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Author(s): Edward H. Miller
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A COMPARATIVE STUDY OF FACIAL EXPRESSIONS OF TWO SPECIES OF PINNIPEDS

by

EDWARD H. MILLER[1][2]
(Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada)

(With 23 Figures)
(Rec. 15-VI-1974)

INTRODUCTION

More than a century ago, DARWIN (1872) suggested that the 'expression of the emotions' of animals could be understood by assuming a causal connection between such expressions and underlying motivational and physiological states. He stressed repeatedly that expressions need have no original or derived signal functions. Intervening research supports many of his basic theses, though we now appreciate that 'expression of emotions' through postures, movements, and facial appearance often has communicative importance and hence may reflect the operation of natural selection favouring information transfer. Such appears to be true at least for many primate species (*e.g.* ANDREW, 1963b; VAN HOOFF, 1967 and 1972), though good evidence is sparse for other taxa of mammals. Nevertheless, circumstantial evidence is suggestive: there seems to be a rough correlation between the complexity and permanence of social organisation of a species and the diversity and degree of stereotypy of facial expressions used in social contexts by members of that species (FOX, 1970; KLEIMAN, 1972; MOYNIHAN, 1967).

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2) Data on *A. forsteri* were gathered while affiliated with the Zoology Department, University of Canterbury, Christchurch, New Zealand. Those on *Odobenus* were gathered while affiliated with the College of Biological Sciences, University of Alaska, Fairbanks, Alaska.

Vibrissae and facial expressions of Pacific walruses, *Odobenus rosmarus* (Linnaeus), and New Zealand fur seals, *Arctocephalus forsteri* (Lesson), and the contexts in which facial expressions occur, are described and compared here. Both species are gregarious, the walrus exceptionally so, but their gregariousness reflects adaptation to different ecological problems. That of walruses is probably related largely to the need for energy conservation in the cold environment they inhabit (FAY & RAY, 1968) and probably also to mutually beneficial effects of group integrity on locating and maintaining contact with favourable food and ice conditions. Fur seals are gregarious in large part because of the necessity to return to a location fixed in space for purposes of breeding and raising the young (BARTHOLOMEW, 1970; PETERSON, 1968). Whereas fur seals show few or no anatomical modifications related directly to intraspecific visual signalling, walruses have their upper canines hypertrophied for that function (F. H. FAY, in prep.).

Species names used follow RICE & SCHEFFER (1968).

METHODS

Male fur seals were observed on the Kaikoura Peninsula, South Island, New Zealand, in July 1970. Seals of various ages and both sexes were studied on the Open Bay Islands, South Island, New Zealand, in August 1970, from October 1970 to February 1971 (over the breeding season), and in May and June 1971. Specimens were collected at both locations, and vibrissae from these were measured and examined.

Observations of walrus behaviour were made in the Bering Sea pack ice, south of St. Lawrence Island, Alaska, during March 1972 (in the latter part of the breeding season). Male walruses were observed on Round Island (Walrus Islands), Bristol Bay, Alaska, in June and July 1972 and 1973. Herds of mixed sexes and ages were studied at the ice edge in the Chukchi Sea, approximately from Wrangell Island, U.S.S.R., in the west to Point Barrow, Alaska, in the east, during August and early September 1973.

RESULTS

VIBRISSAE

Arctocephalus forsteri.

Vibrissae in *A. forsteri* are present only in superciliary and mystacial positions. The slender superciliary vibrissae vary in number from none to two per side (Table 1). Upper ones are usually about twice the length of the lower, the former varying in length from 6 to 32 mm, and the latter from 7 to 17 mm. These vibrissae, black in pups, tend to become pale as the animal ages, though throughout life they appear predominantly dark.

In specimens of *A. forsteri* that I examined mystacial vibrissae were distributed in five or six horizontal rows per side, totalling 22 to 31 vibrissae per side (Table 1, Fig. 1). Mystacial vibrissae are usually black at birth, though some pups are born with a long white whisker in one or both

TABLE 1

Number of vibrissae in A. forsteri

Specimen number	Sex	Side	Number of superciliary vibrissae	Number of mystacial vibrissae 1)	Total mystacial vibrissae	C.L. 2)	Body weight (kg)
K1	M	L	2	3-4-6-7-7-4	31	195	134.5
		R	2	3-5-6-5-6-4	29		
K2	F	L	0	1-3-6-6-6-4	26	136	37.3
		R	2	2-4-6-6-6-3	27		
K3	M	L	2	0-4-6-6-6-4	26	107	19.5
		R	2	0-4-6-6-6-4	26		
K4	M	L	2	1-4-6-6-7-4	28	140	35.9
		R	2	0-4-6-7-7-4	28		
K5	M	L	2	2-5-6-6-6-4	29	117	17.3
		R	2	1-5-6-6-6-4	28		
K6	M	L	2	1-4-6-6-6-4	27	105	19.1
		R	2	1-4-6-6-6-4	27		
OBI1	M	L	0	0-3-5-6-5-3	22	90	20.5
		R	2	0-4-5-6-5-3	23		

1) Counted in rows from the dorsal-most to the ventral-most row.
2) C.L. = curvilinear length (in cm) as defined in Journal of Mammalogy 48: 459-462 (1967).

mystacial pads. Mystacial vibrissae become paler distally as the animal ages, probably due to bleaching (SCHEFFER, 1961), and eventually become completely yellowish-white. However, not all sexually mature seals ashore during the breeding season have pale vibrissae, for the young breeding females characteristically have dark vibrissae with tawny tips. The longest and thickest vibrissae are in posterior parts of the mystacial pads (Fig. 1). For example, from anterior to posterior positions on the left mystacial pad of male K1, vibrissa lengths (in mm) were: (12, 16, 16)-(7, 16, 25, 78)-(18, 28, 42, 73, 73, 78)-(11, 32, 53, 73, 88, 96, 179)-(13, 32, 42, 69, 101, 136, 191)-(30, 61, 98, 93) (brackets correspond to rows: cf. Table 1).

