

Remarks on display functions of the snout of the grey seal, *Halichoerus grypus* (Fab.), with comparative notes

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Adult males of the grey seal, *Halichoerus grypus* (Fab.) (Phocidae), display the large snout conspicuously in threats. The male's snout has probably evolved through sexual selection as a visual display organ, as in some other extant phocids: the hooded seal, *Cystophora cristata* (Nilsson) and the two species of elephant seals, *Mirounga* (Gray). This may also be true of the extinct desmatophocid *Allodesmus* Kellogg. Cephalic display organs in the form of long tusks have also evolved twice in the Odobenidae (walruses). Comparable display structures do not occur in the Otariidae (fur seals and sea lions). However, the massive neck of adult male otariids is important in undirected static-optical threat displays, especially at long range, and in some kinds of short-range threats. Also, adult otariids show sexual dimorphism in facial appearance, which varies interspecifically.

Pinniped species in which large mature males have prominent, constant-growing cephalic display structures show fluid spacing among rutting males, and much agonistic communication at the water surface and on land or ice. This correlation may reflect selective pressures on males to affirm social status repeatedly, through displays which communicate their age (hence strength and experience), and their resource-accurring abilities.

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Les mâles adultes du phoque gris, *Halichoerus grypus* (Fab.) (Phocidae) se servent de leur museau comme moyen d'intimidation durant le comportement de menace. Le développement inusité du museau chez le mâle est probablement le résultat d'une sélection sexuelle vers un organe visuel de parade, comme c'est le cas chez le phoque à capuchon *Cystophora cristata* (Nilsson) et les deux espèces d'éléphants de mer *Mirounga* (Gray). Il en est peut-être de même du desmatophocidé disparu *Allodesmus* Kellogg. Les organes céphaliques de parade en forme de défenses sont apparus deux fois chez les odobenidés (morses). De telles structures n'existent pas chez les otariidés (otaries et lions marins). Cependant le cou imposant des mâles adultes d'otariidés sert d'instrument de parade lors de menaces statiques-optiques non dirigées, surtout à longue portée, et lors de certains types de menaces à courte portée. En outre, chez les otariidés adultes, il y a un dimorphisme sexuel de l'apparence faciale, variable selon les espèces.

Chez les espèces de pinnipèdes dont les mâles adultes de grande taille portent des structures céphaliques de parade à croissance constante, il s'établit un espacement entre les mâles en rut dans le milieu aquatique ainsi que des manifestations agonistiques à la surface de l'eau, sur la terre et sur la glace. Cette corrélation est peut-être le reflet d'une pression sélective exercée sur les mâles qui les pousse à affirmer fréquemment leur statut social par des manifestations révélatrices de leur âge (et par conséquent de leur force et de leur expérience) et de leur capacité à cumuler des ressources.

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Introduction

Signalling adaptations mark the appearance of many mammal species (Geist 1966, 1971a, 1971b, and included references; Hailman 1977; Smith 1977). These include simple modifications in piloerection and in hair colour and pattern, plus ornamentation like manes, beards, tail tufts, tusks, and horns. The aquatic life of pinnipeds sets limits

to their 'social morphology.' For example, long hair would increase drag during locomotion, and displays using elaborate colours or patterns would be effective underwater for short distances only, and may also alert predators or prey. Nevertheless, special display structures adorn some pinniped species which communicate much when at the water surface or out of the water (Miller 1975a, 1975b; Sandegren 1976a).

Males of the grey seal, *Halichoerus grypus*, are larger than females and have much heavier chests

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and necks and more massive snouts. The snout of large adult males has earned the species the generic names 'horsehead' and 'tête cheval' (Fig. 1). In this paper we suggest that the large snout of male grey seals is a display structure, and that cephalic display structures occur in pinniped species with fluid spacing among rutting males, where this is effected fully or partly through threat displays in air.

