

## Walrus ethology. I. The social role of tusks and applications of multidimensional scaling

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Social behavior of male Pacific walruses, *Odobenus rosmarus* (L.), summering (i.e. outside the breeding season) on an Alaskan hauling ground is described. Social interaction on land is mostly agonistic. Visual presentation of tusks and striking with tusks feature prominently in most agonistic interactions; vocal communication occurs in a minority of them. Agonistic interactions are analyzed in R- and Q-approaches with MINISSA, a fully non-metric multidimensional scaling procedure programmed in the Guttman-Lingoes series. Large body size and long tusks characterize dominant walruses. Dominants are most frequently aggressive and threatening, and least frequently exhibit submissive, defensive, protective, and avoidance behavior. Subordinate walruses show the opposite trend. Walruses are bullies; individuals strongly disadvantaged in body size or tusk length, or both, receive numerous strikes and visual threats. Walruses tend to initiate agonistic interactions with smaller individuals. Walrus tusks are important in fighting, a fact which constrains evolutionary ritualization of their visual display.

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On décrit ici le comportement social de morses du Pacifique, *Odobenus rosmarus* (L.), mâles (hors de la saison de reproduction) dans une de leurs zones terrestres en Alaska. L'interaction sociale sur terre est surtout de nature agonistique. La plupart des interactions agonistiques se manifestent surtout par la présentation visuelle des défenses et l'administration de coups de défenses; on remarque aussi une certaine communication vocale chez une minorité d'entre eux. On analyse les interactions agonistiques en utilisant la méthode MINISSA (techniques R et Q), un test non-paramétrique multidimensionnel d'ordination faisant appel aux séries Guttman-Lingoes. Les morses dominants sont caractérisés par l'aspect très massif du corps et la longueur des défenses. Les individus dominants sont plutôt agressifs et menaçants et ne manifestent que rarement des comportements de soumission, de défense, de protection ou d'évitement. On remarque les tendances inverses chez les morses dominés. Les morses sont brutaux; les individus très désavantagés au point de vue taille ou longueur des défenses, ou les deux, reçoivent de nombreux coups et menaces visuelles. En général, les morses dirigent leurs interactions agonistiques contre des individus plus petits. Les défenses de morse ont beaucoup d'importance pour le combat, ce qui empêche la ritualisation phylogénétique de leur parade.

[Traduit par le journal]

### Introduction

Little is known of the social life of walruses, *Odobenus rosmarus* (L.). This is due primarily to their inaccessibility to man; walruses sometimes haul out on land, but they associate with pack ice during critical periods of their annual cycle. In the Pacific, mating occurs in late winter (February-March) in the Bering Sea pack ice south of St. Lawrence Island, and impregnated females give birth in the spring (April-May) of the next calendar year while moving north with the receding ice edge (Brooks 1954; Burns 1965; Fay, unpublished data). Despite the paucity of de-

tailed information about walrus behavior at those seasons, the numerous general accounts suggest some consensus. Walruses are polygynous. Females may nurse calves for more than 2 years, and are extremely solicitous of their offspring's welfare. Males (and some females) have large pharyngeal pouches which are involved in sound production underwater, and are used for buoyancy during in-water sleep. Walruses sometimes cooperate in attacking man and other predators, and are altruistic in shepherding young individuals from danger. Walruses can sleep in the water, but while molting must spend much time hauled out on ice or land. Large tusks (upper canines) occur in both sexes and are used in defence against predators, for breaking through

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ice, in intraspecific strife, for hooking over the edge of ice for stability while sleeping in the water, and as aids to hauling out and locomotion on ice (Belopolsky 1939; Burns 1965; Chapskii 1936; Collins 1940; Fay, unpublished data<sup>2</sup>; Loughrey 1959; Nikulin 1941, 1947; Ognev 1935; Pedersen 1962). It is widely believed that tusks function most importantly in feeding, by digging food out of the sea floor. Detailed studies of feeding ecology and functional anatomy dispel this notion, and suggest that walrus tusks have evolved chiefly for social communication (Fay, unpublished data). It is this suggestion which I examine in this paper.

### Materials and Methods

From 5 June to 12 July 1972 and 26 June to 1 August 1973, assistants and I camped on Round Island, Bristol Bay, Alaska (56°02' N 160°50' W) to observe male walruses summering there. We made most observations with 7 × 35 binoculars, at distances of 10–50 m from herds. In March 1972, I made limited observations on walrus herds in pack ice south of St. Lawrence Island.