The mystacial vibrissae of pups are shorter, thinner, and more flexible than those of adults.

Odobenus rosmarus.

Walruses possess one to three superciliary vibrissae per side, especially as foetuses and young calves, and these may reach 10 mm in length (FAY, *op. cit.*). These vibrissae disappear as the animals age, perhaps due to breakage (*ibid.*).

There are about 600 to 700 vibrissae in the mystacial pads of a walrus, arranged in 13 to 18 rows (YABLOKOV & KLEVEZAL', 1964; Fig. 2). Vibrissae in walruses are yellowish-white throughout life, although calves may have

Fig. 1. *Arctocephalus forsteri*, adult female.

Fig. 2. *Odobenus rosmarus*, young adult male.

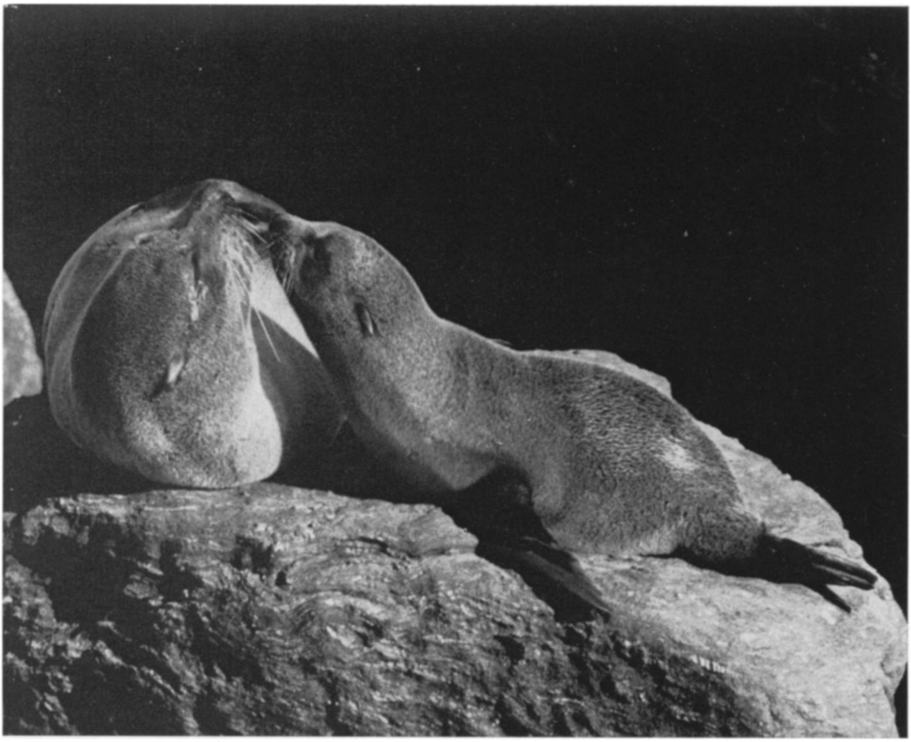

Fig. 3. Beginning of a naso-nasal greeting between female *A. forsteri* and her 10-11 month-old pup.

Fig. 4. Naso-nasal greeting between subordinate young male (left) and dominant adult female.

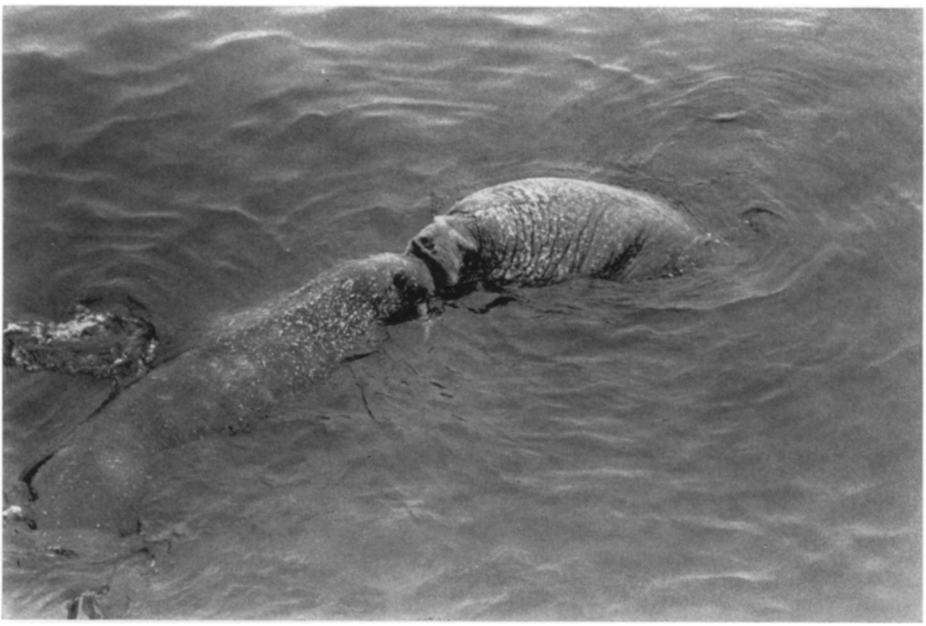

Fig. 5. Naso-nasal greeting between young adult male walruses.

