Miller, E.H. (1974) Social behaviour between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. Australian Journal of Zoology **22**: 155-173.

Aust. J. Zool., 1974, **22**, 155–73

Social behaviour between Adult Male and Female New Zealand Fur Seals, *Arctocephalus forsteri* (Lesson) during the Breeding Season

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Abstract

Observations on social relations between territorial adult male and adult female *A. forsteri* were made on the Open Bay Islands, Westland, New Zealand, during the breeding season 1970–71. Threats comprised about 80% of all social encounters between males and females. Attempted and successful olfactory investigations of females by males, herding of females by males, and 'peace-keeping' by males accounted for about 18% of all encounters, and such interactions usually had agonistic overtones. Less than 2% of all encounters were not agonistic from their inception. Herding responses of males were vigorous and frequent, and are interpreted as serving two functions: containment of females and communication of certain of the herding males' characteristics to the females. Because herding occurs throughout the Otariidae, and is rarely effective in containing females, the second function is probably more important. Males showed much individual variation in their herding tendencies. The frequency of herding behaviour was depressed at warm temperatures. Olfactory investigations of facial and perineal regions of females were common and were not restricted to peri-oestrous females. Only oestrous females were sexually receptive to and showed little aggression toward territorial males, and males detected their physiological state mainly through olfaction. A few oestrous females solicited males with mock threats or by rubbing against them. Precopulatory and early copulatory behaviour was characterized by a moderate amount of mutual contact-seeking behaviour, multiple mounts by the male, and 'activation' of the female by the male biting her. Copulations appeared to be terminated through physical resistance by the female, which resulted in ejaculation and subsequent dismounting by the male. At the time of female resistance, the male commonly had to physically control her. The sudden return to aggressive behaviour typical of non-oestrous females may be mediated through a neural inhibitory process resulting from cervico-vaginal stimulation, as has been proposed for the guinea pig.

Introduction

Members of the family Otariidae (order Pinnipedia) are among the most polygynous and gregarious of mammals. Characteristics common to otariid societies have resulted largely from competition among males for access to oestrous females, and from the need for a terrestrial habitat in which to give birth, nurse the young, and copulate (Bartholomew 1970). Social encounters between adult females and adult territorial males form a numerically and socially important part of the social matrix during the breeding season. Appreciation of the ecological, evolutionary and sociological significance of such encounters cannot be made without detailed knowledge of their forms, social contexts, and results.

Arctocephalus forsteri (Lesson) is found in Australia, New Zealand, and certain of the subantarctic islands lying south of them (King 1969). Recent studies on the behaviour and ecology of Australian *A. forsteri* have been made by Stirling (Stirling

1971*a*, 1971*b*; Stirling and Warneke 1971) and Gentry (1973), and of New Zealand *A. forsteri* by Stirling (1968, 1970) and Crawley (1972).

At the beginning of the austral summer there is intense competition among adult male *A. forsteri* for territories on land or in shallow water next to the colonies. Through chases and fights, the territories are kept free of other males of all ages except for pups and the few male yearlings still at the colony. Territorial males typically fast throughout their period of tenure [see, however, Mate (1973)] which may exceed 2 months. Within a few weeks after the firming of territorial relations among adult males, pregnant females arrive ashore to bear pups. Females copulate once (rarely twice) 1–2 weeks post partum and nurse their progeny regularly for up to, and sometimes over, 12 months (Miller 1971).

This report describes and analyses social encounters between territorial male and adult female New Zealand *A. forsteri* observed during the austral summer of 1970–71. Some data on the Bass Strait fur seal, *A. pusillus* (Schreber), are included.

Species names for pinnipeds follow Rice and Scheffer (1968) except where changed by Repenning *et al.* (1971) or Burns and Fay (1970).

Materials and Methods

Observations were made daily from 27 October 1970 until 13 February 1971 on Taumaka, the larger of the two Open Bay Islands lying off Haast, Westland (South Island), New Zealand. Fur seals haul out on the leeward limestone shelves of the island throughout the year. The top of Taumaka is covered with a dense growth of kie-kie, *Freycinetia banksii*, with a leeward edge of low forest consisting largely of *Hebe elliptica*, *Schefflera digitata* and *Fuchsia excorticata* (cf. Burrows 1972). Although some fur seals penetrate the vegetation as far as 50 m in places, most seals haul out only on the limestone shelves or in the various guts and crevasses along these shelves. Most social encounters between territorial males and adult females (hereafter simply termed 'males' and 'females') occur there.

Two observation hides were erected in the forest, overlooking different parts of the colony. A grid of squares, each of area 10 m^2, was painted on the main study area. This facilitated accurate mapping of boundaries of males' territories and the recording of movements of individually known animals (recognized from scars, characteristics of the vibrissae, etc.). Records of activities and movements of recognizable seals were entered on maps of the study area, and descriptive and quantitative notes were made as appropriate.

Observations on the behaviour of *A. pusillus* were made at a large breeding colony at Seal Rocks, Victoria, from 13 to 18 December 1971.

Results

Nomenclature for Vocalizations

Throughout the paper, 'whimpering' will refer to a rapidly repeated, high-pitched nasal sound produced while the mystacial vibrissae are moved between, alternately, positions of moderate and extreme erection, each sound occurring while the vibrissae are in the extreme position (Bonner 1958, 1968) [This sound is termed 'barking' by Stirling and Warneke (1971)].

'Trumpeted roaring' will refer to a loud, generally long-range vocal threat used by various species of the fur seal genera *Callorhinus* (Peterson 1965) and *Arctocephalus* (Stirling and Warneke 1971) (these authors term it the 'full threat call').

'Oral snorting' describes rapid and forceful expiration of air through the mouth (*v.* 'nasal snorting'), and 'growling' will refer to a call of low pitch, given with the

mouth open, and usually directed at another seal at close range. This is the 'male low intensity threat' of Stirling and Warneke (1971).

These sounds are neither sex- nor age-specific, though the first two are used most often by males (Miller 1971).

Herding

(i) *Description*

Herding was the most vigorous of the classes of social encounters recorded, and accounted for about one-sixth of total recorded social encounters (Table 1).

Table 1. Summary of social encounters between males and females
Based on 43·25 h of observation, 7 December–8 January. 1033 females and 351 males were involved in the encounters

Type of encounter	Number	Percentage[A]
Non-aggressive	15	6·1
Peace-keeping	29	11·8
Approach-herding	202	82·1
Total non-aggressive and herding	246	19·8
Female-to-male threats	344	34·4
Mutual threats	655	65·6
Total threats[B]	999	80·2
Total encounters	1245	—

[A] Relative to total encounters in each group, except for percentages for each group, which are relative to the total number of encounters.
[B] Encounters which involved threat alone; many herding and peace-keeping encounters developed into threat encounters, but these are not included under 'Threats'.