I noted the following for each of 912 dyadic agonistic interactions occurring on land: body sizes of interactants, distinguished as small (S), medium (M), and large (L) in 1972, and very small (VS), S, MS, M, ML, and L in 1973; presence and extent of tusk breakage; relative tusk lengths of interactants (0 = little or no difference, 1 = moderate difference, 2 = much difference); movements of interactants subsequent to interaction; and circumstances in which interaction occurred (e.g. attempted displacement of one walrus by another). I maintained less detailed records for a further sample of agonistic interactions.

To appraise the relative frequencies of agonistic interaction for walruses of different body size, I observed groups of walruses (from 15 to 27 animals) within large herds. These groups were generally not naturally delimited, though I often chose a natural feature (e.g. boulder) as a marker for the group. For each group I noted composition by body size; sizes of interactants; and frequencies of interaction in a 15-min period. I gathered 38 such samples, which totalled 9.5 h of observation time.

I observed 136 walruses moving seaward through herds, and noted the following: body size; number of walruses passed; number of walruses passed that threatened; number of strikes received per walrus passed; number of strikes received per threat; and number of strikes received per threat with strikes.

Body-size classifications between years were not perfectly congruent, but in general terms 1972 S corresponds to 1973 VS, S, plus MS; 1972 M corresponds to 1973 M; and 1972 L corresponds to 1973 ML plus L. I will refer to these three classes as small, medium, and large, respectively, for general descriptive purposes.

<sup>2</sup>Unpublished report filed with the Arctic Institute of North America, Washington, D.C. 1960.

### Data Analysis

Since the landmark papers by Shepard (1962a, 1962b) and Kruskal (1964a, 1964b), techniques of multidimensional scaling have proliferated and have been found widely applicable (Green and Carmone 1970; Green and Rao 1972; Shepard *et al.* 1972; Romney *et al.* 1972), but rather few have been applied to biological data (Sneath and Sokal 1973). I know of only three published studies of animal behavior in which techniques of multidimensional scaling have been used: Golani (1973), R. Guttman *et al.* (1969), and Lieblich *et al.* (1973). Each used a program of the MSA (for Multidimensional Scalogram Analysis) family, MSA-1, developed by Lingoes and L. Guttman (Lingoes 1972, 1973). MSA-1 “starts with a purely qualitative characteristic function denoting presence or absence, but produces an Euclidean space into which person-types can be mapped in such a way as to require a minimum number of coordinates to partition subjects by categories over all items simultaneously” (Lingoes 1973, p. 219). Golani’s data on jackals, for example, were ordered as profiles of items, each profile corresponding to one subject jackal and each item (character) taking one of three to nine possible states.

In this study, I used MINISSA (for Michigan–Israel–Netherlands Integrated Smallest Space Analysis), a program in the SSA-1 family of the Guttman-Lingoes series (L. Guttman 1968; Lingoes 1965, 1966a, 1966b, 1967, 1968, 1971, 1972, 1973; Lingoes and Roskam 1971, 1973; Roskam and Lingoes 1970). Like MSA-1, it uses fully non-metric techniques to find the smallest Euclidean space for a set of subjects. I applied MINISSA in two ways: R-technique, in assessing affinities among behavior components; and Q-technique, in evaluating relationships among behavior of walrus classes which were defined by tusk characteristics and body size (Table 1). See the Appendix for information on data input, proximity coefficients, and theoretical rationale.

In simple terms, the objectives of MINISSA as used herein are the ordering of subjects (behavior components in R-technique, walrus classes in Q-technique) in Euclidean space in which, when all  $\binom{n}{2}$  distances among  $n$  subjects are considered simultaneously, subjects similar to one another and bearing like sets of similarities to other subjects fall close to one another, while

those unlike one another in those ways fall far apart; computation of measures of stress ( $S$ ,  $K$ : see Appendix) to indicate how well the spatial configuration preserves relationships embodied in the proximity matrix  $P$ ; and the ordering of subjects such that 'odd' ones lie peripherally while ones bearing like sets of similarities to all other subjects lie centrally.

Statistical symbols and methods of testing follow Sokal and Rohlf (1969); statistical tables consulted are those of Rohlf and Sokal (1969). In this paper, I accept a probability level of 0.10 as significant.

## Results

### *Description of Behavior*<sup>3</sup>

In discussing dyads, I will refer to the interactant under consideration as the *subject walrus*, and the other walrus as the *other interactant*.

