

Annual Cycle of Fur Seals, *Arctocephalus forsteri* (Lesson), on the Open Bay Islands, New Zealand¹

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ABSTRACT: Fur seals, *Arctocephalus forsteri* (Lesson), were studied on the Open Bay Islands, South Island, New Zealand in 1970-1971. Few adult males were present at the colony site during the winter, but many arrived ashore in November to vie for territories. Individual territorial males remained ashore and fasted for up to 63 days before losing or abandoning their territories. A few adult males reappeared briefly at the colony site a few weeks after abandoning their territories, and left again. Subadult males were common at the colony and other parts of the Open Bay Islands at the start of the breeding season, but their numbers declined steadily throughout it. Adult females frequented the colony site throughout the year. Some pregnant females appeared some weeks before parturition in areas where they subsequently gave birth, then left to feed. The tendency of pregnant females to feed heavily in the weeks prior to giving birth resulted in few females being ashore in mid-November. Pregnant females landed ashore about 2.1 days before parturition. After having given birth, they remained ashore with their pup for about 8.8 more days before leaving to feed. Parturient females entered estrus and copulated about 7.9 days postpartum; sexual receptivity was observed to last up to 14 hrs. Parturient females were absent for about 4.4 days on their first feeding trip after having given birth, and were ashore with their pups for about 2.8 days immediately thereafter. Subsequent feeding periods at sea were longer. Mothers nursed their pups for about one-third of the time that the former were ashore. The fraction of time spent with mothers by pups on land changed little between December and May, and the female-pup nutritional bond extended in some cases for up to a year.

Nonbreeding adult (?) females increased in numbers near the colony as the summer progressed, then declined near the end. Very young males and some older subadult males were common at the colony site in May, but relatively few very young females were then present. An estimated effective sex ratio of 6.1:1.0 (females:males) prevailed in the colony during breeding. Sex ratios based on census data consistently underestimated this figure. The annual cycle is characterized by marked synchrony of births: about three-fourths of them fall in a 22-day period. A temporal equivalent of McLaren's "marginal male effect" may selectively favor a short period of pupping and copulation by females, helping to maintain a brief breeding period in the face of ecological determinants of breeding synchrony that are weaker for *A. forsteri* in New Zealand than for populations of some other pinnipeds.

OUTSTANDING STUDIES of the annual cycle of the fur seal *Callorhinus ursinus* have been made

by Bartholomew and Peterson (Bartholomew and Hoel 1953; Peterson, unpublished, 1965, 1968), but there is only limited information on feeding and nursing rhythms, seasonal movements, and seasonal changes in population composition of *Arctocephalus* species. Some information is available on population com-

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position and the annual cycle of an Australian population of *A. forsteri* (Stirling 1971a, b), but only scattered and generally vague data have been published on New Zealand populations (for references, see "Discussion"). In this paper, I discuss the annual cycle of *A. forsteri* as based on research performed on the Open Bay Islands, South Island, New Zealand, which support a colony of 2,000 to 3,000 animals (Crawley and Brown 1971).

Species nomenclature follows that of Reppening, Peterson, and Hubbs (1971).

MATERIALS AND METHODS

Censuses and observations were carried out on Taumaka, the larger of the two Open Bay Islands, from 27 October 1970 to 13 February 1971 and from 26 May to 2 June 1971. General observations were made there from 17 to 24 August 1970. (For descriptions of habitat see Burrows 1972 and Miller 1971.)

During the 1970-1971 austral summer, early morning censuses (0400-0700 hrs) regularly provided for each day the highest census figures. Therefore, these figures are used in the following data descriptions. Censuses were made almost daily for a grassy clearing near the north end of Taumaka, for the rocky reefs off the north end of Taumaka, and for the trail connecting the hut to the observation blind overlooking the main study area on the colony site. Daily censuses were made on the main study area.

During May and June 1971, it proved necessary to capture juvenile seals in order to confirm their sex. This had been unnecessary during the preceding summer because most immature seals then present were large enough to display diagnostic sexually dimorphic features (e.g., shape and massiveness of the face, shoulders, and foreflippers).

All territorial males and certain subadult males (SAMs) could be individually distinguished on the basis of features such as color of the pelage, broken canines, scars, shape and other characteristics of the face, and vocalizations. Individual adult females were more difficult to identify regularly, but a small number was identifiable by similar features.

Low numbers of some classes of seals,

missed censuses, and influences of circadian, tidal, and meteorological factors on patterns of haul-out necessitated, for parts of the study, the summing of several days' data throughout the summer period. Some kinds of data, therefore, were summed over 5-day periods (see below). Where censuses were missed, estimates for day-blocks were made based on the mean figures for sampled days within the day-blocks. Correspondences between dates and day-blocks are as follows: 1, 1-5 Nov.; 2, 6-10 Nov.; 3, 11-15 Nov.; 4, 16-20 Nov.; 5, 21-25 Nov.; 6, 26-30 Nov.; 7, 1-5 Dec.; 8, 6-10 Dec.; 9, 11-15 Dec.; 10, 16-20 Dec.; 11, 21-25 Dec.; 12, 26-30 Dec.; 13, 31 Dec.-4 Jan.; 14, 5-9 Jan.; 15, 10-14 Jan.; 16, 15-19 Jan.; 17, 20-24 Jan.; 18, 25-29 Jan.; 19, 30 Jan.-3 Feb.; 20, 4-8 Feb.; 21, 9-13 Feb.