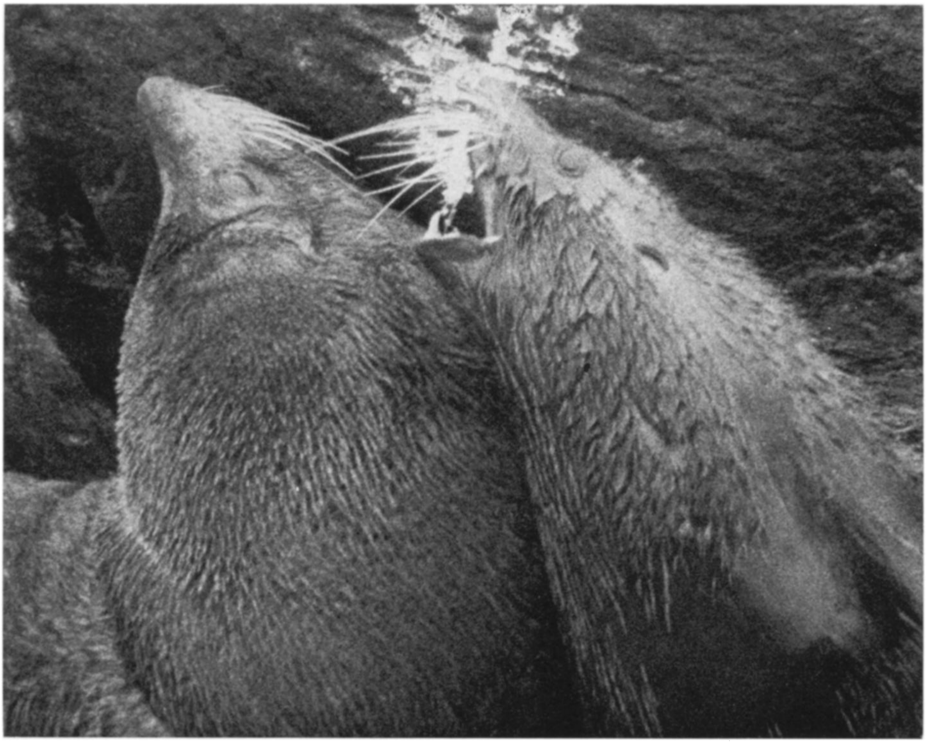

Fig. 6. High intensity submission in young adult male *A. forsteri* (right) after being defeated in a fight.

Fig. 7. Moderate intensity submission in young adult male *A. forsteri* being approached by a dominant male in low intensity threat (in right foreground, out of photograph).

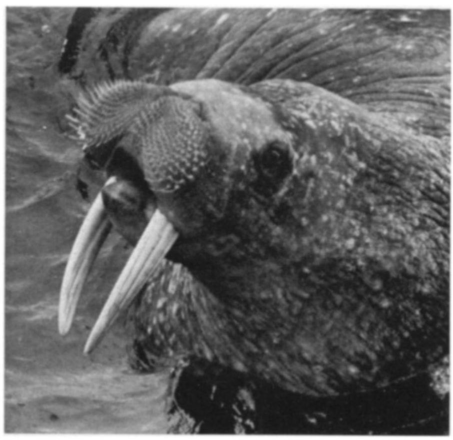

Fig. 8. High intensity submission and direct orientation by young male walrus in response to threat by a dominant male (in left foreground, out of photograph).

Fig. 9. High intensity closed-mouth submission in young male walrus (background) in response to threat by a dominant male (foreground).

Fig. 10. High intensity submission and defensive orientation in young male walrus (foreground) in response to threat by a dominant male (background).

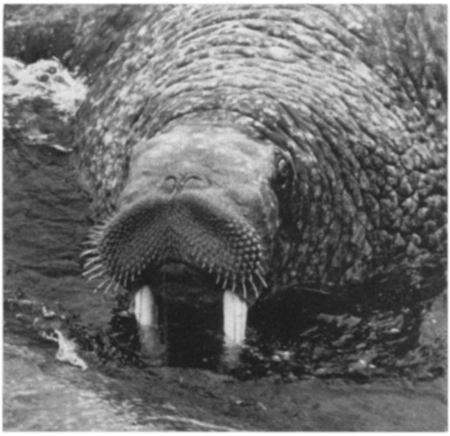

Fig. 11. Low intensity submission by young adult male walrus in response to approach by non-threatening dominant male (to right, out of photograph).

Fig. 12. Protective responses in *A. forsteri*. Adult female (left) lunged toward the face of the adult male (right) due to his persistence in attempting to olfactorily investigate her perineal region.

Fig. 13. Moderate intensity whimpering by adult male *A. forsteri*.

Fig. 14. High intensity whimpering by adult male *A. forsteri*.

Fig. 15. Moderate intensity threat by adult male *A. forsteri*, during latter stages of mutual threat with another adult male (right foreground, mostly out of photograph).