About 3000 male walrus haul out on Round Island each summer, and form large densely packed herds in which agonistic social interactions occur frequently (Fig. 1). Most social interactions occurring on land are solely agonistic. A typical interaction starts when a walrus comes ashore and tries to insinuate himself into the crowded seaward periphery of a herd, by squeezing in or by displacing a resident walrus: "Walrus 1 (w1) approaches rear of recumbent w2, lying at seaward edge of herd, and utters monosyllabic guttural expiration. W2 no response. W1 strikes with tusks rump of w2. W2 quickly rises and twists, raising tusks to horizontal to point at w1, who had assumed tusk-point posture while w2 turned. W1 strikes w2 in upper throat . . ." (from field notes). Other stimuli that evoke aggressive and threatening responses are the visual effect of one walrus moving by or approaching another (Fig. 15), the jostling of one walrus by another, and the sounds and movements of highly submissive walrus. Visual and tactual communication with tusks are the most obvious forms of communication on land, but numerous subtle exchanges occur. For example: "S w1 approaches rear of recumbent L w2. W2 lifts head and looks back at w1. W1 stops, regards w2, then lowers head away from w2 and appresses mystacial pads against neighbouring walrus. W2 lowers head

back to resting position. W1 lifts head and looks at w2 . . ." (from field notes). The contexts and forms of such communications among walrus strongly resemble those known for other mammals with well-developed visual communication, and need not be detailed here (for an exemplary account, see Poirier 1970). Such interactions were included in samples of agonistic behavior analyzed below.

Most agonistic interactions involve *static visual tusk threat*, in which the head of the sender is raised and thrown back so that the tusks are held roughly horizontal and point directly or obliquely toward the recipient (Figs. 2, 15). The levels of arousal, and the relative postures and orientations of the interactants modify the basic tusk-point response (Fig. 4); at low intensity, the sender may show only slight and brief intention-raising of his tusks in the direction of the recipient. Visual tusk threats are commonly accompanied by leaning toward the recipient (Figs. 5, 6), especially when he is clearly subordinate or the sender is very aggressive. During such leaning, one or both forms of *kinesic visual tusk threat* may occur. In one of these, the head is shaken laterally, rapidly and repeatedly, as though to contact the recipient's tusks. The other form is a rapid movement downward in the direction of the recipient, as though to strike his face or throat. The downward movement is commoner than the lateral, and usually occurs during mutual tusk-pointing bouts.

*Striking* with the tusks is usually performed with a downward motion, so that the recipient is usually struck with the tips of the tusks. Only 9 of 1048 strikes to the body were recorded as being made otherwise ("prod" and "press into" in field notes). A sender contacts a recipient's tusks by rapid lateral shakes of the head while leaning toward him, though many tusk contacts occur as walrus parry feints or attempted strikes to their throat and face. Strikes commonly draw blood, but probably only rarely result in serious injuries during the summer. Young walrus, even those without visibly external tusks, exhibit motor patterns resembling those used by adults in visual and tactual tusk threat (Fig. 3). In agonistic interactions on land, most strikes are received on the rump (24.6%), back (19.4%), and dorsal and lateral neck (24.2%) ( $N = 1086$ ). This distribution of strikes received is discordant with the observed scarring pattern, which is heaviest on the forequarters (compare,

<sup>3</sup>To improve comprehensibility of this section, I have incorporated without comment some interpretations made through MINISSA, R-technique.