We studied grey seal behaviour on Sable Island, Nova Scotia (43°53' N 59°55' W) during the winter breeding seasons from 1973 to 1977 (DJB from 1973–74 to 1976–77, EHM in 1974–75). Our other observations which have led to this paper have been on walruses, harp seals, and harbour seals, plus five otariid species (EHM, 1968–78), and on harp and hooded seals (DJB, 1977–78).

Observations and Discussion

The Social System of Grey Seals

The breeding system and life history of grey seals on Sable Island resemble those of other pinniped species which give birth and copulate on land (fur seals, sea lions, elephant seals). They show polygyny, physical competition among males for mating privileges, and deferred physical and social maturity in males (Bartholomew 1970; Laws 1956; Miller 1975c; Peterson 1968; Stirling 1975). Social relations among breeding males are mainly agonistic, and involve many threats and fights. Spacing among breeding males is fairly uniform but is quite fluid as they attempt to stay near particular females or small groups of females, up to and through their oestrus, which lasts several days. Females in turn form patchwork aggregations of constantly changing composition (Boness 1978; Boness and James 1979). About one-fifth of the world's grey seals breed on pack ice, where the male reproductive strategy of remaining with pupped females is probably very similar, though the spatial dynamics of female aggregations differ.

Threat Displays by Grey Seals during the Breeding Period

Hewer (1957, 1974) describes some kinds of aggressive interactions of grey seals. In this section we describe typical forms and contexts of threats, especially those involving adult males.

Distant threats take place from as few as 5 to as many as 25 m. The simplest are direct or oblique orientation without locomotion, and with the head lifted off the ground with mouth open. Other kinds are rapid partial approach or intention movements of approach, with closed mouth. Adult males which are established on the breeding grounds (tenured

males) commonly threaten mildly like this in response to movements or activity of distant males.

Close-up threats are more intense. They occur frequently between tenured males and between tenured and transient males. These often begin with mutual or one-way approach with closed mouth (Fig. 2), and with a characteristic enlargement of the neck, due to retraction of the head (and inhalation?). Threatening males typically shift orientation while slowing their speed as they approach more closely, and assume parallel or antiparallel postures about 0.5–3 m apart. Numerous variations occur. For example, a male may stop approaching and assume an oriented open-mouthed posture, while the other male displays in broadside orientation (Fig. 3).

Males at close quarters tend to avert their heads into at least oblique orientation (Figs. 7 and 8). Slightly oblique or nearly direct orientation may occur in low-intensity parts of a threat, but this is replaced quickly by strongly oblique or parallel–antiparallel orientation when threat intensity increases (see sequence, Figs. 5, 6, 7, and 8). Most often, males threatening at close quarters hold their heads off the ground and roughly parallel to it, while they are strongly oblique or parallel–antiparallel to one another. Heads are lifted highest during high-intensity threats (Fig. 7), but they drop as threats wane (Figs. 7 and 8). Fighting males often swing the forequarters and heads into strong parallel alignment quickly, and each places his inside foreflipper against the shoulder of the other (a typical context in which this occurs is as in Fig. 7, following the brief fighting bout in Fig. 6). Facial appearance during open-mouthed threats varies, though mouths are usually open to some extent. Also, the posterodorsal region of the lips may be lifted, imparting a distinctive profile.

Adult males threaten subordinate males similarly at close quarters. Subordinates often respond by rearing up and away with the mouth closed (Fig. 4). They may also stretch toward and smell the dominant's neck or shoulder. Subordinates in such situations generally open the mouth only when dominants move rapidly, *e.g.* as they lunge, bite, or advance rapidly while at close quarters; then subordinates orient defensively and gape briefly, and generally back off. This defensive gape is similar to that in submissive fur seals and sea lions (Otariidae) (Gentry 1974; Miller 1971, 1975a; Sandegren 1975, 1976b), and elephant seals (*Mirounga*) (Sandegren 1976a), but in *Halichoerus* is much briefer.