Movement of a female within a territory and near its boundary usually caused the male to try to place himself between the female and the boundary. Males showed good abilities in judging the speed and angle of approach necessary to intercept a female before she reached the territorial boundary. Males whose territories abutted on male-uninhabited forest generally permitted females to move unhindered in that direction. In contrast, females approaching the sea from within territories situated on the shoreline were usually approached and herded by the males whose territories they were leaving.

During herding, a male whimpered continually and usually placed himself in a broadside upright posture between the female and the boundary (Fig. 1*a*). When so positioned, the male performed a sideways 'shuffle' in the direction of the female, forcing her backwards either through or without bodily contact; or else the male remained stationary in the posture described, often giving rapid ventrolateral head and neck movements of small amplitude ('head flicks') in the direction of the protesting female (Fig. 1*a*). Rapid sideways shufflling was used by active and aroused males; others tended to remain motionless and upright, whimpering. Females that vigorously resisted being herded tended to evoke greater activity and more frequent and intense threats from herding males.

Herding males whimpered almost continually, except when they threatened the females. At such times, they usually growled or, exceptionally, gave a trumpeted roar. Vocal threats usually accompanied head flicks and open-mouthed threats directed at the female. The most extreme herding response occurred when one male threw himself on top of a female that was leaving his territory. An identical sequence was seen in *A. pusillus*, although herding in that species was generally less frequent and less intense than in *A. forsteri* [cf. Rand (1967) on African *A. pusillus*.]

The responses of females to being herded varied. Some simply backed away quietly and tried to leave the territory elsewhere. Others acted aggresively by biting and shaking the skin of the male's chest or neck, while growling and snarling. A number of females stopped worrying the forequarters of the male and quickly moved to nip more sensitive regions such as the hip, flank, and rear flippers. Males bitten in those places generally turned back to threaten, whereupon the females tried to run around them. Such a ploy by a female was usually ineffective. Occasionally, a male was confronted by an exceptionally aggressive female and would permit her to leave even after showing incipient herding. More usually, a female had to escape elsewhere and frequently did so surreptitiously, with head and neck lowered, glancing uneasily at the male whose territory she was leaving. Females that were about to cross a territorial boundary and saw or heard a male approaching ran quickly across the boundary unless the male was quite close (see below).

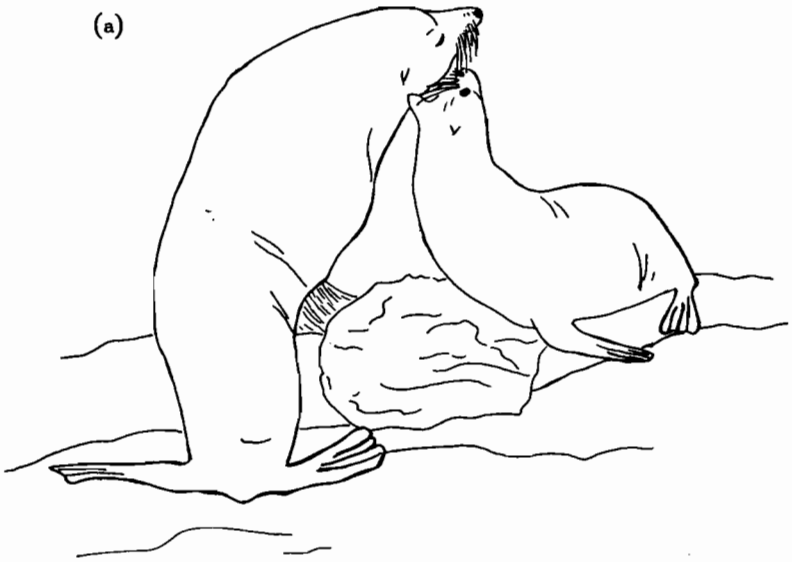
The response of a female to an approaching male was to wheel around and orient directly, visually and bodily, keeping her hindquarters away from him, and to threaten with open mouth and growls or oral snorts, or both, with snapping and jabbing in the direction of his face (Figs 1*a* and 1*c*). So automatic was this wheel-and-orient response that a female about to cross a boundary, and perceiving a male especially close, would turn to confront the male rather than quickly leave the territory.

Despite the sometimes protracted herding efforts by males, all females that were observed being herded finally escaped. For example, in early November, male PH herded the lone female in his territory for about 8 h, an unusually long period. Finally, he relaxed and permitted her to leave. She gave birth 2 days later in a distant territory.

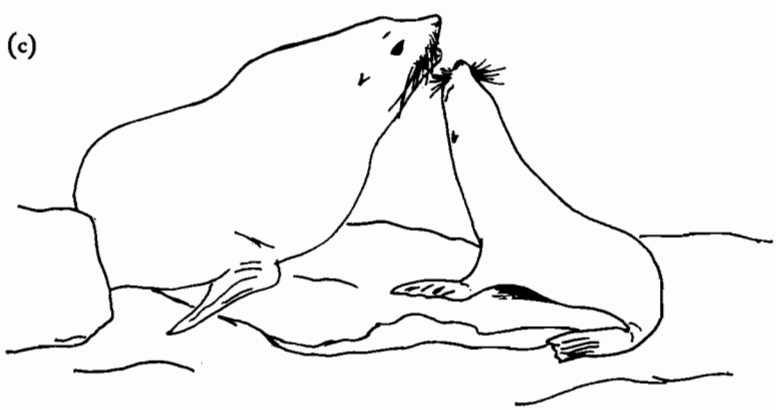
(ii) *General analysis*

In an attempt to isolate factors contributing to assiduousness and relative frequency of herding, records of herding (or approaches to females with apparent intention to herd) were obtained for individual males under a variety of seasonal and thermal conditions. Large differences among males were noted. For example, males AL and BCH held territories in which no pups were born and in which, therefore, there were no resident populations of females, yet BCH herded transient females about three times as often as did AL. Two injured males with impeded locomotion herded relatively little and with low vigour, but uninjured male NG attempted herding in only two of 23 recorded instances of females leaving his territory. Sizes of territories,

Fig. 1. Herding, olfactory investigation, and male threat. (*a*) Male intervening between female (on right) and territorial boundary. Note the direct facial orientation of the female. (*b*) Male investigating perineal region of female, before latter can turn to threaten. (*c*) Male threatening small female. Note the slight rotation of the male's head, and the slightly erect vibrissae of the female.


(a)


(b)


(c)

duration of time with territorial status, and topographical characteristics of territories did not systematically influence the extent or intensity of herding. Whether a female left a shoreline territory to go to sea or to an adjacent territory, she had about the same likelihood of being approached or herded. In the former case, males responded 54·8% of the time ($N = 62$); in the latter, 44·0% of the time ($N = 159$). These percentages do not differ significantly by t_s estimate (cf. Sokal and Rohlf 1969, pp. 607 ff.).