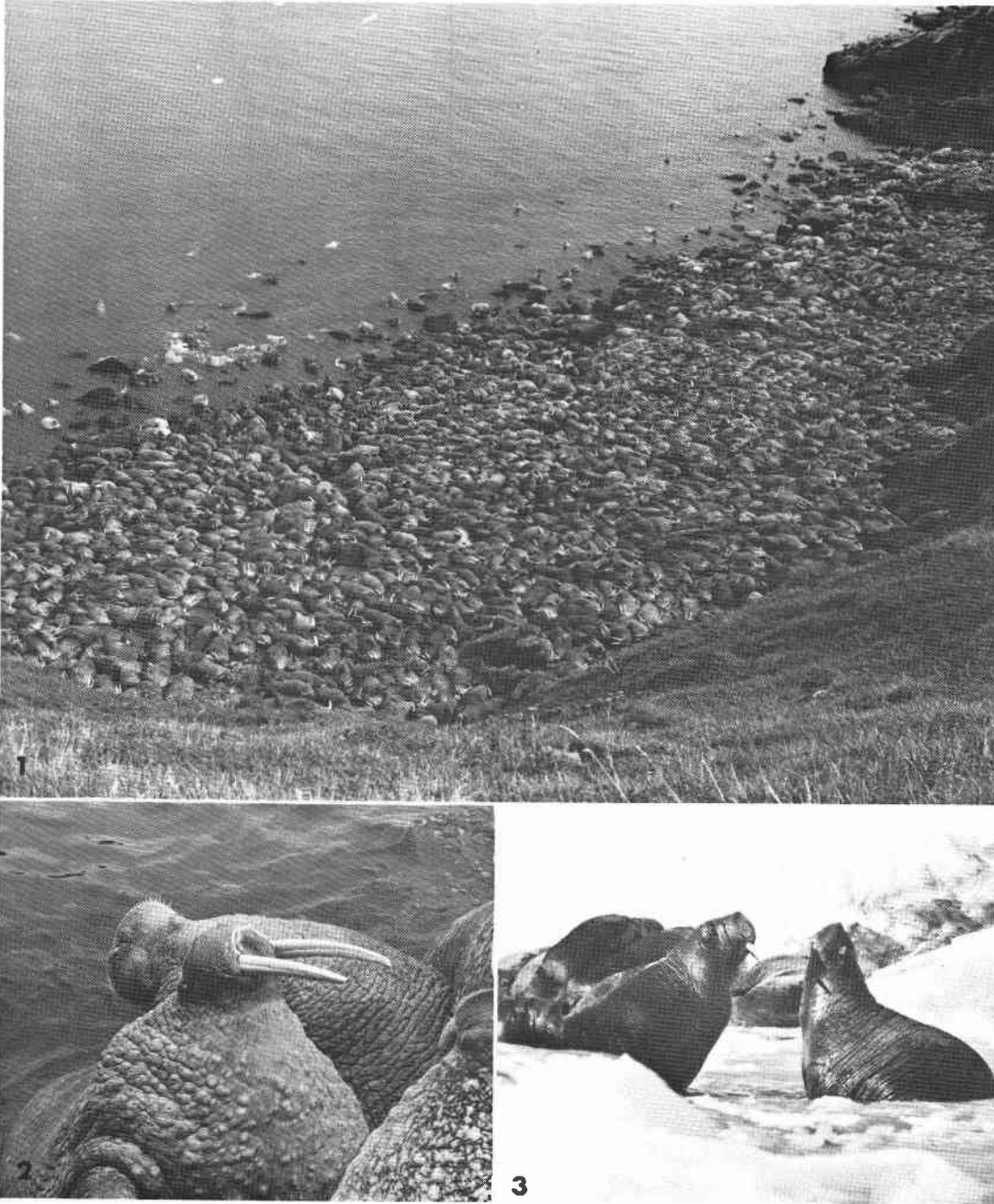


FIG. 1. Large herd of male walrus. FIG. 2. Large male walrus in frontally oriented static visual tusk threat posture. The recipient is partially visible in the right foreground. FIG. 3. Young walrus play-fighting (Bering Sea, March 1972).

sequentially, the young males in Figs. 3, 5, and the male on the right in Fig. 7).

Only 34.3% of 528 walrus that were engaged in agonistic interactions made threatening

sounds. These varied from nearly silent expirations to deep vocal roars. They were often difficult to detect, and are not included in the following analyses.