RESULTS

Census figures for females, yearlings, and adult territorial males present on the colony study areas are summarized in Figure 1. Some territorial males were present on the islands in late October, and their numbers increased slowly until mid-December. Yearlings, some still nursing, were seen most days until 9 December. Some gaunt starveling yearlings were seen but most yearlings appeared to be well fed. The female population reached a local maximum in mid-November, reached a minimum about 1 week later, then increased rapidly until the end of the 1st week in December. It then fluctuated erratically and declined slowly until late January. A second increase and subsequent decline in female numbers occurred in early February.

Male seals encountered on the trail and grassy clearing ("plateau") could be unequivocally classed as adults or subadults but I found it difficult to distinguish members of these classes when censusing the outlying reefs through binoculars. The general similarity between the shapes of the curves for total males and for SAMs (Figure 2a) suggests, however, that errors in distinguishing members of the classes were minor. The SAM population fluctuated erratically until about day-block 7, then declined steadily.

A SAM "arrival" at the main study area

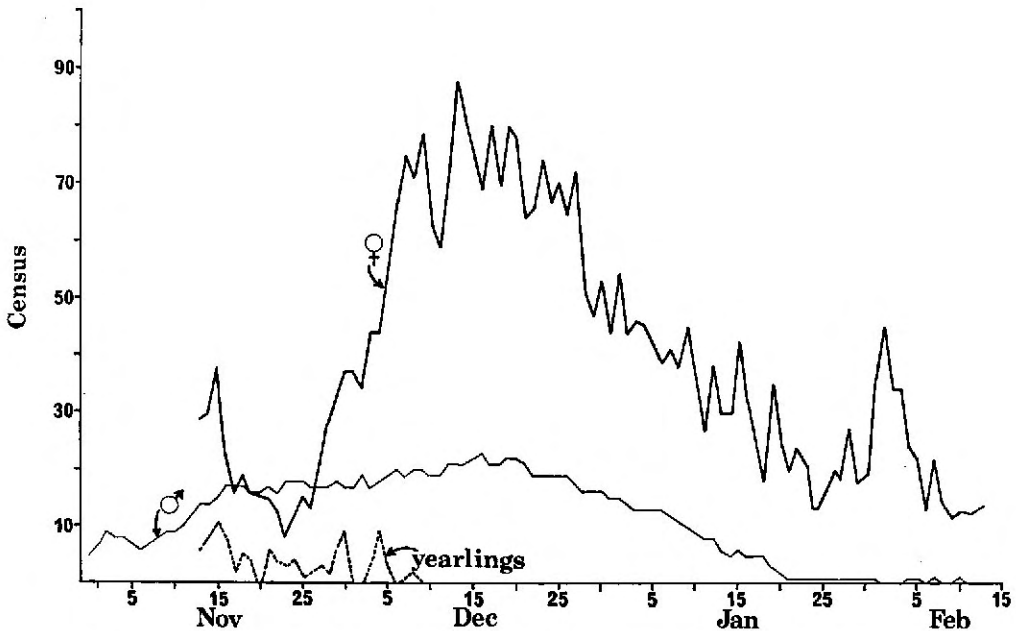


FIGURE 1. Seasonal trends shown in census figures taken during early morning for adult females, territorial males, and yearlings on the main study area.

was considered to be the arrival or hitherto unrecorded presence of a SAM there. Seven individually recognizable SAMs were recorded as returning to the main study area after as long as 56 days, and 12 SAMs were recorded there on from 2 to 8 consecutive days. The number of SAM arrivals per hr on the main study area declined steadily over the summer (Figure 3). Only one SAM was recorded landing on the main study area after day-block 8, although SAMs were then still common on noncolony census areas (Figure 2a). However, census figures for SAMs on the main study area were highest before the population decline on noncolony census areas became apparent (Figure 2a), suggesting that the dispersion of SAMs over the islands as a whole obscured a decline in population that was present from early summer. This being so, the number of SAMs arriving on the main study area was proportional to their numbers on the islands.

When seals on the outlying reefs, path, and plateau could not be reliably sexed, they were classed as "neuters." A general increase in the census figures for this class occurred over the summer, with a sharp decline near the end

(Figure 2b). The class was probably comprised largely of females, for the following reasons. When the outlying reefs were visited and censused at close quarters, most classifiable seals were females. Thus, on 31 October two females were seen there, none was present on 2 or 3 November, 18 were counted on 20 December, 17 on 13 January, 20 on 4 February, and 27 on 5 February. Second, since the SAM population declined over the summer (Figure 2a) it can be inferred that the population of unrecognized male "neuters" also declined. Finally, female BT, who gave birth on the main study area and whose pup died, was twice observed on the outlying reefs in the weeks following her pup's death, suggesting some use of that location by females who have lost their pups.