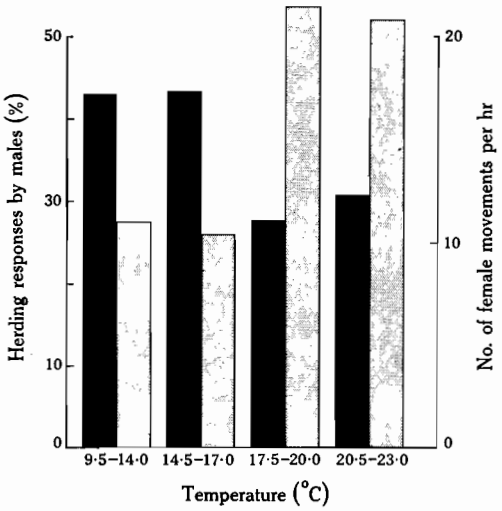


Fig. 2. Effect of air temperature on movements by females near and across territorial boundaries (stippled bars), and on herding responsiveness of males (solid bars).

Table 2. Effect of ambient temperature on rate of encounter between moving females and herding males

Based on 43·25 h of observation, 7 December–8 January

Quantity	At ≤ 17°C	At > 17°C
Number of territorial males present	476	245
Percentage involved in herding encounters with females	31·1	35·1
Total number of herding encounters	468	240
Number of encounters per male	0·98	0·98

Males were relatively inactive during the hot mid-day when air temperatures sometimes exceeded 25°C, except for those holding shoreline territories and able to cool themselves in the sea. Conversely, females tended to move frequently when it was warm, shuttling between young pups and the sea, or moving to the sea until the cool evening (Fig. 2). Those males that held territories at the water's edge showed greater responsiveness under warm ambient conditions to moving females than did males holding inland territories and without access to the sea. Territorial males in the former situation showed 65 approach–herd responses to 149 female movements, against 51 to 188 for males in the latter situation ($\chi^2 = 5{\cdot}96$; $0{\cdot}01 < P < 0{\cdot}025$). The increased activity of females and decrease in herding responsiveness of males produced similar male–female encounter frequencies (due to herding) at all temperatures (Table 2).

Non-herding Encounters

(i) *Olfactory investigation*

Males frequently attempted to sniff at the perineal and facial regions of females. This could sometimes be accomplished before the female could resist (Fig. 1*b*) but usually males had to contend with a resisting female. Typically, a whimpering male approached a female, leaned toward her while nodding his head up and down, and avoided her jabs and snapping jaws. A male's interest sometimes waned at once, but some males persisted in their attentions for up to an hour. Often a male was content to displace a female from her place of rest and smell the rock upon which she had lain.

As in herding, males generally showed aggression only toward females that strongly resisted. Most obvious aggression in encounters involving male attempts at olfactory investigation resulted from the reluctance of females to leave their resting places. In such situations, males usually assumed a threat posture characterized by: a stiffening of the neck; orientation of the neck at about 45–65° relative to the ground, with the snout pointing up along the same axis; oblique orientation of the face relative to the female due to slight lateral rotation of the head; and a slightly open mouth accompanied by growls (Fig. 1*c*). Rapid head flicks, with or without bodily advance, were indicative of a more highly aggressive state and usually made the female withdraw quickly. Displaced females often waited nearby until the male finished his inspection of their former resting spot, then quickly reclaimed it.

Females usually resisted the approach of an investigating male with jabs and open-mouthed threats (rarely, biting) in the direction of the male's face. Persistence or overt aggression by the male invariably evoked some elements of submissive behaviour: retraction of the corners of the mouth; widely gaping mouth; relaxed lower lip; averted wide-eyed stare; highly pitched whining vocalization (high-intensity submission only); and full erection of mystacial vibrissae (high-intensity submission only: Fig. 1*c*) (Miller, unpublished data). In this study, males spent up to 4% of their daylight hours interacting overtly with females (Miller 1971) and, despite its irregular and non-systematic occurrence, investigation appeared to be the only means by which males regularly assessed the reproductive states of females.

(ii) *Displacement and dispersion*

Males preferred certain locations within their territories for resting. Shaded locations or those with pools of water were preferentially used under warm conditions. Females also favoured such locations during the heat of the day, so altercations over their use were common.

Displacement of females usually involved a higher order of threat than was used in the types of encounter described above. A male approached a desired location and threatened, with head up, oblique visual orientation, rapid head flicks, and open-mouthed threats, any female present, especially those that disputed the intrusion. Such encounters were usually very brief and unambiguously settled in favour of the male.

Non-oestrous females, even at rest, were utterly intolerant of the close proximity of males, though they tolerated smaller distances when both were at rest than at other times, allowing, rarely, slight physical contact (e.g. overlap of parts of the flippers). Even then, however, females oriented away from males' heads and anterior body parts.

Small distances between resting males and females were most commonly seen under warm conditions, when they sought relief in the few sources of shade and water available (cf. Gentry 1973).

(iii) *Peace-keeping*

Agonistic encounters among females, but not those involving pups and yearlings, attracted the attention of territorial males, and the latter commonly approached the sites of such encounters. In *A. forsteri*, such peace-keeping accounted for about 2% of recorded encounters between males and females (Table 1).

Females that were involved in agonistic encounters among themselves, and that were approached by a male, transferred their attention to him and oriented in a typically defensive manner, often showing indications of submission (Fig. 3; note the facial expression of the female in the background). For his part, the male would at the most threaten (usually) the aggressor in the encounter or at the least, try to sniff at one or both of the females. There was no apparent attempt to 'reconcile' the females, although male intervention generally caused termination of the dispute.

Males did not preferentially drive away non-oestrous females that interacted agonistically with oestrous females over the use of space, and there was no evidence that the behaviour permitted dense concentrations of females to build up.

(iv) *Miscellaneous*

There are few reports of non-sexual behaviour of pinnipeds not involving threat or attack by the female. In *A. forsteri*, a male walking near resting females invariably elicited open-mouthed threats, oral snorts, and growls from them, even if the male showed no interest in them (such threats are entered as unidirectional in Table 1). Females sometimes spontaneously ran toward nearby males and nipped them, usually evoking mild threat responses from the males.

Contact-seeking behaviour outside of sexual contexts was not observed.

Naso-nasal greetings, usually initiated cautiously by males, comprised only about 1% of observed encounters (Table 1) and these commonly led to typical agonistic encounters.

Copulatory Behaviour

(i) *Introduction*

Part or all of 59 copulations was observed, all but two of which were performed by territorial adult males. Females were sedentary during the birth–oestrus interval (about 8 days) and consequently tended to copulate with the male in whose territory they pupped. Of nine females observed to pup and copulate, two copulated with males other than the ones in whose territories they had given birth. Of six other females that gave birth but that were not seen to copulate, only one moved to a different territory within 8 days after parturition. Combining these figures, three of 18 females (16·7%) may have copulated with males other than the ones in whose territories they gave birth.

The frequency of copulation tended to be lowest in the hot early afternoon. Copulation frequencies, per 2-h interval throughout the day were ($N = 59$): 0500–0700, 10; 0700–0900, 6; 0900–1100, 13; 1100–1300, 10; 1300–1500, 3; 1500–1700, 2; 1700–1900, 10; 1900–2100, 5.