Another common form of threat occurs when an adult or large subadult male captures a female

moving to sea. This happens when a female finally abandons her pup and moves toward the sea, after several days of oestrus around the end of lactation (Boness 1978; Boness and James 1979). Females are then approached and mounted by many males, especially untended males. A male lies across the female's back with his chest resting on her, and lowers his head and neck, with open mouth and with the back of the head depressed slightly, so that the snout is just below the horizontal.

Finally, males threaten females in a way slightly less formalized than in mild close-up threats between males. This is especially common when females resist their approaches and investigations (Fig. 1). Parallel posturing of the head occurs only incidentally in threats between females, and there is no formalized lateral or oblique presentation of the head and snout.

To summarize, the 'Roman nose' in *Halichoerus* is characteristic of large, mature males, though it is detectable even in 1st-year males upon close study. Threatening adult males display the snout prominently in numerous short-range agonistic encounters in the breeding season. They also show a distinctive open-mouthed expression and posture, with the head fairly low, and these contrast with the appearance of submissive subordinates. These observations suggest that the snout of male grey seals has a substantial visual signal function.

Cephalic Display Organs and Social Systems in Other Pinniped Species

(a) Phocidae and Odobenidae

Halichoerus joins three extant phocid species (the hooded seal, *Cystophora cristata*, plus the two elephant seal species, *Mirounga leonina* and *M. angustirostris*), and possibly also the extinct desmatophocid *Allodesmus* (Mitchell 1966), in having the snout of adult males modified (enlarged) apparently solely for visual signalling of threat in air. King (1972) and Briggs and Morejohn (1976) review cranial anatomy in these phocids. The snout of male hooded and elephant seals is not fixed in size and shape as is true of *Halichoerus*, but can be expanded, and is expanded maximally during high-intensity threats (Fig. 9; Berland 1966; Sandegren 1976a). Furthermore, the snout of male elephant seals changes in size throughout the year,

and is largest during rut (Laws 1953, 1956; Sandegren 1976a). Male hooded seals can extrude the bright red nasal septum as a large balloon in threat, but this is apparently less common than snout expansion (see Berland 1958, 1966).

Extant walruses (*Odobenus rosmarus*) possess long tusks which are used in threats and fights (Miller 1975a, 1975b). Tusks evolved independently (as display organs?) in the extinct dusignathine odobenids (Mitchell 1975). They are constant growing and are thus approximate indicators of age and size, like the snouts of male grey, hooded, and elephant seals. However, walruses differ from those species in two ways: tusks occur in both sexes, and they are weapons.²

The species discussed differ ecologically and in their cephalic adornments, but share characteristics related to male spacing and the medium in which threats among males occur. Threats and fights between male hooded seals usually occur on the pack ice surface near a pupped female, and involve snout expansion (Fig. 9; Mansfield 1964; D. E. Sergeant, personal communication; Terhune and Ronald 1973). Male hooded seals may consort with pupped females until oestrus, like grey seals, and they fight and threaten one another over access to females. Female hooded seals have a briefer nursing period than do female grey seals (ca. 10–12 days), which probably permits some sequential polygyny even though the pupping season is brief (Emlen 1976; Emlen and Oring 1977; Stirling 1975). Adult male elephant seals threaten and fight in breeding colonies on land or fast ice (the latter in parts of the range of *M. leonina*), and they expand the snout as they rear high in threats and in long-range vocal threats (LeBoeuf and Petrinovich 1974; Sandegren 1976a). Male elephant seals show fluid movements on land near females, and establish a hierarchy through which dominant males become situated closest to many females (LeBoeuf and Peterson 1969). The social system of walruses is poorly known, but some generalizations can be

²V. Geist (personal communication) has suggested that it may be to the advantage of females to mimic males in this highly social species. This could enhance their competitive abilities, especially with respect to young males, and reduce harassment by them (Geist 1974; Geist and Karsten 1977).