Records of sightings of individually known females, excluding those for females first identified on the day they gave birth (when special efforts were made to search for identifying features), are summarized in Figure 4. It is unlikely that a female would have been recorded as a mother (at some time observed with a pup of the year) if she had not borne a pup, since

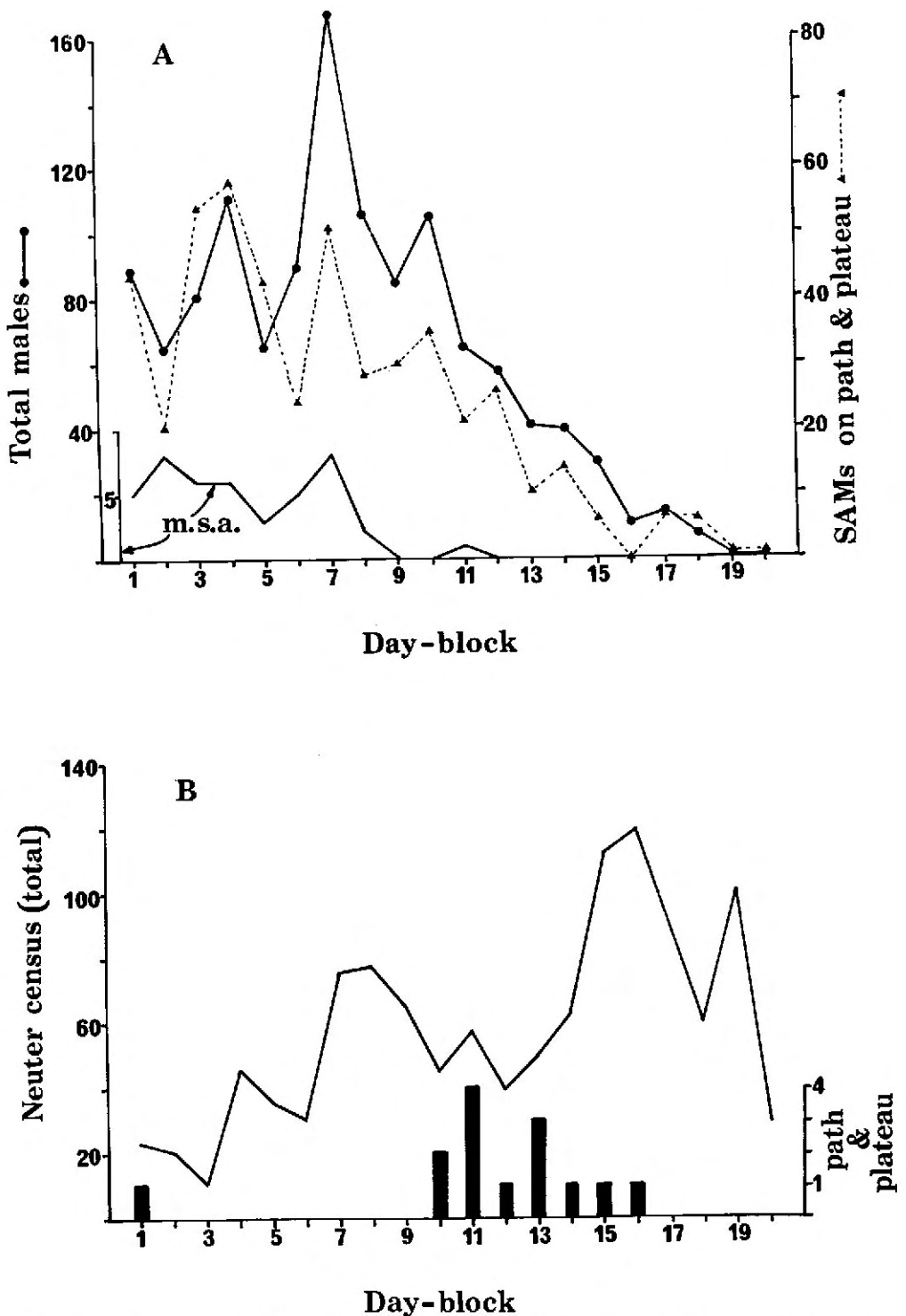


FIGURE 2. *A*, seasonal trends in the number of males censused on noncolony study areas. Census figures for subadult males (SAMs) on the main study area (m.s.a.) also are shown; *B*, seasonal trends in the number of seals not able to be sexed by distant visual inspection (—neuters) for all noncolony census areas, and for the path and plateau (vertical bars).