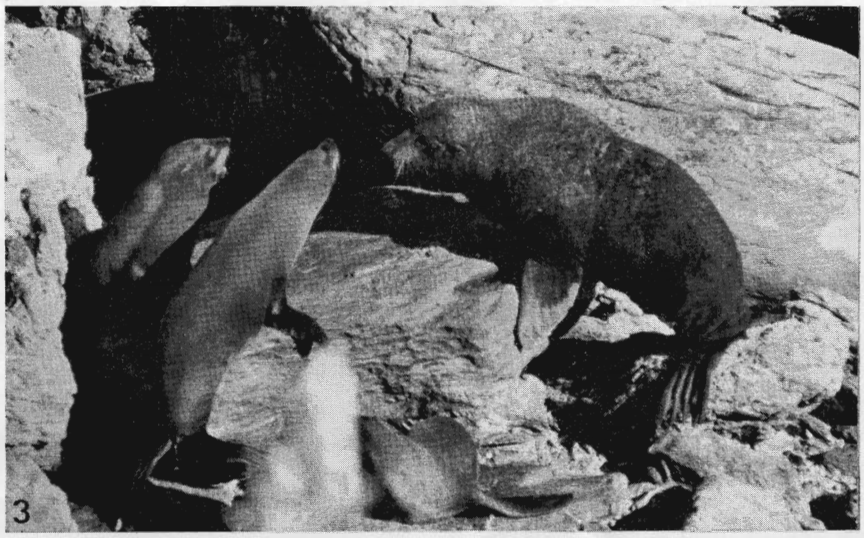


Fig. 3. Adult male approaching two females that had been squabbling over the rock shown. Note how the females' attention is directed to the male, and that they have backed away from him.

Fig. 4. Adult male biting back of neck of female in early phase of copulation.

(ii) *Sexual receptivity and precopulatory behaviour*

Female *A. forsteri* were sexually receptive only during a brief period of oestrus, lasting up to about 24 h, and usually copulated but once (Miller 1971). In this study, of 10 females kept under intensive observation during oestrus, one copulated twice, yielding a mean copulation rate of 1·1 per female.

To the human observer, oestrous females behaved very similarly to non-oestrous ones, except during locomotion and when interacting with males. Oestrous 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 tucking the flippers beneath the body. They showed a lower level of aggressiveness toward males and a 'playfulness' not seen at other times. However, such characteristics were generally made apparent only after males initiated encounters with them; very few oestrous females sought out encounters with males (see below). Female *A. forsteri* that did not respond aggressively to investigating males were always sexually receptive, though not all sexually receptive females were initially unaggressive toward investigating males.

A few females actively solicited males by approaching them silently with mouth slightly ajar and eyes widely opened and seemingly unfocussed, gently grasping the males' lateral neck skin or flank, and slowly twisting their heads from side to side while maintaining a grip. One female bounded, with mouth ajar, toward a male and silently made some slow lateral swings of the head and neck at him in mock threat. Another rolled onto her back and placed her fore and rear flippers against the chest of the male. When in close contact with males, some oestrous females leaned or rubbed against them.

There were no conspicuous changes in the appearance of the vulva coinciding with oestrus.

Since oestrous females were generally silent and not actively involved with courtship, either visually or tactually, males must have ascertained their reproductive states through scent, taste, or both. Male *A. forsteri* were never observed to lick any part of females, although one male *A. pusillus* was seen to extrude his tongue when his snout was thrust into the vulva of an oestrous female. Sexual receptivity in *A. forsteri* could be reliably inferred from the level of interest shown by a male in smelling her vulva, face, or both, even when the female showed incipient resistance to such investigation. The male's whimpering became more high-pitched, and he nodded his head more rapidly and with greater amplitude, often shifting his weight from side to side. He sometimes stopped whimpering to smell the female's face or perineum, and prolonged or repeated smelling of this region served to excite the male further. As a male became more excited, he would push against the female with his chest or lower his head and neck to rub against her. The female, in turn, would become quieter and more passive.

Oestrous females copulated with the first male they contacted and showed no preference for particular males.

(iii) *Copulation*

Some males mounted immediately upon finding that a female was sexually receptive. Others excitedly smelled the facial and perineal regions of females for up to 15 min before mounting. Early mounts in a copulatory sequence were typically brief (Fig. 5) and unaccompanied by intromission or pelvic thrusting. Males mounted up to nine times before the copulation was terminated (Fig. 5) and 67·3% of 53 copulations involved multiple mounts.

Females often maintained an upright posture early in a copulatory sequence and not infrequently leaned back to rub against the male. Males often forced the passive females into a prone position by pressing against them with the neck, then mounted, and as quickly dismounted. Although female passivity occurred in and was probably

a part of the stimulus situation necessary for successful copulation, males appeared to try to invigorate females by 'gnawing' or biting the neck or upper back (Fig. 4). Such biting usually increased in vigour until the female responded, for example, by lifting the head to weakly threaten the male with open-mouthed threat and growling (as in Fig. 4). Such resistance further excited the male who remounted or, if mounted, increased the rate and amplitude of pelvic thrusting. Biting appeared not to function in restraining females and was never strong enough to injure them.

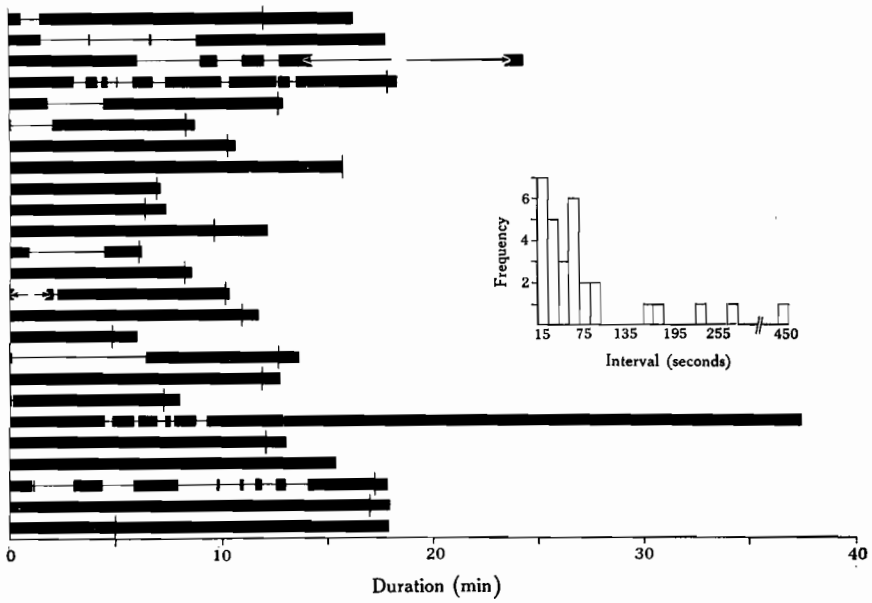


Fig. 5. Temporal patterning in copulatory sequences. Each record represents one copulation. Thick lines indicate mounted, thin lines unmounted phases. Broken thick lines, observations incomplete. Short vertical bars, onset of resistance (when present) by the female. Inset: frequency distribution of durations of the intervals from onset of female resistance to final dismount by the male.