Fig. 16. High intensity threat by adult male *A. forsteri*, after being bitten by and consequently swinging at another adult male, during mutual threat display (other male to right, out of photograph).

Fig. 17. Typical posturing and facial expressions used by adult territorial male *A. forsteri* during mutual threat demarcating boundary between territories.

Fig. 18. High intensity aggressive facial expression in adult male walrus in response to being hindered in moving through a herd by another male (lower left, flipper visible).

Fig. 19. High intensity aggressive facial expression and oral (plus nasal?) expiration in adult male walrus while moving through a herd and threatening another male (to the left).

Fig. 20. Adult female *A. forsteri* scratching face.

Fig. 21. Adult male walrus scratching neck.

Fig. 22. Adult male walrus yawning. Note the eversion of the vibrissae on the left side of the left mystacial pad.

Fig. 23. Adult male walrus yawning.

a few dark ones, and they tend to be longer and more slender in young calves than in older animals. Vibrissae in adults are short, stout, and little flexible.

The arrangement of mystacial vibrissae on the face of the walrus differs markedly from the 'typical' Carnivore-Pinniped pattern, in that the mystacial pads are arranged on the anterior surface of the face and anteroventral to the nostrils (Fig. 2).

In neither of the species studied did superciliary vibrissae appear to have social function, and hereafter 'vibrissae' will refer only to mystacial vibrissae.

FACIAL EXPRESSIONS

Naso-nasal greetings.

A. forsteri.

In fur seals engaged in naso-nasal greetings not involving whimpering, the nostrils are opened and the vibrissae are typically extended partially or entirely forward (Figs 3, 4) (nostrils of pinnipeds are opened through muscular action and are generally open only during breathing). Extreme erection of the vibrissae typifies cautious attempts by subordinates to instigate naso-nasal greetings with dominants (*e.g.* Fig. 4). Erection to varying degrees is shown by seals engaging in naso-nasal greetings with others of approximately equal dominance status. Erection occurs weakly and sporadically in naso-nasal greetings between females and their offspring (Fig. 3), and little erection is shown by dominants in greeting subordinates (Fig. 4).

O. rosmarus.

Naso-nasal greetings between walruses are usually accompanied by slight tilting of the head downward, thereby bringing the dorsally positioned nostrils in proximity. In walruses, unlike in fur seals, the nostrils are not always brought into contact or near contact (Fig. 5). Mutual apposition of much or of only the dorsal margins of the mystacial pads accompanies most naso-nasal greetings, the nostrils are opened, and the vibrissae moved slowly but obviously throughout the engagement. No other modification in facial appearance is apparent.

Submission.

A. forsteri.

Extreme submissive behaviour by fur seals, such as is typical of males defeated in fights over territorial status during the breeding season, is characterised by the following: extreme erection of the vibrissae; widely opened eyes; limply hanging lower jaw; relaxed lower lip; and posteriorly retracted corners of the mouth (Fig. 6). In a situation of high intensity submission, the submissive seal typically gives a highly pitched screech and sporadically shakes the head laterally, rapidly and with small amplitude, all the while retaining direct orientation toward the face of the dominant. As the dominant lessens his threat or as the distance between the two seals increases, the screeching vocalisation, erection of the vibrissae, and shaking of the head disappear.

Low intensity submission, such as occurs when a subordinate is approached by a dominant, is illustrated in Fig. 7. Note the subordinate's widely opened eyes, oblique visual orientation, gaping mouth, relaxed lips and mystacial pads, and retracted corners of the mouth. These elements of submissive behaviour are not evoked only by overt threat. For example, a female may show them in response to the proximity of an adult male, even though the latter may be showing no apparent interest in or orientation to her.

Generally, direct facial and visual orientation are used by submissive seals being threatened at close range, and that are thus in immediate danger of being struck or bitten. Consequently, in such a context, the tactic can be considered as defensive orientation. Oblique facial and visual (or averted stare) orientation are used by most submissive animals when some distance from a dominant; 'facing away' as a distinct component appears as a stereotyped component only following mutual threat displays between seals of about equal dominance status (see below, p. 275).

Recognisable submissive facial expressions appear in pup *A. forsteri* within a few weeks of birth.

O. rosmarus.

Facial expressions accompanying high intensity submissive behaviour are striking: the mystacial pads are drawn up dorsomedially causing a lateral narrowing, and the vibrissae are erected (Figs. 8, 9). The dorsal margin of the mystacial pads is raised, imparting a 'pig snout' appearance (Fig. 10). Submission of high intensity is also accompanied by a loud repeated vocalisation, 'bellowing', occurring about four times per second, with the mouth opening and closing with each call (Fig. 8; note also the incipient opening of the mouth of the submissive walrus in Fig. 9). Generally, high intensity submission given at some distance from the dominant(s) evoking that behaviour is unoriented or oriented only obliquely toward the dominant(s) (Fig. 9). In the context of immediate or close range threat, submissive walruses rear the head and face up and away from a threatening dominant but maintain approximately direct orientation to the face of the dominant, raising and pointing the tusks more or less directly at him (Fig. 10). As in the fur seal, this tactic seems to be solely defensive in nature. Feint strikes by a dominant toward a subordinate evoke increased leaning away and extreme erection of the vibrissae.