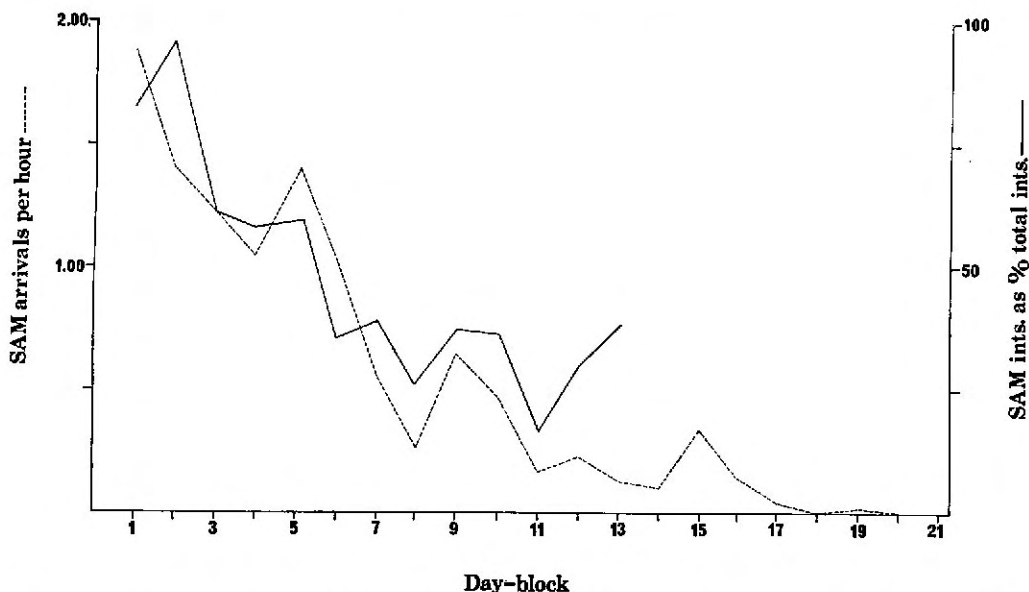


FIGURE 3. Seasonal trends in the rate of arrival of subadult males (SAMs) on the main study area, and in the percentage of total male-male social interactions (ints.) involving territorial males, in which SAMs were involved.

no fostering was observed (Miller 1971); however, some females who gave birth may have mistakenly been classed as nonmothers (never seen with a pup of the year). The effect of this possible error would be to minimize differences between the curves, rendering observed differences more reliable. Prior to day-block 6, many nonmothers were sighted. No mothers were identified until day-block 4, after which this class increased steadily in size (the low value in day-block 9 is interpreted as sampling error). The increase after day-block 10 of the nonmother class may be due to the inclusion of females who had lost their pups, but some of the nonmothers clearly showed a pattern of being present on the colony site in early to mid-November, and again in January and February for short periods: female ZG was present 15-16 November, 5, 7, 14 January; CHF was recorded 9, 12, 15-18 November, 25 December, 9, 14, 16, 22 January; NF was seen 29 November and 12 January. Other well-marked nonmothers were recorded early (OF, 17-21 November; OJ., 9 November; PUG, 4 November) or late (ZZ, 2-6, 8, 9 January; TT, 10, 12, 14, 29 January; PX, 25 January). Thus, nonmothers tended to be ashore in greatest numbers in early or late summer or both, and

mothers were most abundant in midsummer. Some nonmothers appeared to be old, being large and having teeth and vibrissae worn. None of the old females was seen to copulate, although they localized at the colony site. Presumed virgins (small, vibrissae dark and light, some with distinctive light brown pelage) tended to be less sedentary in their movements, and two females of this class were collected in early November while in association with groups of small SAMs around the periphery of the colony. One identifiable young female was observed to copulate.

A stillbirth occurred on 31 October, and live births occurred in the 42-day period from 18 November to 29 December. The mean date of pupping was 9 December (S.D. = 9.8, $N = 117$), with 76.9 percent of the births occurring from 29 November to 19 December (22 days). The seasonal distribution of births closely approximated a normal curve ($D = 0.10216$).

Females localized in their movements before giving birth, and some even did so prior to their last feeding trip before giving birth. Thus, female ACE was first identified in male LH's territory on 3 December. She remained until 5 December, then disappeared until 15

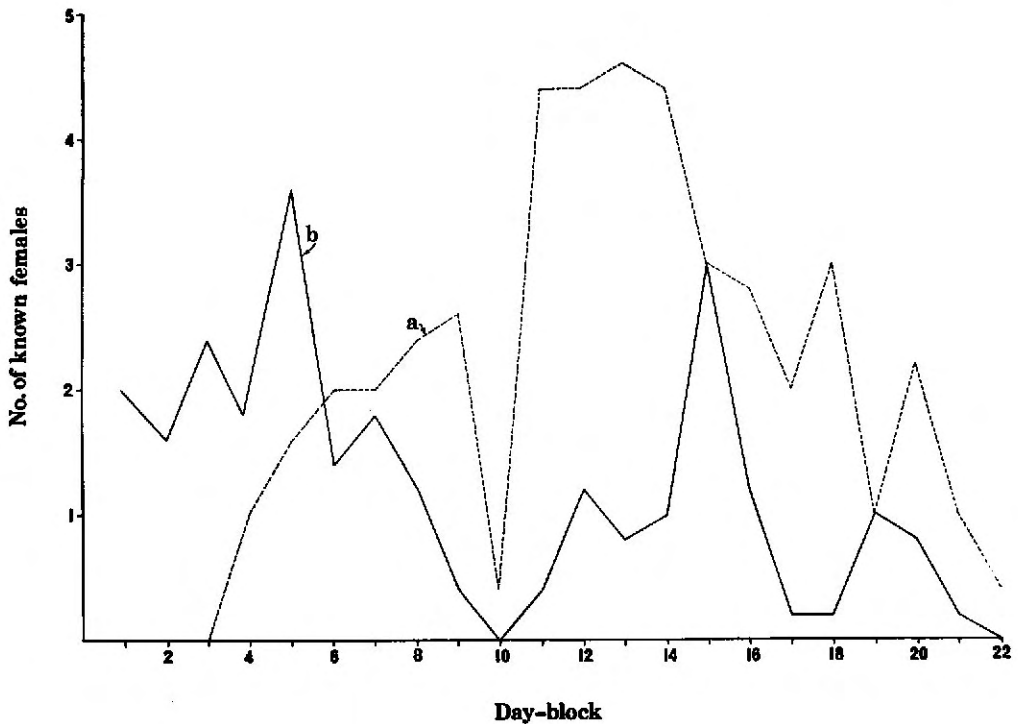


FIGURE 4. Seasonal trends in the mean number of identifiable mothers (a) and nonmothers (b) sighted per day. (See text for definitions of mother and nonmother.)