If a female rose and started to slowly walk away, as sometimes occurred when males showed little activity during an unmounted phase, or when the uneven ground prevented intromission, the male would rush after her, force her down, and quickly mount. It never seemed as though the female was actually trying to escape the male's attentions so much as trying to accommodate him by moving to a more suitable location, or to interest him by token resistance (cf. Stirling, 1971*a*).

Males mounted females dorsally, with a single exception. In that instance, the female was on her side, but immediately upon intromission, shrieked and turned to lie on her ventrum. Interestingly, female *A. pusillus* were not uncommonly mounted while lying on their sides.

Female *A. forsteri* showed no postural responses, such as straightening of the spine in the lumbar region or spreading of the rear flippers, in response to precopulatory activities of males.

Males remained upright throughout early stages of copulation, whimpering and shifting their weight from side to side. When a female started resisting late in copulation the male lowered his neck so as to completely cover her, thereby controlling her,

presumably until ejaculation. It appeared essential to use this ploy to control large females that resisted. Males were able to prevent females from leaving copulation by assuming this posture, despite their attempts to wriggle out. A male *A. pusillus* was seen to mount and hold down by force a non-oestrous female for 7 min, despite her vigorous protests.

The first indication of impending resistance by a female *A. forsteri* was her increased alertness; she opened her eyes and looked up at the male, sometimes lifting her head off the ground. This was followed by growling or snarling, then by stretching up and twisting to bite the male's chest. This response occurred in 88·6% of 35 copulations. If the male did not dismount, the female would squirm ineffectually and snarl with varying pitch. It was at this stage that a male often lowered himself onto the female. In *A. pusillus*, females frequently bit males, twisting up and to the side, or arching dorsally to bite the male's midventral region (cf. Rand 1955 on African *A. pusillus*). Male *A. forsteri* did not often lean down to rub the chest against the female with broad lateral motions as did *A. pusillus*.

Most (83·9%) of the copulations terminated within 90 s of the commencement of female resistance, the longest time being 7 min 47 s (Fig. 5, inset). Intervals between initial female resistance and dismounting by male *A. pusillus* were similar: 0, 2, 8, 20, 34, 50 and 76 s. When female *A. forsteri* started to resist but the male had apparently not yet ejaculated, the male would lower himself and increase the amplitude and rate of pelvic thrusting. There were no overt signs of ejaculation, and thrusting was often so weak and intermittent as to render meaningful counts impossible, unlike *Eumetopias* (cf. Gentry 1970).

The sex responsible for the termination of a copulation was difficult to determine. Usually a male dismounted or permitted the female to wriggle out soon after she started resisting. In both cases the male was directly responsible for the termination of the sequence, though the female, in exciting the male to ejaculation by her resistance, may be indirectly responsible. Since both sexes apparently play a role, it may be artificial to assign the role of 'termination of copulation' to one sex. It is clear, though, that females of normal size cannot physically terminate a copulation with an adult male.

The briefest copulation, measured from the beginning of the first mount to the final dismount, was 5 min 25 s (single mount), and the longest was 38 min. Some copulations were protracted, with brief series of mounts and intermittent periods of apparent loss of interest by the male.

After a copulation that ended with female resistance, the female usually bit and threatened the male actively with open-mouthed threat and growls. Such energetic antagonism contrasts with the behaviour of female *A. pusillus*, which usually lay placidly after a copulation, and did not (or only very mildly) attack the male. The few female *A. forsteri* that did not resist in the latter stages of a copulation acted similarly before and after the copulation, moving with jerky and uncoordinated actions. The responses of males varied with those of females. Males that were threatened were prone to respond in kind. Females that started to leave territories after copulating seemed to be herded no differently from non-oestrous females.

Males were never seen to leave a copulation in order to chase or threaten other males. Other males took advantage of the reluctance of males to forego interactions with oestrous females. Most of the territorial transgressions observed among terri-

torial males took place when one male was interacting with females, both oestrous and non-oestrous.

Discussion

Herding

Attempted control of female movements by male pinnipeds is best developed and most conspicuous in the Otariidae, though most species of the Phocidae probably show this tendency in some form (e.g. Laws 1956; Kenyon and Rice 1959; Carrick *et al.* 1962; Cameron 1967; Darling and Boyd 1969). This difference between the families relates directly to the otariids' greater capacity for movement on land and to the prevalence of terrestrial territoriality in that family as compared to the phocids. Within the Otariidae, all species show herding behaviour to some extent, but there appears to be a major difference in the degree of development of this behaviour between the Arctocephalinae (fur seals) except *A. pusillus* on the one hand, and the Otariinae (sea lions) plus *A. pusillus* on the other. Of the arctocephalines, *Callorhinus* shows the most aggressive and vigorous herding behaviour (Bartholomew 1953; Bartholomew and Hoel 1953; Peterson 1965, 1968). Herding in *A. forsteri* is milder and resembles that reported for other species of *Arctocephalus* (Bonner and Laws 1964; Paulian 1964; Bonner 1968). All arctocephalines except *A. pusillus* breed on rocky seacoasts, in sea caves, and generally in extremely irregular and rugged habitats (Kenyon 1960; Paulian 1964; Bartholomew 1966; Bonner 1968; Peterson *et al.* 1968; Miller 1971). Sea lions and *A. pusillus* breed on sandy beaches or relatively smooth flat rock benches (Waite 1909; Hamilton 1934; Warneke 1966; Peterson and Bartholomew 1967; Rand 1967; Gentry 1970; Sandegren 1970; Cooper 1972), situations which must render the efficacy of herding very low. In typical arctocephaline habitat, males' territories often have only a few exits and entrances, which facilitates herding. Thus, Paulian (1964) described how a female *A. tropicalis* was trapped in a male's territory because the male could easily block the only exit. Habitat differences between the two groups of otariids can thus account for the difference in development of herding. The subfamily Otariinae, and perhaps *A. pusillus* (cf. Repenning *et al.* 1971), is more highly derived than the Arctocephalinae, and one of the distinctions between them is body size; otariines (plus *A. pusillus*) are considerably larger than other *Arctocephalus* species and *Callorhinus* (King 1964; Warneke, personal communication). Evolution of increased body size may have reduced ease of movement on land to the point where vigorous herding became less effective and imposed a significant energy drain on fasting males. Considered together with the characteristics of breeding habitats of *A. pusillus* and otariines, it can be appreciated that herding beyond a certain level of activity may have come to be selected against in those species.

