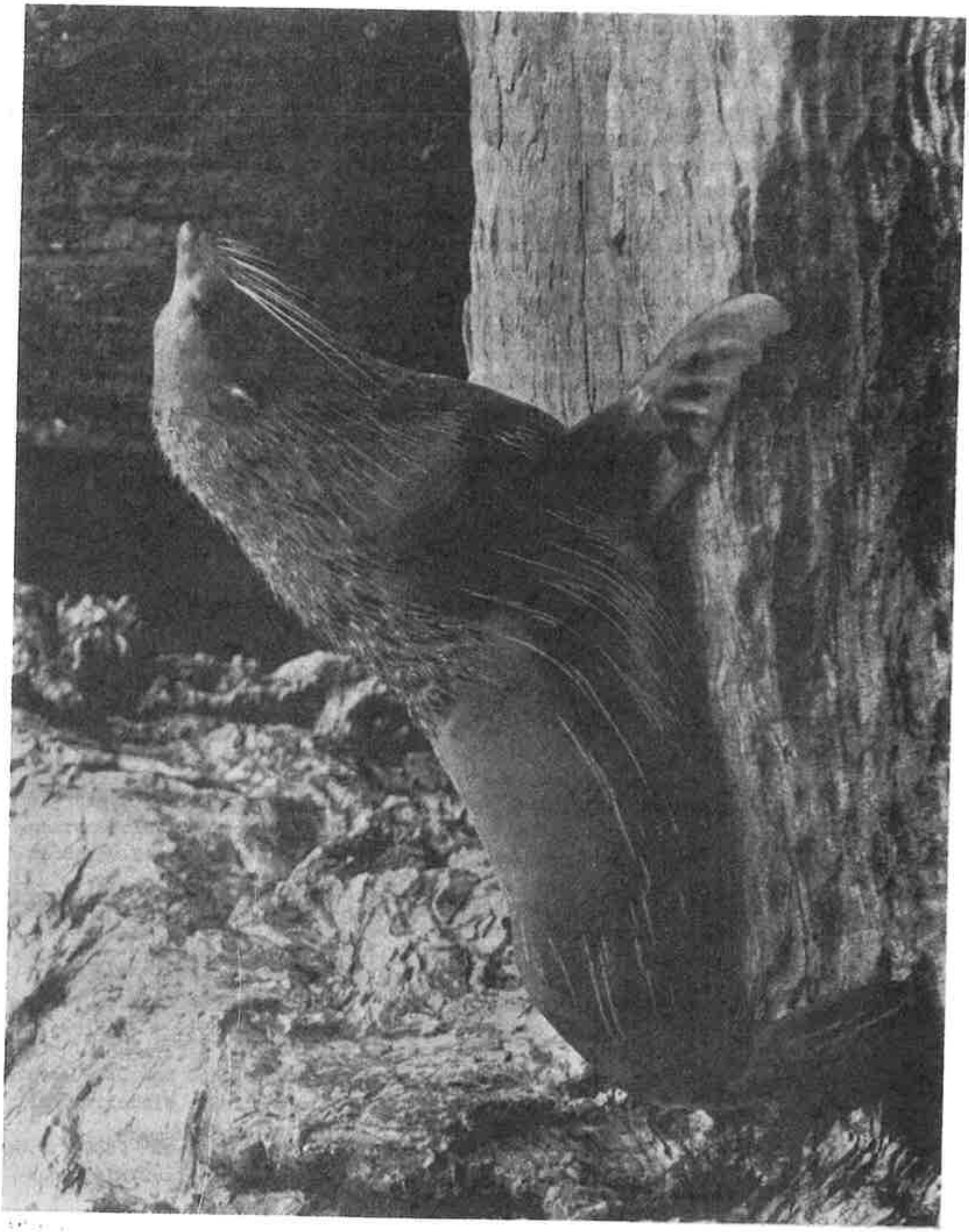

Plate 8 Medium-sized sub-adult male, recently out of the sea. Compare the shape, size and proportions of his fore-quarters and head, with the female in Plate 9.