TABLE 1

SUMMARY OF INTERVALS BETWEEN BIRTH AND COPULATION FOR FEMALES OF *Arctocephalus forsteri*

| FEMALE | DATE OF PARTURITION (1970) | DATE OF COPULATION (1970) | ROUNDED INTERVAL (DAYS)* | EXACT INTERVAL† |
|--------|----------------------------|---------------------------|--------------------------|----------------------|
| CL | 20 November | 26 November | 6 | 5 days, 17 h, 40 min |
| 14 | 30 " | 7 December | 7 | — |
| 41 | 6 December | 13 " | 8 | 7 days, 17 h, 10 min |
| 38 | 6 " | 13 " | 7 | 7 days, 0 h, 67 min |
| F2 | 9 " | 17 " | 7 | 7 days, 5 h, 29 min |
| WV | 17 " | 23 " | 7 | 7 days, 5 h, 29 min |
| 74 | 13 " | 24 " | 11 | — |
| PB | 17 " | 24 " | 7 | 6 days, 23 h, 37 min |
| CR | 17 " | 24 " | 7 | 7 days, 10 h, 11 min |
| " | 17 " | 25 " | 8 | 8 days, 0 h, 21 min |
| 65 | 14 " | 26 " | 12 | 12 days, 5 h, 25 min |

* $\bar{Y} = 7.9$ days.

† From the onset of observed labor to the onset of estrous behavior (cf. Miller 1974).

December, when she reappeared in the same place. She gave birth there the following day. For nine identifiable females, the mean time ashore prior to parturition was 2.1 days (range

1–5 days), and this time was usually spent near the site where parturition subsequently occurred. Females copulated an average of 7.9 days after giving birth (range 6–12, $N = 10$: see

TABLE 2
SUMMARY OF TIME ON LAND FOR FEMALES OF *Arctocephalus forsteri*

| FEMALE | DAYS ON LAND AROUND BIRTH | | | SUBSEQUENT RECORDS | | | | |
|-----------|---------------------------|-------|-------|--------------------|-------|--------|-------|--------|
| | 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* | — | 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 | — |
| \bar{Y} | 1.9 | 9.4 | — | 4.4 | 2.8 | — | — | — |

* Pup died in the third feeding interval.

Table 1), and left the colony site about 0.9 days later ($\bar{Y} = 8.8$ days after giving birth, range 6-12, $N = 21$). Female CR copulated twice within 14 hrs. Copulations were observed from 13 November to 18 January ($\bar{Y} = 16$ December, S.D. = 12.0, $N = 54$); the associated variance is insignificantly greater than that for pupping ($F_s = 1.50$). The four copulations observed prior to day-block 6 involved very small females with light brown pelage, and two of these copulations were performed by SAMs. One member of this distinctively colored class of females had been tagged 2-3 yrs previously by Dr. I. Stirling (Stirling 1970), so the class consisted at least partly of virginal females (by analogy with *Callorhinus* [Kenyon, Scheffer, and Chapman 1954]).

Data collected on postparturient returns to the colony site by females and time on shore around birth are summarized in Table 2. Except for female BT, whose pup weakened and died, the first absence of females from land varied from 3-5 days, and nursing visits ashore were consistently briefer than adjacent periods of feeding at sea.

From 29 December to 13 February information was gathered on the amount of time females spent with their pups while ashore, and the fraction of time spent nursing. Females were accompanied by their pups 67.0 percent of their time ashore ($N = 2,568$), and pups nursed 51.2 percent of the time they were with their mothers ($N = 1,519$). Thus, females

known to have live pups were being nursed for 34.3 percent of their time ashore in the observation period.

Adult males held territories for as long as 9 weeks, during which period of fast they lost much body weight (cf. Miller, in press). Throughout their period of tenure, adult males excluded all other males except pups and most yearlings from their territories. The extent of social involvement of territorial males with nonterritorial males corresponded closely to the frequency with which members of the latter class entered the colony (Figure 3). A few territorial males returned briefly to their former territories some weeks after abandoning them, but the majority did not (Miller, in press).