FIG. 1. Adult female grey seal (left) threatening a large adult male that had approached her. The relative size and shape of the snout is typical for adult seals. FIG. 2. Simple direct approach with closed mouth, by one young adult male grey seal (background) threatening another. FIG. 3. Static open-mouthed threat at close range between two medium-sized adult male grey seals. FIG. 4. Young adult male grey seal (left) threatening a younger, subordinate male. Note the latter's closed mouth, orientation, and head reared defensively. The dominant male is inching closer, and the subordinate is about to back away.



made (Miller 1975b, 1976; and footnote 3). Mild threat interactions involve tusk display and blows, and are given by both sexes and all ages throughout the year. Intense threats between rutting males seem to predominate at the water surface, and these space out adult males in temporary mating territories in the water adjacent to herds hauled out on ice. Intense threats and fights among rutting males also occur while herds are travelling in the water.

(b) *Otariidae*

Nothing obviously comparable with the six independent evolutions of display structures in phocids and odobenids exists in the 14 extant otariid species. All adult male otariids have massive necks and, especially in some sea lions, long neck hairs. Male otariids have maximal neck size at about the start of breeding because fat deposition increases in late winter (Howell 1930; Rand 1956; Schusterman and Gentry 1971). The huge necks of tenured males make them conspicuous in a posture used commonly on land, when they rest upright with the head pointed up (Fig. 10). The necks are also displayed in some kinds of static and kinesic threats at close range. Males of species whose pelage contrasts with the breeding habitat are especially conspicuous in these various postures and threats. This occurs in the following, at least: *Otaria flavescens*, *Phocarcos hookeri*, and *Zalophus californianus*, in all of which males are much darker than females, and in which the dominant breeding habitat is light coloured; *Eumetopias jubatus*, a pale species which breeds on dark rocky islands in the north Pacific; and *Arctocephalus tropicalis*, whose lemon-yellow venter (especially pronounced in adult males) contrasts with the dark breeding rocks (for the last, see Paulian (1964); for the others, see photographs in Hamilton (1934), Marlow (1975), Peterson and Bartholomew (1967), Sandegren (1975, 1976b), and Vaz Ferreira (1975)).

Male otariids display their faces and heads during short-range threat encounters during the breeding season (Fig. 11). These encounters occur fre-

quently between neighbouring males and define their common territorial boundaries. It is possible that the facial appearance of males has been modified for purposes of visual display, for strong sexual and species differences exist (Figs. 10, 11, 12, and 13). However, this suggestion is unsubstantiated at present.