Facial expressions accompanying submission are graded. Under conditions of mild or distant threat, a walrus shows only slight and transient erection of the vibrissae and incipient drawing-up of the mystacial pads. In Fig. 11 note these characteristics, and also the slight eversion of the vibrissae on the sides of the mystacial pads. The walrus illustrated is regarding a dominant out of the photograph to the right. Visual orientation by subordinates in such cases is normally averted or oblique with respect to the dominant, and rearing of the head up and away may appear in mild form.

Young walruses (up to 1+ years) show poorly developed facial expressions associated with submission, with no apparent movement of the mystacial pads or erection of the vibrissae after being struck, and with simple avoidance of threatening dominants.

Protective responses.

A. forsteri.

Seals that are threatened by jabs or blows to the face show narrowing of the eyes, erection of the vibrissae, and wrinkles in the facial skin (Fig. 12).

O. rosmarus.

Walruses receiving tusk blows in the sensitive region around the eyes, rostrum, cheeks, and mystacial pads generally show partial eye closure and slight erection of the vibrissae. Facial avoidance of the animal responsible for the blow follows and accompanies such behaviour, for example, by leaning back and away and orienting the tusks toward the striker, or by burying the face among other animals.

Whimpering.

A. forsteri.

All species of otariids have a facial expression that involves erection of the vibrissae accompanied by a sound variously termed (for fur seals) honking (RAND, 1967), whimpering (BONNER, 1958 and 1968), whickering (KENYON, 1960; PETERSON, 1965 and 1968), and barking (STIRLING & WARNEKE, 1971). In *A. forsteri,* the sound and accompanying facial expression are most frequently used by males during the breeding season, but both sexes and all ages of seals, even pups a few weeks old, use them in concert.

Whimpering by adult males consists of a series of similar highly pitched sounds, each sound accompanied by contraction of the flanks, expiration through the nostrils, and extreme erection of the vibrissae. Moderate intensity whimpering is illustrated in Fig. 13; high intensity (frontal view) in Fig. 14. Normally, expiration through the nostrils probably follows the sound and does not contribute to its production. The sound varies in pitch, loudness, and frequency of occurrence directly with the degree of arousal. In addition, the mouth may be opened during whimpering which results in a lowered pitch and almost a bisyllabic sound (the mouth of the seal in Fig. 14 is opened in such a way). Typically, the sound is given two to three times per second, each lasting about a fifth of a second (STIRLING & WARNEKE, 1971). A similar duration has been reported for the sea lion *Zalophus* (PETERSON & BARTHOLOMEW, 1969). During whimpering, the head is erect, tilted up slightly (Figs 13, 14), and nodded vertically with each sound. Nodding is especially pronounced during high intensity whimpering, such as occurs during social encounters with females.

Whimpering is most often given by males that are engaged in encounters with females, males engaged in general locomotory activity within their territory, males mildly disturbed, and males in the low intensity latter stages of ritualised threat displays with neighbouring males (see next section). Among females and young males, whimpering usually only occurs following mutual threats in which the whimpering seal was co-dominant. In pups, the elements of whimpering that appear earliest are the repeated contraction of the flanks and associated nasal expirations.

O. rosmarus.

Nothing resembling whimpering was observed.

Threat.

A. forsteri.

At close range, threatening seals have the mouth open, though less widely than in high intensity submission (compare Fig. 6 with 15, 16, 17). In threats where the mouth is open, the lips are tense and the corners of the mouth are not posteriorly retracted. When a seal threatens with mouth closed or open only slightly, the mystacial pads are slightly expanded, the corners of the mouth are drawn forward, and the face assumes an 'aggressive pucker' (Fig. 16; cf. FOX, 1970 and KLEIMAN, 1967). Generally, a slightly open mouth with accompanying expansion of the mystacial pads accompanies higher intensity threat than does a more relaxed facial appearance (compare Figs 15, 16). This judgement is based on the apparently greater frequency of aggressive acts such as biting, feinting, or slashing with the teeth, associated with such an expression: the male in Fig. 16 had just completed a swing at another male (to the right, out of the photograph) in response to being bitten by him.

During mutual threats, seals usually have their snout and head angled up and rotated so that they are obliquely oriented to one another (Fig. 17). During the course of a typical threat between territorial males, the seals threaten as described, often making feints or attempting quick bites. Early phases of such a sequence are most often accompanied by tension of the face and slight opening of the mouth. As the encounter progresses, facial expressions become more relaxed (*e.g.* Fig. 15), and eventually one or both animals close their mouths and start to turn away. Turning away by one male often evokes more intense threat by the other, such as a lunge or open-mouthed threat. Males turning away generally start whimpering and move away from the site of the encounter (which takes place across territorial boundaries). Females, after mutual threats among themselves, also may turn away whimpering but tend to stay in about the same location as prior to the encounter.

During a threat encounter in which dominance is quickly established, a threatening seal frequently shows direct or nearly direct visual and facial orientation, a posture suggestive of imminent closer approach, and neck 'hunched' as if in preparation for attack.

The basic characteristics of threat are similar for both sexes and all ages. However, stereotypy and predictability of events within threat sequences are far greater for threats between territorial males than for others (MILLER, 1971).