For the period of time in which estrous females were known or assumed, on the basis of knowledge of when births occurred, to be present in the colony, the mean number of territorial males present per day was computed. This figure was divided into the total number of births to provide an estimate, slightly modified from that of Kenyon, Scheffer, and Chapman (1954), of the degree of polygyny (Figure 5). The sex ratios computed from census data fall below the "average harem size" (see legend, Figure 5) except for five dates for the subsidiary study area. The number of births that occurred on the latter area was probably greater than recorded, but, because of restricted visibility and relatively few hours spent in observation there, greater accuracy was not

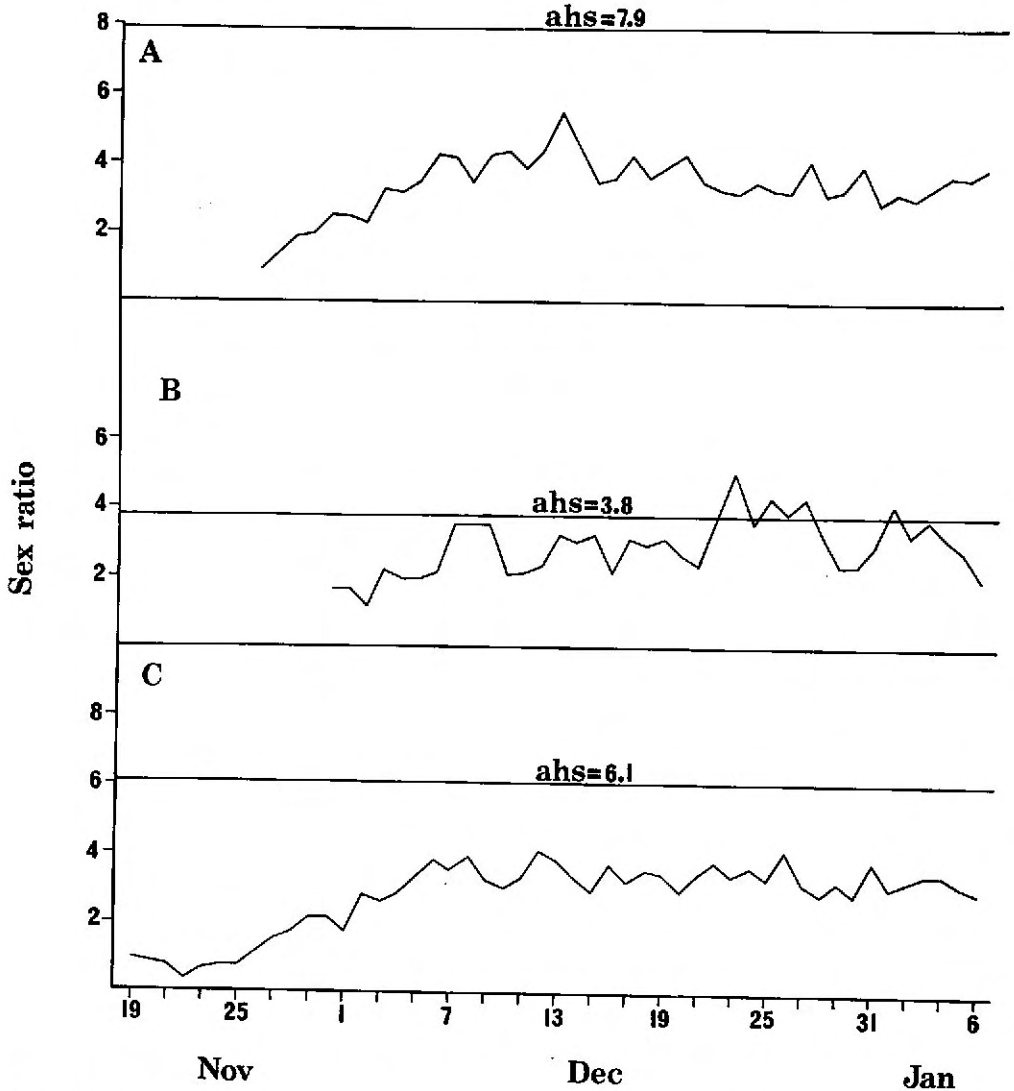


FIGURE 5. Seasonal trends in the sex ratio based on census figures for the main (A), subsidiary (B), and both (C) colony study areas (ahs = average harem size; modified from Kenyon, Scheffer, and Champan 1954).

possible. Furthermore, females from the main study area tended to move into the gully of the adjacent subsidiary study area at low water, further inflating the sex ratio estimate calculated from census data for some dates. It is apparent from the curves in Figure 5 that census data yielded an unreliable assessment of the extent of polygyny, and that seasonal factors imposed additional errors.

As they matured, and when their mothers were absent from the colony, pups tended to

congregate and rest in areas used little by adult seals. Data gathered from 26 December to 13 February and in May indicated that more than three-fourths of pup pods contained five pups or less, and never more than one-fifth of those pups whose mothers were absent from the colony site were in pods of larger size. There was a decline in mean pod size and in the fraction of pups resting in pods over this period, coincident with an increase in the relative frequency of lone pups (pups not with

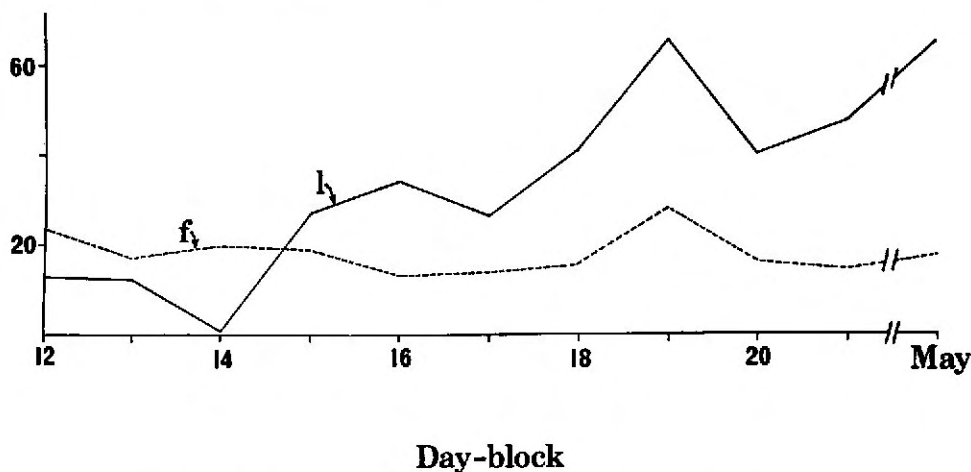


FIGURE 6. Seasonal trends in the percentage of pups with females (f) and alone (not with female and not in pup pod [l]).