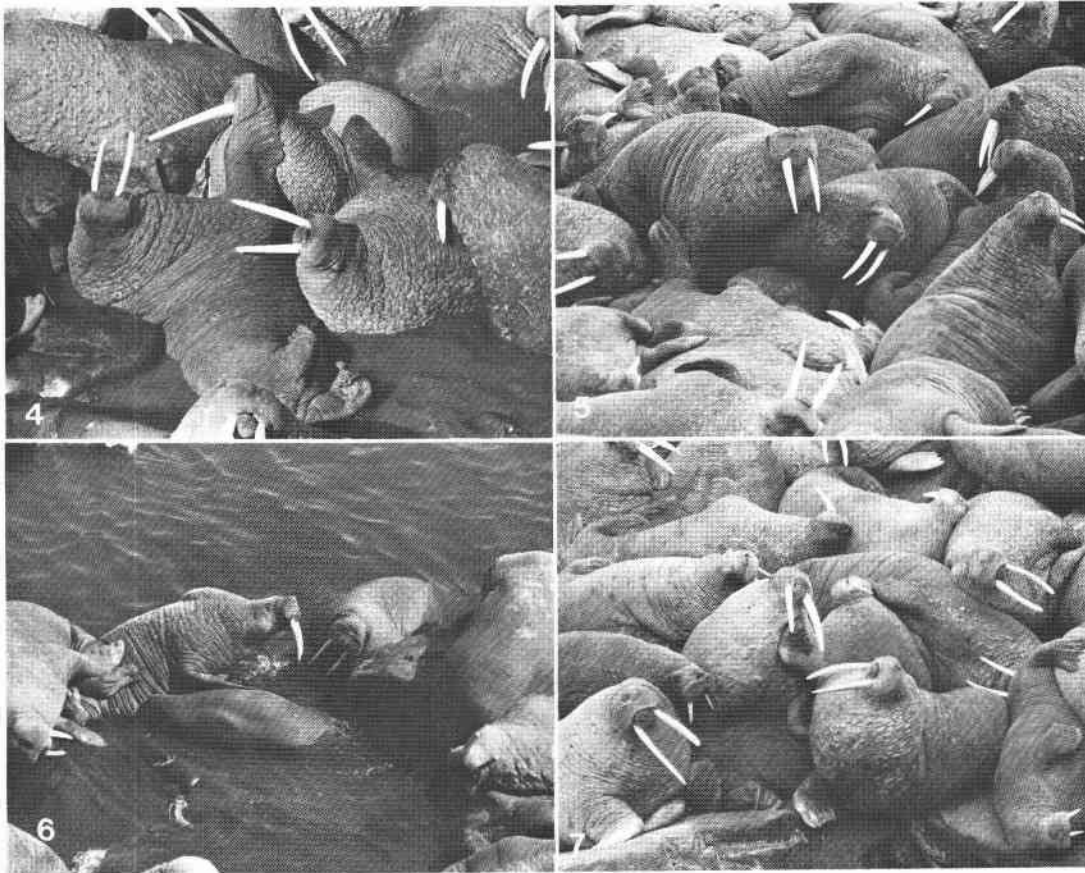


FIG. 4. Mutual static visual tusk threat between one-tusked and two-tusked walrus. The latter is flippering the former. FIG. 5. Facing away and leaning laterally away by a walrus (on right) in response to leaning visual tusk threat (from walrus on left). FIG. 6. Adult female walrus (on left) nursing her 2-year-old calf and stretching threateningly toward male walrus (on right), who responds by protectively leaning and twisting head away. FIG. 7. Agonistic encounter between two large male walrus. One (in foreground) is flippering, leaning away, and showing a suggestion of facing away, in response to static visual tusk threat by the other (on left). The animal on the right subsequently moved away, vibrissae erect.

Walrus often respond to close-up threat by *leaning away* and protectively *facing away* (Figs. 5, 15B). Subordinate walrus often lean away, but the action often seems to be one of simple avoidance (Fig. 6). Highly submissive walrus erect the mystacial vibrissae and emit a loud, rapidly repeated monosyllabic vocalization, *bellowing*, while *stretching the neck* vertically up (Fig. 8) or up and away (Fig. 10) from the sender of a threat (cf. Miller 1975b). In *head-tucking*, a walrus suddenly brings his head and face down to rest, mystacial pad down, among or against other walrus (Fig. 9). This is a common response to being struck about the face or head, or being suddenly threatened at close quarters. It

protects the strongly innervated mystacial pad and the face, which is covered with soft thin skin (F. H. Fay, personal communication; E. H. Miller, unpublished data). Subordinate walrus can often protect themselves from being struck by leaning against the side and upper back or dorsal neck of a threatening superior (*lean protectively against*; Fig. 10). Walrus respond to numerous disturbances by *flippering* the other interactant, with fore (usually) or hind flippers, or both (Fig. 4). Flippering is used strategically by submissive and aggressive animals, and walrus commonly flipper those walking close to or over them, even though there is no other apparent communication.