O. rosmarus.

During threat, walruses show a lateral broadening and dorsoventral deepening of the mystacial pads, and slight inflation of the rostrum lying lateral and posterior to the nostrils (Figs 18, 19). As a result, the skin of the upper lip, especially around the bases of the tusks, is more exposed and appears laterally stretched (Fig. 18). The dorsal margin of the mystacial pads is more nearly horizontal in threat than in a relaxed position (compare Fig. 2 with 18, 19). The mouth remains closed, except during occasional short oral expirations (and nasal? — note open nostrils and mouth in Fig. 19). Orientation during threat varies greatly and depends on the relative positions and postures of the interacting animals. The basic high intensity threat consists of a head-high posture with tusks pointed directly or almost directly toward the face of the receiver. Mild threats range from slight elevation of the tusks in the direction of the receiver to the extreme posture described. Often, a walrus lands ashore and walks with tusks slightly elevated and a typical threatening facial expression, but without threatening any individual.

Play.

A. forsteri.

Social play in fur seals generally consists of mock fighting. Submissive and dominant roles are generally evident, and facial expressions used are indistinguishable from those seen in non-play social encounters.

O. rosmarus.

Play was observed infrequently and often took place underwater. Young walruses engaging in mock fighting showed no obvious changes in facial expression, but older individuals showed threatening facial expressions just prior to striking with the tusks.

Investigation of objects.

A. forsteri.

Fur seals commonly erect the vibrissae when smelling objects such as rocks, pieces of driftwood, *etc.* The same is true of captive and wild *Callorhinus* (personal obs.).

O. rosmarus.

Walruses commonly tactually investigate rocks, ice, and bodies of other animals by pressing the mystacial pads against the object and moving the vibrissae slowly. They sometimes press the mystacial pads against their own foreflippers and respond similarly. Such investigation may or may not be accompanied by opening of the nostrils. Olfactory investigation of walrus carcasses has been observed to occur from a distance of a few metres, with the investigating walrus lifting the head, nostrils open, repeatedly in the direction of the carcass. No alteration in the mystacial pads was observed at such times.

Autogrooming and yawning.

A. forsteri.

During scratching of the facial region and upper throat, *A. forsteri* often slightly erect the vibrissae and close the eyes partially or entirely (Fig. 20). Yawning is often terminated with erection of the vibrissae.

O. rosmarus.

Walruses scratching their forequarters or head may have the eyes partially closed, and usually show some degree of erection of he vibrissae and their movement dorsally, but not dorsomedially (Fig. 21).

Walruses sometimes yawn after social encounters in which they showed submissive behaviour, but most yawning appears in strictly non-social contexts. Even that occurring after agonistic encounters appears simply to be 'primed' by the preceding submissive behaviour, and to have no social function. In yawning, the mystacial pads are drawn up dorsally and the mouth is opened widely (Figs 22, 23). From the dorsal aspect, yawning imparts a facial expression similar to, though broader than, a submissive one (compare Fig. 10 with 22).

DISCUSSION

Vibrissae.

Pinnipeds possess the largest and most strongly innervated mystacial vibrissae of the mammals (HUBER, 1930; SCHEFFER, 1958). A length of 48 cm for single mystacial vibrissae has been reported for *A. gazella* (BONNER, 1968) and *Eumetopias* (SCHEFFER, 1958). This is much longer than any I measured in *A. forsteri,* but the general positioning and development of the vibrissae in that species accord with what is known about other species of otariids (BONNER, 1968; RAND, 1956; SCHEFFER, 1961) and pinnipeds in general (LING, 1966 and 1972; MOHR, 1950). The importance to otariids of mystacial vibrissae in underwater feeding, orientation, and tactile investigation of objects seems clear (HUBER, *op. cit.*). Thus, captive sea lions, *Zalophus,* reportedly use mystacial vibrissae in responding to food items close to the face (EVANS & HAUGEN, 1963), and have been observed swimming with vibrissae erect while running the nose along the sea bottom (LINDT, 1956). Similarly, in the bearded seal, *Erignathus* (BURNS, 1967) and the sea otter, *Enhydra* (KENYON, 1969), vibrissae are used as tactile organs during feeding.

In the natural state, walrus mystacial vibrissae are short and stout (Fig. 2), but they can attain monstrous length and form in captivity (*e.g.* Fig. 2 in MOHR, 1950; BROWN & ASPER, 1966). Under natural conditions they are worn down due to the manner of feeding on the sea bottom, which is believed to resemble 'rooting' by pigs (BROWN & ASPER, *op. cit.*; FAY, *op. cit.* Vibrissae of *Erignathus* and *Enhydra* become similarly worn: cf. BURNS, *op. cit.* and KENYON, *op. cit.*). The mystacial vibrissae are probably used mainly in tactually investigating and grossly manipulating objects and potential food items (KING, 1964) and rarely or not at all in dismembering (HOWELL, 1930) or 'straining' food (King, *op. cit.*; SCHEFFER, 1958).

The arrangement and degree of development of mystacial vibrissae of odobenids and otariids can thus be most simply appreciated as reflecting adaptations to problems of orientation and food and object manipulation underwater, and there seems to be no need to invoke social factors as a major selective agent affecting their form.

Facial expressions.

This part of the Discussion will attempt to distinguish between facial expressions that may have display function and those not. In agreement with ANDREW (1972), 'display', referring to a behaviour pattern, will imply that that pattern's form and/or contextual use have been moulded by natural selection favouring information transfer. 'Communication' and 'signalling' will carry similar connotations.