TABLE 3

SUMMARY OF CENSUS DATA OF *Arctocephalus forsteri*, 26 MAY–2 JUNE 1971

| CLASS | N | PERCENTAGE |
|-------------|-----|------------|
| Adult Males | 6 | 1.0 |
| SAMs | 112 | 19.0 |
| Females | 173 | 29.3 |
| Pups | 299 | 50.7 |
| Total | 590 | 100.0 |

NOTE: Totals of daily census data taken on part of the colony site and forest behind it.

females and resting more than 1.5 m from the nearest pup) (Figure 6). The proportion of pups with females changed little over the sample period (Figure 6), suggesting that the feeding-nursing rhythms of females also changed little from late December to May.

Numerous SAMs were ashore from 26 May to 2 June 1971 (Table 3). Most of them were very small and I found them to be difficult to distinguish from females without capturing them for examination. Few adult males were present, and some very small females were recorded.

Also during the winter observations, some large SAMs were present on the main study area for 3 days in succession, during which time they engaged in unsteretyped threat displays with one another across topographically

distinct "territorial boundaries," mildly chased away smaller SAMs, and herded females. During the winter observations, the proportional representation of males in the forest behind the colony site varied inversely as their size (Table 4). There seemed to be a much larger fraction of pups in the forest during the winter work ($101/299 = 0.338$) than during the summer, although comparable figures were not compiled for the latter period.

DISCUSSION AND CONCLUSIONS

Population Trends in the Reproductive Period

Numbers of adult females declined in mid-November, then increased rapidly. This trend probably resulted in part from the tendency for pregnant females to feed heavily in the weeks before giving birth, as also has been suggested for *A. pusillus* (Rand 1956, 1967). The arrival ashore in late November of pregnant females a few days prior to their giving birth accounts for the rapid increase in numbers after 23 November. Many females were ashore throughout December, for two reasons. First, the period that a female spends on shore with her newborn pup is probably the longest continuous association they will ever have together on land. Since births occurred in a brief period, many females were in this post-

TABLE 4

HABITAT PREFERENCES OF DIFFERENT CLASSES OF *Arctocephalus forsteri*, MAY-JUNE 1971

| CLASS | BREEDING ROCKS | FOREST | TOTAL |
|------------------------|----------------|-----------|-------|
| Adult males | 6 | 0 | 6 |
| Large SAMs | 20 | 0 | 20 |
| Medium and Large SAMs | 32 | 2 | 34 |
| Medium and Small SAMs | 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 |

* Percentage of pups in association indicated, in habitat type.

partum association with their pups simultaneously. Second, pregnant females continued to arrive ashore throughout December. The decline in the female population in late December was due to the lower rate of recruitment of pregnant females, the increased amount of time that mothers were spending away from the colony while feeding, and probably the tendency of females who had lost their pups to stay away. Rand (1959) presented evidence of such a tendency in *A. pusillus*. Similarly, some *Liometopias* females with pups were on shore 63 percent of the time during the summer, whereas some without pups were ashore only 47 percent of the time (Gentry 1970).

The Female Cycle

Pregnant females of a number of species of otariids haul out a few days before giving birth (e.g., Bonner 1968, Gentry 1970, Peterson and Bartholomew 1967, Rand 1955). Reported intervals between birth and copulation are 5.3, "5 or 6," "3 to 7," 7.9, and 8 days for *Callorhinus*, *A. pusillus*, *A. tropicalis*, *A. forsteri*, and *A. gazella*, respectively (Bonner 1968; Paulian 1964; Peterson 1965, 1968; Rand 1956, 1959; this study) but in sea lions are between 11 and 30 days in duration (Gentry 1970, Odell 1972, Peterson and Bartholomew 1967). After copulating, *A. forsteri* females remained ashore for about 0.9 days, a period similar to those reported for *A. gazella* (Bonner 1968) and *Callorhinus* (Peterson 1965). Crawley (1972: 122)

reported that females of *A. forsteri* on the Snares Islands, New Zealand, "remained in constant attendance for at least three weeks" after birth, a figure hard to reconcile with other published figures, including my own, for arctocephalines.

A. forsteri pups suckled their mothers for about one-third of the time that the latter were ashore. This compares with figures of 75 percent for *Zalophus* (Peterson and Bartholomew 1967) and 30-45 percent for *Callorhinus* (computed from data in Peterson, unpublished). *Zalophus* and other sea lions commonly nurse the young for longer than 1 year (Gentry 1970, Hamilton 1934, Marlow 1968, Peterson and Bartholomew 1967, Sandegren 1970), as contrasted with *Callorhinus* (about 4 months) and *A. gazella* (about 3 months). At about 6 months of age, *A. forsteri* pups spend as much time with their mothers as when they are about a month old. More detailed comparative and ontogenetic studies on this matter clearly are needed.