Because herding behaviour is still present in all species of otariids, and because even in the arctocephalines it rarely serves to contain females within territories, it is likely that there is a selective advantage to its presence common to both subfamilies. This common feature may be communicative; herding may serve to display to herded females certain attributes of herding males, such as vigour, experience, etc. This could provide, in theory at least, a basis for ultimate choice of mate by females, in affecting their movements in the birth–oestrus interval and their choice of pupping location. Since there is no good evidence of mate choice in the Pinnipedia (cf. Miller

1974), however, it seems likelier that herding provides herded females with criteria for 'normal' males. Thus abnormally active male *Eumetopias* may repel females (Gentry 1970).

Body Contact, Peace-keeping, and Aggression

Adult male and female *A. forsteri* seek and tolerate body contact with each other only when the female is in oestrus. This is characteristic of arctocephalines except *A. pusillus*, but is less marked in *Callorhinus* (cf. Stirling 1972; Gentry 1973). All otariines, walruses (Odobenidae), and, to a lesser extent, *A. pusillus* tolerate and even seek (e.g. Hamilton 1934; Sandegren 1970; Ross 1972) body contact with unrelated conspecifics. Whereas in walruses this propensity seems to be due to the need for conservation of body heat (Fay and Ray 1968), its adaptive basis in other species, particularly those inhabiting climates less extreme than does the walrus, is unknown and needs comparative study.

Peace-keeping is widespread in the Otariidae, having been reported for both subfamilies (Hamilton 1934; Eibl-Eibesfeldt 1955; Rand 1955; Ferreira 1956; Kenyon 1960; Rand 1967; Marlow 1968; Schusterman and Dawson 1968; Sandegren 1970). Peterson and Bartholomew (1967, p. 31) suggest that in *Zalophus* this reflects nothing more than 'a general reaction to heightened activity', and my observations on *A. forsteri* support this interpretation for otariids. It thus does not seem to occur for the purpose of terminating agonistic encounters among females, though such is a typical result.

The dominant quality in male–female social encounters is aggression, particularly on the part of the female. The low percentage of interactions in which this was absent, and the relatively large number of unidirectional threats directed by females at passing males, bear this out (Table 1). Considering the lack of pair-bonds and social cooperation in this species, the absence of amicable behaviour is not surprising. There is little reason for females not to react aggressively toward males, whether in herding or investigation. Unprovoked antagonism by females toward males is the rule among pinnipeds (for otariids: Bonner 1958; Bonner and Laws 1964; Gentry 1970; Stirling 1971*a*; for phocids: Laws 1956; Hewer 1957; Kenyon and Rice 1959; Hewer and Backhouse 1960; Cameron 1967, 1969, 1970; Cline *et al.* 1971; LeBoeuf 1972).

Copulatory Behaviour

The midday decline in sexual activity observed in *A. forsteri* agrees with that known for *Eumetopias* in Alaska (Sandegren 1970) and California (Gentry 1970). In *A. forsteri*, the decline was not due to a decreased frequency of encounter between females and territorial males (Table 2). The tidal cycle influences sexual activity in some phocids (Venables and Venables 1957, 1959; Hewer and Backhouse 1960), and northern elephant seals show heightened sexual activity in early morning, around noon, and again in the evening (LeBoeuf 1972). Similar proximate environmental stimuli could conceivably affect diurnal trends in *A. forsteri* as well. It may be operationally difficult to separate effects of such stimuli from effects due to a fairly inflexible birth–oestrous interval; *A. forsteri* shows a diurnal trend in frequency of births similar to that of copulations (Miller 1971).

Active seeking of males by oestrous females may sometimes occur in grey seals and southern elephant seals (Laws 1956; Curry-Lindahl 1970) and in the otariids *A. pusillus*, *Zalophus*, *Eumetopias*, and perhaps *Callorhinus* (Bartholomew and Hoel 1953; Peterson and Bartholomew 1967; Rand 1967; Gentry 1970; Sandegren 1970, 1974). In this study, it took place before a minority of observed copulations and never reached the high levels reported for *Eumetopias* (Sandegren 1974).

Precopulatory behaviour of female *A. forsteri* resembles displays used by oestrous female sea lions (Peterson and Bartholomew 1967; Gentry 1970; Sandegren 1970, 1974), but occurs far less frequently. The tactile components, in particular, are much less developed than in the otariines. Similarly, during and preceding copulation, male *A. forsteri* rub against the female far less than do the more thigmotactic *A. pusillus* (personal observation) and otariines (Peterson and Bartholomew 1967; Sandegren 1970).

Chemical cues used by males to assess the reproductive state of females before copulation may be absent in northern elephant seals (LeBoeuf 1972), but olfactory (and gustatory?) investigation of oestrous females by males is the rule among otariids (Rand 1955; Bonner and Laws 1964; Paulian 1964; Bonner 1968; Sandegren 1970). Investigation of the perineal region usually precedes copulation, although male *Callorhinus* may mount after smelling only the face (Bartholomew and Hoel 1953). No scent glands have been found in pinnipeds (Frechkop 1955), and at this time the nature and source of the chemical substance(s) signalling sexual receptivity in otariids are unknown.

In *A. forsteri*, the colour and degree of swelling of the vulva are unchanged at oestrus; the vulva of oestrous female *Callorhinus* becomes bright pink (Bartholomew 1953; Bartholomew and Hoel 1953; Peterson 1965, 1968) and could conceivably have a visual signal function at that time.

Token resistance by oestrous female *A. forsteri* serves to excite the male further, as in other species of otariids (Rand 1955; Peterson 1968; Gentry 1970; Sandegren 1970; Stirling 1971*a*). Nevertheless, the passivity of oestrous females presumably also carries stimulus value: male *Eumetopias* (Gentry, personal communication), *Phoca groenlandica* (Sivertsen 1941), and *Mirounga leonina* (Carrick *et al.* 1962) have been observed to copulate with corpses, which presumably emitted sexual stimuli related to passivity.

Unlike *A. pusillus* (personal observation) and *Zalophus* (Peterson and Bartholomew 1967), no female *A. forsteri* were observed to complete copulation in any posture other than lying fully on the ventrum. Biting of the neck was not used in *A. forsteri* to restrain females, as in the phocids *Halichoerus* (Backhouse 1969) and *Mirounga* (Matthews 1929; Paulian 1953; Laws 1956; LeBoeuf 1972). Nor was biting ever strong enough to scar or kill females, unlike in Phocidae (Paulian 1953; Carrick and Ingham 1962; Marlow 1967; Cline *et al.* 1971).

Other species of arctocephalines behave similarly to *A. forsteri* at the end of copulation, when female resistance is soon followed by male dismounting (Rand 1955; Bonner 1958, 1968; Paulian 1964; Peterson 1965). In the Otariinae, females are reported to actively terminate copulations (Peterson and Bartholomew 1967; Gentry 1970), but it is not known if this indicates a basic difference from arctocephalines in terms of the suggested correlation between female resistance and male ejaculation. In *A. forsteri*, the resistance was not token by any means. It involved elements of

aggression as well as submission, e.g. biting, open-mouthed threats, high-pitched vocalizations and submissive facial expressions. Sandegren (1970) observed female *Eumetopias* to defaecate at such a stage, a behaviour typical of frightened mammals (Eisenberg and Kleiman 1972).