There is a number of facial expressions common to the two species and used in clearly non-communicative circumstances: yawning and olfactory/tactual investigation of objects; and, while grooming the forequarters, an expression strongly resembling in form and context the 'consummatory face' described for canids (FOX, *op. cit.*). The sudden erection of vibrissae when struck or threatened at close quarters (*e.g.* Fig. 12) can be interpreted as a fundamentally protective response. In fur seals, protective erection of vibrissae may serve to transfer information, but it seems more parsimonious to postulate a protective rather than a display function in such instances. ANDREW (1963a, b, and 1972) has pointed out the fundamental nature of sudden erection of mystacial vibrissae in the Carnivora whenever anything is brought very close to the face.

Threatening fur seals open the mouth, thereby exposing the primary fighting weapons, the lower canines. However, the intensity of threat does not vary simply with the degree of exposure of the canines, since their visual conspicuousness is least when the likelihood of their use is highest (compare Figs 15 and 17 with 16). The extent and manner of presentation of mouth-opening and canine exposure are fairly stereotyped and predictable in many types of short-distance moderate intensity threats (Figs 15, 17), and only grade with slight closing of the mouth as the intensity of threat increases and stereotypy breaks down. In the former context, threatening fur seals are oriented to the interactant in a manner favourable for display, but this too diminishes as stereotypy of threat encounters declines at high intensities. It therefore seems reasonable to assign display function to facial expressions as used by fur seals in Figs 15 and 17, but to question whether that illustrated in Fig. 16 is communicative as defined. Further support for this interpretation comes from knowledge of canids, in which threatening facial expressions are remarkably similar in form and context to the high intensity threatening expression of *A. forsteri* (FOX, *op. cit.*; KLEIMAN, 1967): it would be remarkable if such evolutionary conservatism were due to the natural selective maintenance of common display functions, considering species differences in social structure and the role of facial-visual communication in them. Threatening walruses reduce the already potentially slight visual conspicuousness of the expanded and deepened mystacial pads and rostrum, and exposed tusk bases, to the interactant by raising the head into a tusk-point posture. This is only partly shown in Figs 9 and 10, but is clear at high intensity threat, when the tusks point directly or almost directly toward the interactant and are parallel to the ground. It is of course possible that the selectively important point may not be the form of the expression as such, but rather its dissimilarity with submissive expressions. However, on the basis of present evidence I conclude more conservatively that the threatening expression of walruses is not a display.

Submissive facial expressions of fur seals are graded and are clearly visible to the interactant (Figs 6, 7). In walruses, they are also graded, and the postural correlates of submission present an oblique view of a narrow, flat-topped, and conspicuously pale (due to the erection and crowding-together of the vibrissae) image to the interactant (Figs 9, 10). Like high intensity threatening facial expressions, submissive expressions show striking similarities to those described for canids (FOX, *op. cit.;* KLEIMAN, 1967). This is particularly true of fur seals; walruses, because of the limited mobility of their lips (HOWELL, *op. cit.*), are structurally constrained in their abilities to show all features of such expressions. These features may form part of a generalised and evolutionarily ancient response to threat (VAN HOOFF, 1972). As indicated above for high intensity threat, such evolutionary conservatism of form and context across species implies original and nowadays functions that transcend the ecologically labile visual communicative ones. Nevertheless, submissive facial expressions in both species are visually conspicuous and distinctive, and these characteristics alone make a signal function a more compelling possibility. Two further points can be noted: the structural features of the faces of fur seals and walruses have diverged markedly (Figs 1, 2), and what may be expressions with common causation in fact have very different appearances; and dissimilar vocalisations accompany high intensity submission in the two species, that in fur seals being a high-pitched screech and that in walruses being a loud segmented bellow. The first point suggests that evolutionary changes in facial structure by themselves have altered the form of expression; it may not have been evolutionarily necessary for divergence in expression per se to accompany the diverging systems of facial-visual communication. The second point emphasises that the expressions are only components of an overall submissive response and that the response in toto is different between species, so that they do not show the evolutionary constancy initially postulated. (Both points could have been made with respect to threatening facial expressions, but there the general effects, viz. slight increase in tension and apparent size of the face, are rather similar between species, and vocal concomitants of threat seem to have diverged less than is true of submission). It is concluded as likely that submissive facial expressions have signal functions in both species.

Naso-nasal greetings in both species are accompanied by the use of vibrissae. In *A. forsteri*, erection of the vibrissae varies with context and social status, but it apparently occurs regularly and in constant form in the fur seals *A. gazella* (BONNER, 1968) and *Callorhinus* (PETERSON, 1965 and 1968), and the sea lion *Zalophus* (PETERSON & BARTHOLOMEW, 1967). Simply because tactile information is exchanged during naso-nasal greetings, however, is insufficient evidence for assuming a signal function: the 'whiskers-forward' response may occur indiscriminately whether a conspecific or a rock is being smelled. Important tactile information may also be transferred through the rhinarium, which is strongly innervated for mechano-reception (HUBER, *op. cit.*): see Fig. 4. In walruses, movement of vibrissae by both interactants against the interactant's mystacial pads almost always occurs. ANDREW (1972) points out that protective responses are often conspicuous parts of greetings; this agrees with observations on walruses and fur seals but need not imply that the responses are communicative. Tactile signal functions are possible for both species; visual signal functions are likely only for *A. forsteri*.