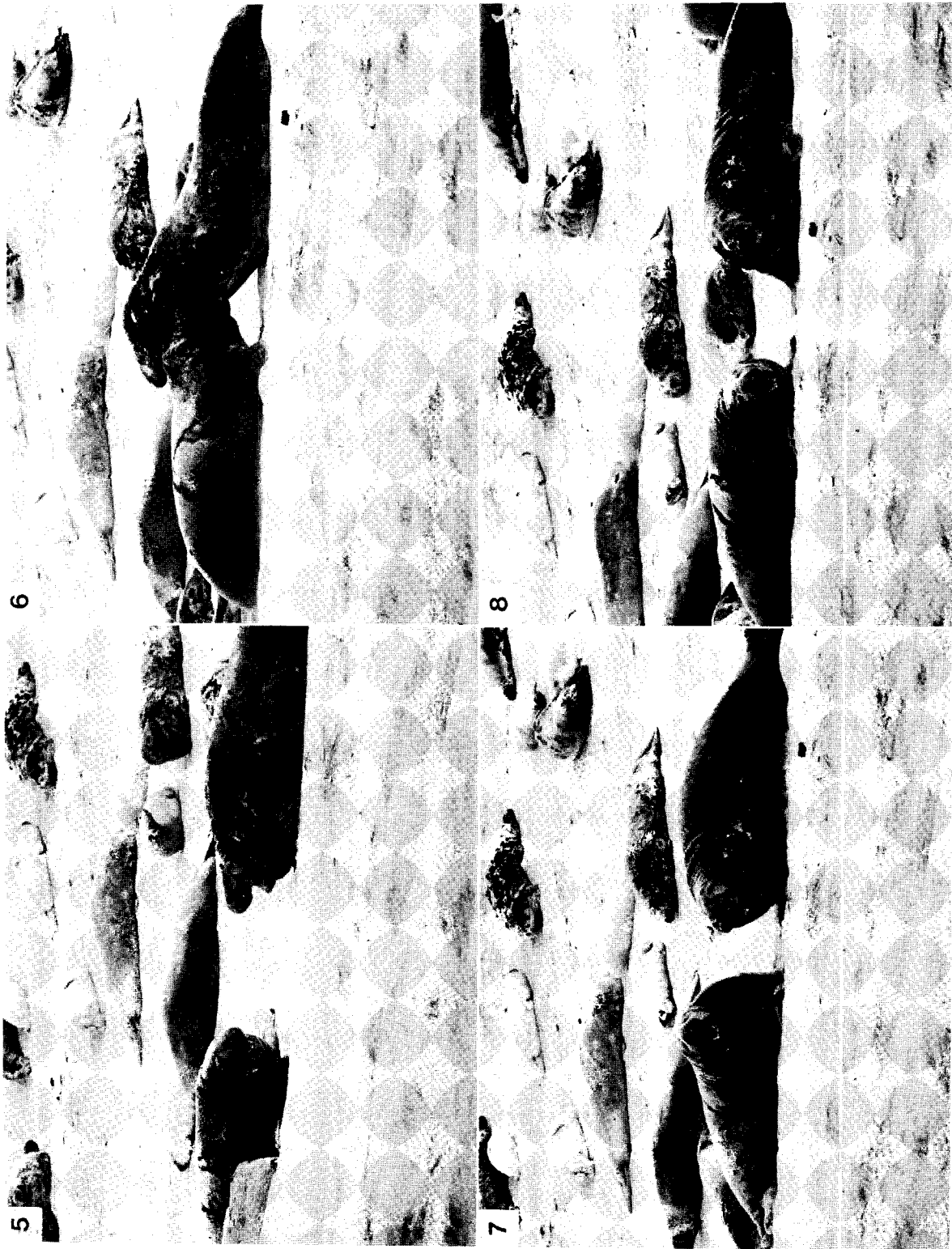
Male otariids are rigidly territorial. They fight and threaten one another to gain and maintain territorial status where females haul out to pup and copulate. Males generally interact repeatedly with their neighbours over particular parts of their common territorial boundaries, and neighbours weaken their threat exchanges as they habituate to one another (Gentry 1970; Miller 1971). Territorial boundaries of otariids often remain the same with turnover of males within seasons, and even from year to year (Peterson 1965, 1968; Gentry 1970).

Rutting males in pinniped species with cephalic display organs show fluid or temporary spacing, or both. This generates uncertainty about their identity and status, so it behooves them to communicate their social status quickly and unambiguously in agonistic encounters. One way to do this is to signal with a structure that changes with age (which in turn reflects both strength and experience), and is connected to aggressive expression. Unsurprisingly, features of the face and head have been modified for communicative purposes in threats of many mammal species (Geist 1966). Grey, hooded, and harp seals, and walruses can be included here. Selective pressures on displays of breeding male otariids differ. Neighbours become familiar with one another quickly and tend to interact as social 'equals' in close-up threats at fixed locations. Identity of interactants, kinds and locations of threats, and postencounter movements are all highly predictable. There is therefore less need to communicate relative competitive ability and aggressive inclination, except when males are untenured or challenged by untenured males.

It is interesting to speculate on the relative importance of intersexual selection in these two schemes. The former exemplifies a form of nonresource-based polygyny, in which a male's resource-acquiring ability can be communicated by his physical characteristics, behaviour, and social "achievements" relative to other males (e.g. posi-

³Fay, F. H., G. C. Ray, V. N. Gol'tsev, A. A. Kibal'chik. 1978. Time and location of mating and associated behavior of the Pacific walrus *Odobenus rosmarus divergens* Illiger. Unpublished manuscript.