Seasonal Timing of Reproductive Activities

In this study, copulations occurred over a greater span of time than did births (as in Australian *A. forsteri* [Stirling 1971a]), due in part to the assumed tendency of virgin females to mate early in the summer. Because most females of that reproductive class were absent from the colony during most intense breeding activity, and presumably copulated elsewhere

with SAMs, the observed span of time is probably an underestimate. Histological evidence in support of this interpretation has been provided for *Callorhinus* (Craig 1964) and *A. pusillus* (Rand 1955). Pinnipeds show delayed implantation of the blastocyst (reviews by Harrison 1969 and Harrison and Kooyman 1968), and it seems reasonable to assume that the narrower range of dates for births than for copulations results from the operation of an exogenous cue triggering implantation (Carrick et al. 1962). This cue is probably related to day-length and pineal function (Bigg and Fisher, in press; Cuello and Tramezzani 1969; Elden, Keyes, and Marshall 1971; Harrison 1963; Reiter 1973). The use of a predictable seasonal cue as a trigger to initiate physiological preparation is a fruitful strategy where the optimum time of raising young is predictable, and where "physiological prognostication" of future conditions is imperative because of a necessary preparatory phase such as embryonic growth (Schreiber and Ashmole 1970). In discussing southern elephant seals and northern fur seals, respectively, Carrick et al. (1962) and Peterson (1965, 1968) suggested that proximate environmental conditions (food availability, weather) are the critical selective factors upon which the annual cycles must hinge (cf. Stirling 1969). New Zealand and Australian populations of *A. forsteri* show synchrony in births fully as marked as do the species mentioned, yet *A. forsteri* inhabits a far less seasonal habitat than do they. Also, weaning in *A. forsteri* is probably less sudden and seasonally discrete than it is for *Mirounga leonina* and *Callorhinus*. A possible population genetical factor may favor synchrony in pupping and copulation by females; females of *A. forsteri* that pup and hence copulate very early or very late have a lower probability of being mated, and if mated, are unlikely to be fertilized by males that are capable of holding territories during the peak of breeding, for reasons of age, infirmity, or physical ineptness in obtaining and maintaining a territory (Bonner 1968, Buen 1947, McGilvrey 1957, Paulian 1964). Such females, therefore, are more likely to mate with a male that deviates from the genetic norm characterizing those males holding territories during the main part of the breeding

season. I have argued elsewhere that mate-choice by female otariids is to some extent obviated by the intensity of competition among adult males, which results in low genetic variance among them (Miller, in press), and suggest that a temporal equivalent of McLaren's "marginal male effect" (McLaren 1967) may help to maintain seasonal synchrony in dates of parturition and hence copulation by females.

Seasonal Changes in Population Composition

SAMs of *A. forsteri* in New Zealand tend to segregate from colonies during the breeding season (Hector 1871, Crawley 1972). It is unlikely that the decline observed for the SAM population at the Open Bay Islands in the summer was a consequence of competition with parturient females for food within feeding range of the colony site—even though SAMs decreased in numbers over the summer, the "neuter" class increased (cf. Abegglen and Roppel 1960 and Paulian 1964). By mid-February, SAMs and "neuters" were few, but nonmothers were more abundant than during midsummer (contributing to the second population peak of females in mid-February; cf. Figure 1). Behavioral exclusion of SAMs by adult males and of nonmothers by mothers may partly explain these trends (cf. Ling 1969).

Juveniles, yearlings with females, as well as old SAMs and some adult males occur in late summer and early winter at such locations as Macquarie Island, but are essentially absent from there over the winter (Gwynn 1953, Csordas and Ingham 1965). Most adult and many juvenile males then concentrate on hauling grounds that are generally situated north of breeding colonies (Singleton 1972; Stirling 1968, 1970; Stonehouse 1965, 1969), whereas a good number of juvenile males locates at the colony site (this study). The distribution of very young females is not known, though some may occur at such places as Macquarie Island (the sex of small juveniles there has not been determined [Csordas and Ingham 1965]).

The significance of seasonal changes in population composition and dispersion of otariids is obscure. Postbreeding movements away from colony sites that are otherwise inhabited

throughout the year are well documented for adult males of a number of species (Bonner 1968, Mate 1973, Odell 1972, Orr and Poulter 1967, Peterson and Bartholomew 1967, Peterson and LeBoeuf 1969, Warncke 1966). Could the rigidly territorial social system of the summer months, the extreme sexual dimorphism in size, and the high levels of intramale aggression that appear during the breeding season, and that are correlated with the proximity of females, be incompatible with year-round residence at colony sites by adults of both sexes? It is interesting to note in this regard that *A. galapagoensis* is a year-round resident of the Galápagos Islands, that its breeding season is poorly defined (Heller 1904), and that it shows little sexual dimorphism in size (Repenning, Peterson, and Hubbs 1971). Adult males in a number of species of fur seals frequent colony sites in the winter in low numbers (e.g., Bonner 1968, Stirling 1971a, Vaz-Ferreira 1956), but information on their social relations and dispersion is lacking.

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