It was not usually possible to determine when intromissions occurred. On other data presented above, the copulatory pattern of *A. forsteri* corresponds to number 10 or 12 of Dewsbury (1972).

Sexual receptivity of female Carnivora is largely dependent upon oestrogen facilitation, but there are important neural contributions to facilitation and inhibition of components of sexual behaviour (Beach 1967). The very rapid change in sexual receptivity of female *A. forsteri*, from passivity to physical resistance, may be due to an afferent neuro-inhibitory process resulting from cervical or vaginal stimulation, or both (cf. Goldfoot and Goy 1970). So rapid is the transition in behaviour that hormonal causation for induced non-receptivity seems unlikely. The brief period of behavioural oestrus characteristic of *A. forsteri* seems to be a time of suppressed aggression, terminated by a certain level of copulatory activity. Aggression toward males may hence be hormonally repressed and neurally derepressed at the onset and end of oestrus, respectively.

Acknowledgments

I thank in particular M. C. Crawley for his patient and firm supervision of this study. R. M. Warneke kindly provided for my stay with *A. pusillus* at Seal Rocks. F. H. Fay, P. C. Lent, J. O. Murie and P. D. Shaughnessy critically read an earlier draft of the paper. Financial support was provided by the University Grants Committee and the Marine Department, Wellington, New Zealand.

References

Backhouse, K. M. (1969). 'Seals.' (Golden Press: New York.)

Bartholomew, G. A. (1953). Behavioral factors affecting social structure in the Alaska fur seal. *Trans. N. Am. Wildl. Nat. Resour. Conf.* **18**, 481–502.

Bartholomew, G. A. (1966). Interaction of physiology and behavior under natural conditions. In 'The Galapagos. Proceedings of the Symposia of the Galapagos International Scientific Project'. (Ed. R. L. Bowman.) pp. 39–45. (University of California Press: Los Angeles.)

Bartholomew, G. A. (1970). A model for the evolution of pinniped polygyny. *Evolution* **24**, 546–59.

Bartholomew, G. A., and **Hoel, P. G.** (1953). Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. *J. Mammal.* **34**, 417–35.

Beach, F. A. (1967). Cerebral and hormonal control of reflexive mechanisms involved in copulatory behavior. *Physiol. Rev.* **47**, 289–316.

Bonner, W. N. (1958). Notes on the southern fur seal in South Georgia. *J. Zool. (Lond.)* **130**, 241–52.

Bonner, W. N. (1968). The fur seal of South Georgia. Br. Antarctic Surv. Sci. Rep. No. 56.

Bonner, W. N., and **Laws, R. M.** (1964). Seals and sealing. In 'Antarctic Research: a Review of British Scientific Achievement in Antarctica'. (Eds. R. Priestley, R. J. Adie, and G. de Q. Robin.) pp. 163–90. (Butterworths: London.)

Burns, J. J., and **Fay, F. H.** (1970). Comparative morphology of the skull of the ribbon seal, *Histriophoca fasciata*, with remarks on systematics of Phocidae. *J. Zool. (Lond.)* **161**, 363–94.

Burrows, C. J. (1972). The flora and vegetation of Open Bay Islands. *J. R. Soc. N.Z.* **2**, 15–42.

Cameron, A. W. (1967). Breeding behaviour in a colony of western Atlantic gray seals. *Can. J. Zool.* **45**, 161–73.

Cameron, A. W. (1969). The behavior of adult gray seals (*Halichoerus grypus*) in the early stages of the breeding season. *Can. J. Zool.* **47**, 229–33.

Cameron, A. W. (1970). Seasonal movements and diurnal activity rhythms of the grey seal (*Halichoerus grypus*). *J. Zool.* (*Lond.*) **161**, 15–23.
Carrick, R., Csordas, S. E., Ingham, S. E., and **Keith, K.** (1962). Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to sex and age. *CSIRO Wildl. Res.* 7, 119–60.
Carrick, R., and **Ingham, S. E.** (1962). Studies on the southern elephant seal, *Mirounga leonina* (L.). V. Population dynamics and utilization. *CSIRO Wildl. Res.* 7, 198–206.
Cline, D. R., Siniff, D. B., and **Erickson, A. W.** (1971). Underwater copulation of the Weddell seal. *J. Mammal.* **51**, 216–18.
Cooper, K. F. (1972). Natural history and behaviour of the Australian sea lion *Neophoca cinerea* (Péron) on Kangaroo Island, South Australia. B.Sc. Thesis, University of Adelaide.
Crawley, M. C. (1972). Distribution and abundance of New Zealand fur seals on the Snares Islands, New Zealand. *N.Z. J. Mar. Freshwater Res.* **6**, 115–26.
Curry-Lindahl, K. (1970). Breeding biology of the Baltic grey seal (*Halichoerus grypus*). *Zool. Gart.* **38**, 16–29.
Darling, F. F., and **Boyd, J. M.** (1969). 'The Highlands and Islands.' (Collins: London.)
Dewsbury, D. A. (1972). Patterns of copulatory behavior in male mammals. *Q. Rev. Biol.* **47**, 1–33.
Eibl-Eibesfeldt, I. (1955). Ethologische Studien am Galapagos-Seelöwen, *Zalophus wollebaeki* Sivertsen. *Z. Tierpsychol.* **12**, 286–303.
Eisenberg, J. F., and **Kleiman, D. G.** (1972). Olfactory communication in mammals. *Annu. Rev. Ecol. Syst.* **3**, 1–32.
Fay, F. H., and **Ray, C.** (1968). Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. *Zoologica* (*N.Y.*) **53**, 1–18.
Ferreira, R. Vaz (1956). Etologia terrestre de *Arctocephalus australis* (Zimmerman) ('lobo fino') en las islas Uruguayas. Ministerio de Industrias y Trabajo Servicio Oceanografico y de Pesca: Trabajos sobre islas de lobos marinos. No. 22.
Frechkop, S. (1955). Ordre des Pinnipèdes. In 'Traité de Zoologie'. (Ed. P. P. Grassé.) Vol. 19. pp. 292–340.
Gentry, R. L. (1970). Social behavior of the Steller sea lion. Ph.D. Thesis, University of California.
Gentry, R. L. (1973). Thermoregulatory behavior of eared seals. *Behaviour* **46**, 73–93.
Goldfoot, D. A., and **Goy, R. W.** (1970). Abbreviation of behavioral estrus in guinea pigs by coital and vagino-cervical stimulation. *J. Comp. Physiol. Psychol.* **72**, 426–34.
Hamilton, J. E. (1934). The southern sea lion *Otaria byronia* (de Blainville). '*Discovery*' *Rep.* **8**, 269–318.
Hewer, H. R. (1957). A Hebridean colony of grey seals, *Halichoerus grypus* (Fab.), with comparative notes on the grey seals of Ramsey Island, Pembrokeshire. *J. Zool.* (*Lond.*) **128**, 23–66.
Hewer, H. R., and **Backhouse, K. M.** (1960). A preliminary account of a colony of grey seals, *Halichoerus grypus* (Fab.) in the Southern Inner Hebrides. *J. Zool.* (*Lond.*) **134**, 157–95.
Kenyon, K. W. (1960). Territorial behaviour and homing in the Alaska fur seal. *Mammalia* **24**, 431–44.
Kenyon, K. W., and **Rice, D. W.** (1959). Life history of the Hawaiian monk seal. *Pac. Sci.* **13**, 215–52.
King, J. E. (1964). 'Seals of the World.' (British Museum (Natural History): London.)
King, J. E. (1969). The identity of the fur seals of Australia. *Aust. J. Zool.* **17**, 841–53.
Laws, R. M. (1956). The elephant seal (*Mirounga leonina* Linn.). II. General, social, and reproductive behaviour. Falkland Is. Dep. Surv. Sci. Rep. No. 13.
LeBoeuf, B. J. (1972). Sexual behaviour on the northern elephant seal *Mirounga angustirostris*. *Behaviour* **41**, 1–26.
Marlow, B. J. (1967). Mating behaviour in the leopard seal, *Hydrurga leptonyx* (Mammalia: Phocidae) in captivity. *Aust. J. Zool.* **15**, 1–5.
Marlow, B. J. (1968). The sea lions of Dangerous Reef. *Aust. Nat. Hist.* **16**, 39–44.
Mate, B. R. (1973). Population kinetics and related ecology of the northern sea lion, *Eumetopias jubatus*, and the California sea lion, *Zalophus californianus*, along the Oregon coast. Ph.D. Thesis, University of Oregon.
Matthews, L. H. (1929). The natural history of the elephant seal with notes on other seals found at South Georgia. '*Discovery*' *Rep.* No. 1.