FIGS. 5-8. Approach, brief fight, and subsequent close-range threat between two large adult male grey seals. The seals pause in threat (Fig. 5), then the scarred male approaches and a brief fight follows (Fig. 6). The animals engage in high-intensity threat immediately thereafter (Fig. 7; note the similarity of the posture of the scarred male here to that of the dominant male in Fig. 4, as though threatening to swing at the other interactant). The threat weakens, and the unscarred male is about to turn away (Fig. 8).



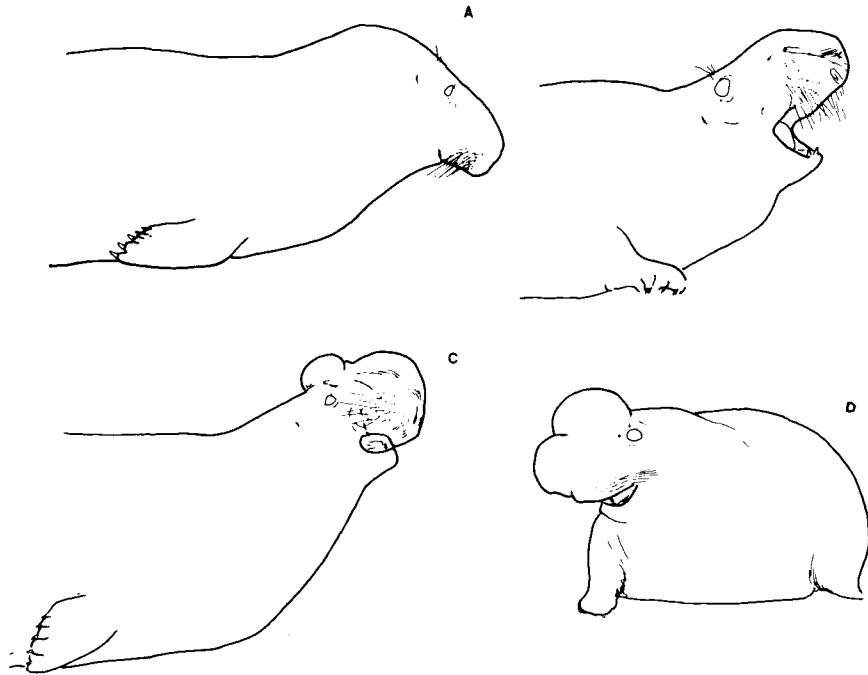


FIG. 9. Differences in the facial appearance of a threatening male hooded seal. Sketches A through D illustrate increasing inflation of the hood. A and B portray a single male photographed a few seconds apart, as he started to threaten the observer.

tion on a lek (footnote 4)). Physical characteristics which change with age can provide such information (see Trivers 1976; Wilbur *et al.* 1978). In contrast, otariid males establish territories where females later give birth and nurse their pups. This is a form of resource-based polygyny, in which resource characteristics can reflect male "quality" (Miller 1975c; review by Cronin and Sherman 1977). Male characteristics *per se* may be relatively unimportant in affecting mate choice by females in such systems (Cronin and Sherman 1977; Itzkowitz 1978).

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⁴Miller, E. H. 1977. Functions of display flights by males of the least sandpiper, *Calidris minutilla* (Vieill.) (Aves, Scolopacidae), on Sable Island, Nova Scotia. *Unpublished manuscript*.

FIG. 10. Adult male Bass Strait fur seal (*Arctocephalus pusillus*) in a relaxed head-up posture. FIG. 11. Typical threat display between adult male Bass Strait fur seals, across their common territorial boundary. FIG. 12. Mutual threat between a small female and an adult male southern sea lion (*Otaria flavescens*). FIG. 13. Adult male Pribilof fur seal (*Callorhinus ursinus*) 'barking' ('whimpering') at low intensity.



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