In whimpering adult male *A. forsteri*, mystacial vibrissae may serve as visual and/or tactile signals during olfactory investigation of facial regions of females. Erection of the vibrissae during whimpering may, however, simply be necessary for sound production, and may be a communicatively insignificant part of a basically acoustic display. Certainly in many contexts a visual communicative function is not likely: turning away following mutual threats; in undirected response to miscellaneous disturbances; and in general movement within a territory. However, the visual conspicuousness and stereotypy of the erection are certainly suggestive of visual signal function.

There is a consistent difference between the sub-families Otariinae (sea lions) and Arctocephalinae (fur seals) in the use of vibrissae in threat.

Vibrissae are erect during boundary displays between adjacent territorial male sea lions (GENTRY, 1970; PETERSON & BARTHOLOMEW, 1967; SANDEGREN, 1970 and in press). Compare an equivalent display for *A. forsteri*: Fig. 17. Female sea lions engaged in close-up mouth-to-mouth threats also have vibrissae erect (SANDEGREN, 1970 and in press; cf. discussion above on protective responses), although in distant threats they do not do so (PETERSON & BARTHOLOMEW, 1967; personal obs.). (Interestingly, female grey seals (Phocidae: *Halichoerus*) have vibrissae erect during distant threats (FOGDEN, 1971)). Within the Otariinae, then, but not within the Arctocephalinae, vibrassa erection may have visual signal function in ritualised threats between males.

Walruses have long been considered to have vision substantially inferior to that of otariids (compare sizes of eyes, Figs 7, 8), which may be related to a social organisation the principal features of which occur in the sea, to the visually conspicuous tusks which appear to have evolved to function solely in the social sphere (FAY, *op. cit.*; MILLER, unpublished data), and to feeding on stationary benthic organisms. In contrast, fur seals have a society that is land-based, they have no structural characters that have evolved solely as social organs (except the long neck hair of males?), and they are active hunters of mobile prey. *Odobenus* and *A. forsteri* clearly owe certain facial expressions in social and non-social contexts to common origins and common causation. A greater fraction of facial expressions used in social contexts is considered to be communicatively important for *A. forsteri* than for *Odobenus*. Despite similar diversity and forms of facial expressions for the two species, the number of communicatively significant ones differs, and this agrees with knowledge of the species' ecological relations, social structures, and (assumed) visual capacities.

SUMMARY

Fur seals *Arctocephalus forsteri* and walruses *Odobenus rosmarus* show similar facial expressions in a variety of social and non-social contexts. In non-social settings, both species modify the facial appearance by erecting the mystacial vibrissae while grooming the forequarters, while yawning, and during olfactory/tactile investigation of objects. During naso-nasal greetings, vibrissae are often erected in fur seals, and are erected and moved against the interactant's mystacial pads in walruses. Highly submissive animals show: for *A. forsteri*, erection of the vibrissae, wide gape, relaxed lips, posterior retraction of the corners of the mouth, wide-eyed stare; for walruses, dorsomedial drawing up of the mystacial pads and erection of the vibrissae, imparting a 'pig snout' appearance. In high intensity threat, both species show facial expressions involving: for *A. forsteri*, slight lateral expansion of the mystacial pads, slight to moderate opening of the mouth, direct or oblique visual orientation from a head-up posture; for *O. rosmarus*, lateral and dorsoventral expansion of the mystacial pads, attendant exposure and stretching of the skin of the upper lip, especially around the bases of the tusks, and inflation of the rostrum posterolateral to the nostrils.

The similarities of form and context of facial expressions used by the two species suggest common causation, but a greater number of those of *A. forsteri* is considered communicative, in agreement with known ecological and social characteristics of the two species.

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RÉSUMÉ

Les Otaries, *Arctocephalus forsteri,* et les Morses *Odobenus rosmarus,* montrent des expressions faciales similaires dans une variété de contextes sociaux et non sociaux. Dans des situations non sociales, les deux espèces modifient leur apparence faciale en dressant les vibrisses de leurs moustaches lorsqu'ils grattent leurs membres antérieurs, lorsqu'ils bâillent, et lors de l'examen olfactif/tactile d'objets. Durant les salutations nez-à-nez, les vibrisses sont souvent dressées chez les otaries, alors que chez le Morse elles sont dressées et frottées contre les coussinets portant les moustaches de l'autre individu en présence. Chez les animaux fortement soumis, on observe: chez *A. forsteri,* une érection des vibrisses, un bâillement prononcé, un relâchement des lèvres, une rétraction des commissures des lèvres vers l'arrière et un regard fixe; chez le morse, un redressement des coussinets des moustaches vers le haut et une érection des vibrisses, donnant l'apparence d'un 'museau de cochon'. Lors de menaces extrêmes, les deux espèces montrent des expressions faciales comprenant: chez *A. forsteri,* une légère expansion latérale des coussinets des moustaches, une légère ouverture de la bouche et une orientation visuelle directe ou oblique alors que la tête est gardée haute; chez *O. rosmarus,* une expansion latérale et dorso-ventrale des coussinets des moustaches, étirant et exposant la peau de la lèvre supérieure, spécialement autour de la base des défenses, et un gonflement du rostre vers les côtés et l'arrière des narines.

Les similitudes dans la forme des expressions faciales et dans le contexte dans lequel elles sont utilisées chez les deux espèces suggèrent une causalité commune mais le plus grand nombre de celles-ci chez *A. forsteri* est considéré comme ayant une fonction de communication, en accord avec les caractéristiques écologiques et sociales connues chez les deux espèces.