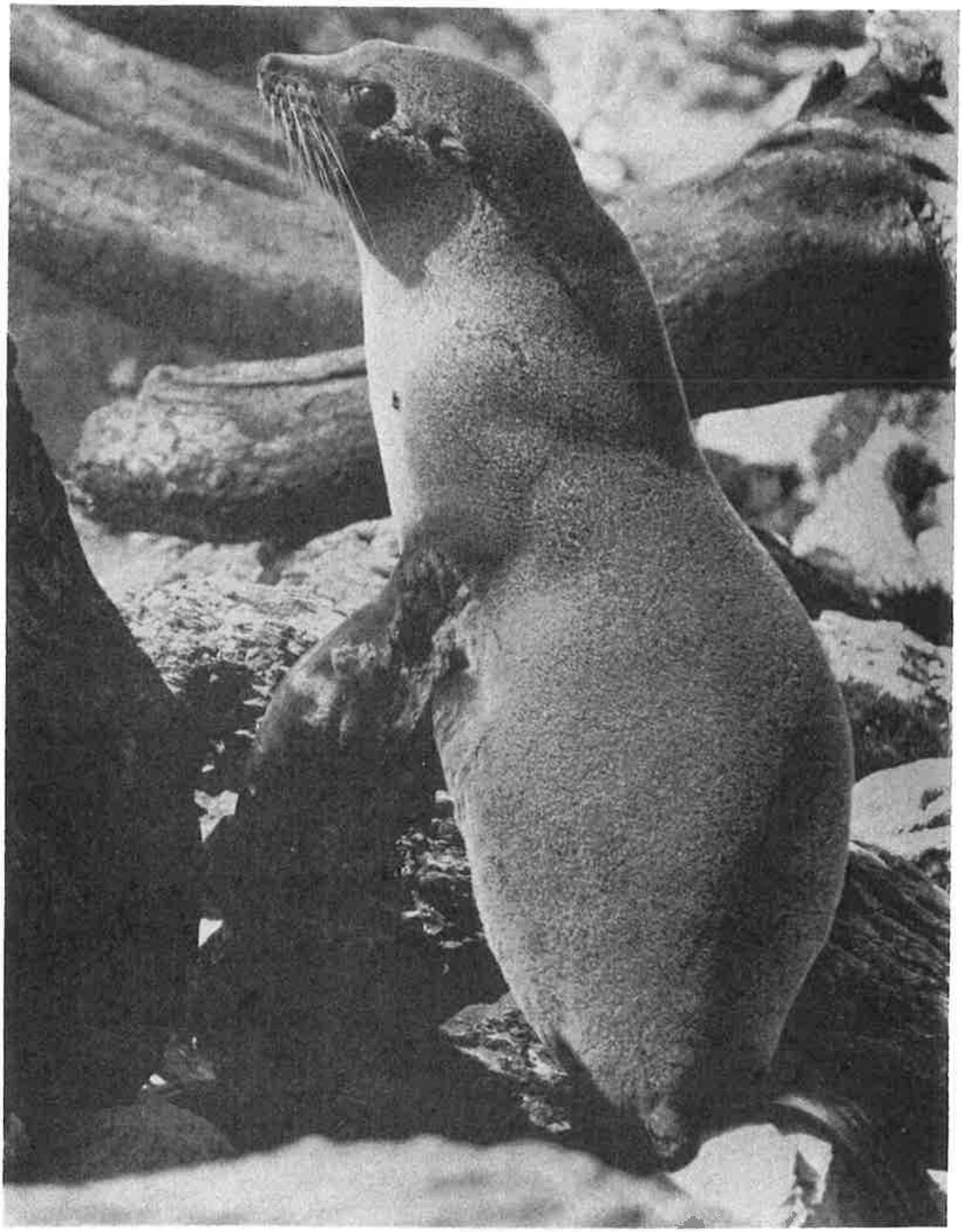

Plate 9 Medium-sized pregnant female. Note the well-proportioned head and forequarters, and relatively slender shoulder region (compare Plate 8).