Miller, E. H. (1971). Social and thermoregulatory behaviour of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828). M.Sc. Thesis, University of Canterbury.

Miller, E. H. (1974). Social and evolutionary implications of territoriality in adult male New Zealand fur seals, *Arctocephalus forsteri* (Lesson, 1828), during the breeding season. In 'Symposium on the Biology of the Seal'. (Eds. K. Ronald and A. W. Mansfield.) (Conseil International pour l'Exploration de la Mer.) (In press.)

Paulian, P. (1953). Pinnipèdes, cétaces, oiseaux des Iles Kerguelen et Amsterdam. *Mém. Inst. Rech. Sci. Madagascar Sér. A Biol. Anim.* **8**, 111–234.

Paulian, P. (1964). Contribution a l'étude de l'otarie de l'Ile Amsterdam. *Mammalia* **28**, Suppl. 1, 1–146.

Peterson, R. S. (1965). Behavior of the northern fur seal. D.Sc. Thesis, Johns Hopkins University.

Peterson, R. S. (1968). Social behavior in pinnipeds with particular reference to the northern fur seal. In 'The Behavior and Physiology of Pinnipeds'. (Eds. R. J. Harrison *et al.*) pp. 3–53. (Appleton–Century–Crofts: New York.)

Peterson, R. S., and **Bartholomew, G. A.** (1967). The Natural History and Behavior of the California Sea Lion. Spec. Publ. Am. Soc. Mammal. No. 1.

Peterson, R. S., Hubbs, C. L., Gentry, R. L., and **Delong, R. L.** (1968). The Guadalupe fur seal: habitat, behavior, population size, and field identification. *J. Mammal.* **49**, 665–75.

Rand, R. W. (1955). Reproduction in the female Cape fur seal. *Arctocephalus pusillus* (Schreber). *J. Zool. (Lond.)* **124**, 717–40.

Rand, R. W. (1967). The Cape fur seal (*Arctocephalus pusillus*). 3. General behaviour on land and at sea. South Afr. Div. Sea Fish. Invest. Rep. No. 61.

Repenning, C. A., Peterson, R. S., and **Hubbs, C. L.** (1971). Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernández and Guadalupé species. In 'Antarctic Pinnipedia'. Antarctic Res. Ser. Am. Geophys. Union. Vol. 18. (Ed. W. H. Burt.) pp. 1–34.

Rice, D. W., and **Scheffer, V. B.** (1968). A list of the marine mammals of the world. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 579.

Ross, G. J. B. (1972). Nuzzling behaviour in captive Cape fur seals. *Int. Zoo. Yb.* **12**, 183–4.

Sandegren, F. (1970). Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubata*) in Alaska. M.S. Thesis, University of Alaska.

Sandegren, F. (1974). Sexual-agonistic signalling and territoriality in the Steller sea lion (*Eumetopias jubatus*). In 'Symposium on the Biology of the Seal'. (Eds. K. Ronald and A. W. Mansfield.) (Conseil International pour l'Exploration de la Mer.) (In press.)

Schusterman, R. J., and **Dawson, R. G.** (1968). Barking, dominance, and territoriality in male sea lions. *Science (Wash. D.C.)* **160**, 434–6.

Sivertsen, E. (1941). On the biology of the harp seal *Phoca groenlandica* Erxl. Investigations carried out in the White Sea 1925–1937. *Hvalradets Skr.* **26**, 1–166.

Sokal, R. R., and **Rohlf, F. J.** (1969). 'Biometry. The Principles and Practice of Statistics in Biological Research.' (W. H. Freeman and Co.: San Francisco.)

Stirling, I. (1968). Diurnal movements of the New Zealand fur seal at Kaikoura. *N.Z. J. Mar. Freshwater Res.* **2**, 375–7.

Stirling, I. (1970). Observations on the behavior of the New Zealand fur seal (*Arctocephalus forsteri*). *J. Mammal.* **51**, 766–78.

Stirling, I. (1971*a*). Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). I. Annual cycle, postures and calls, and adult males during the breeding season. *Aust. J. Zool.* **19**, 243–66.

Stirling, I. (1971*b*). Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). II. Adult females and pups. *Aust. J. Zool.* **19**, 267–73.

Stirling, I. (1972). Observations on the Australian sea lion, *Neophoca cinerea* (Péron). *Aust. J. Zool.* **20**, 271–9.

Stirling, I., and **Warneke, R. M.** (1971). Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. *Aust. J. Zool.* **19**, 227–41.

Venables, U. M., and **Venables, L. S. V.** (1957). Mating behaviour of the seal *Phoca vitulina* in Shetland. *J. Zool. (Lond.)* **128**, 387–99.

Venables, U. M., and **Venables, L. S. V.** (1959). Vernal coition of the seal *Phoca vitulina* in Shetland. *J. Zool. (Lond.)* **130**, 665–9.
Waite, E. R. (1909). Vertebrata of the Subantarctic Islands of New Zealand. In 'The Subantarctic Islands of New Zealand'. (Ed. C. Chilton.) Vol. 2. pp. 542–600. (Government Printer: Wellington.)
Warneke, R. M. (1966). Seals of Westernport. *Victoria's Resour.* **8**, 44–6.

Manuscript received 18 February 1974