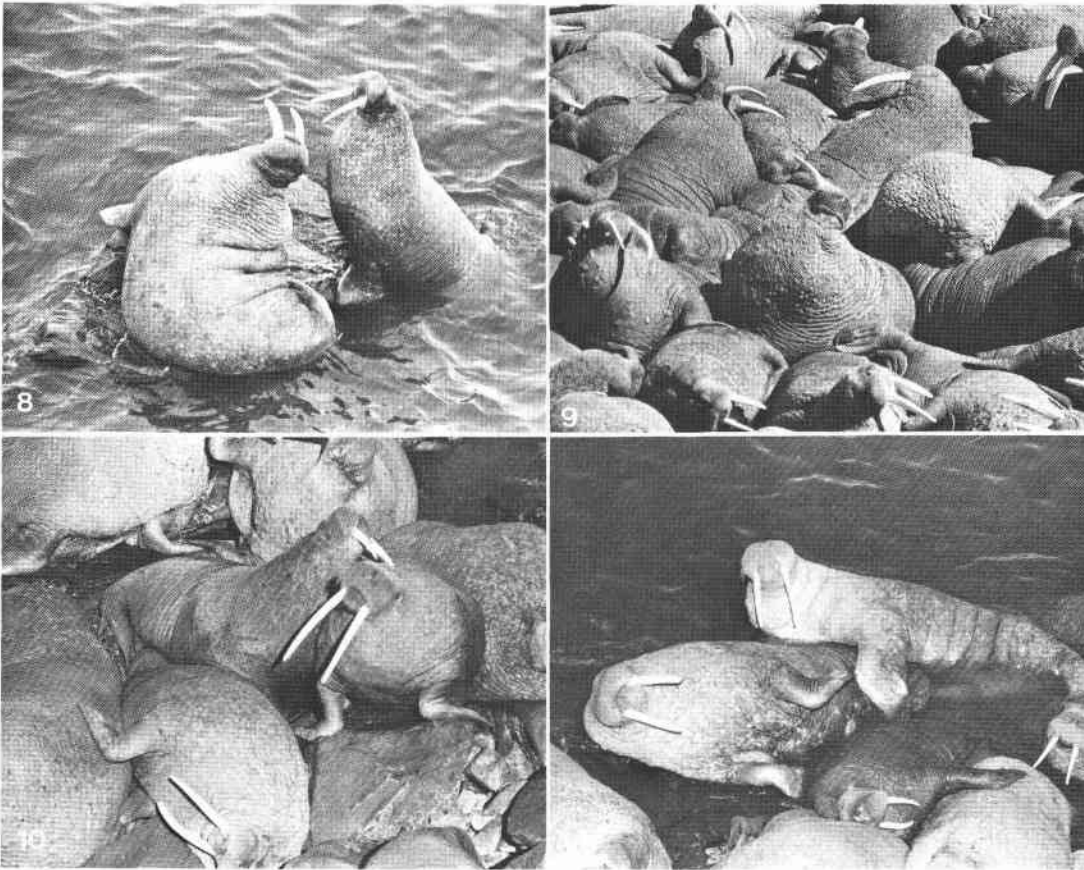


FIG. 8. Static visual tusk threat by walrus (on left) toward a smaller walrus (on right), who is neck-stretching, orienting defensively, and showing incipient vibrissae erection. FIG. 9. Large male walrus (on right) head tucking in response to sudden visual tusk threat by large one-tusked male (in center). FIG. 10. Protective leaning by smaller of two interacting walruses (on left). Note the suggestions of neck stretching and leaning away by the smaller male, and the slight tusk raise and head rotation in the direction of the smaller by the larger male. FIG. 11. Mounting of large by medium-sized male walrus. The latter grasps with his foreflipper the large male and has his penis thrust in the region of the large male's anus.

In shallow water seaward of herds on land, male walruses often rub against others, engage in nasonasal greetings or one-way olfactory/tactual investigations with the mystacial pad, show (one-way) homosexual behaviors such as mounting and pelvic thrusting (Fig. 11), and take part in complex lone and social behaviors underwater and at the water's surface. The significance of observations on these can best be appreciated if I briefly describe display behavior of adult male walruses during the breeding season (Ray and Watkins 1975; F. H. Fay, personal communication; E. H. Miller, unpublished data). This involves repeated dives by males near the edge of ice upon which females are hauled out. Rapid

'knocks,' produced by forceful bringing together of the cheek teeth, and resembling the sound of castanets, are given underwater and are followed by the 'bell tone,' which is somehow produced by means of the pharyngeal pouches (Fay 1960; Schevill *et al.* 1966). Before surfacing, another series of knocks is produced and, upon surfacing, a single loud knock is emitted. The animal then submerges his head for a few seconds, then surfaces and knocks again, submerges, then surfaces and emits a short piercing whistle through his pursed lips (this sequence is sometimes varied and (or) repeated) before diving. Females rub against the male during the surface phase, and some dive and surface in unison with him. At

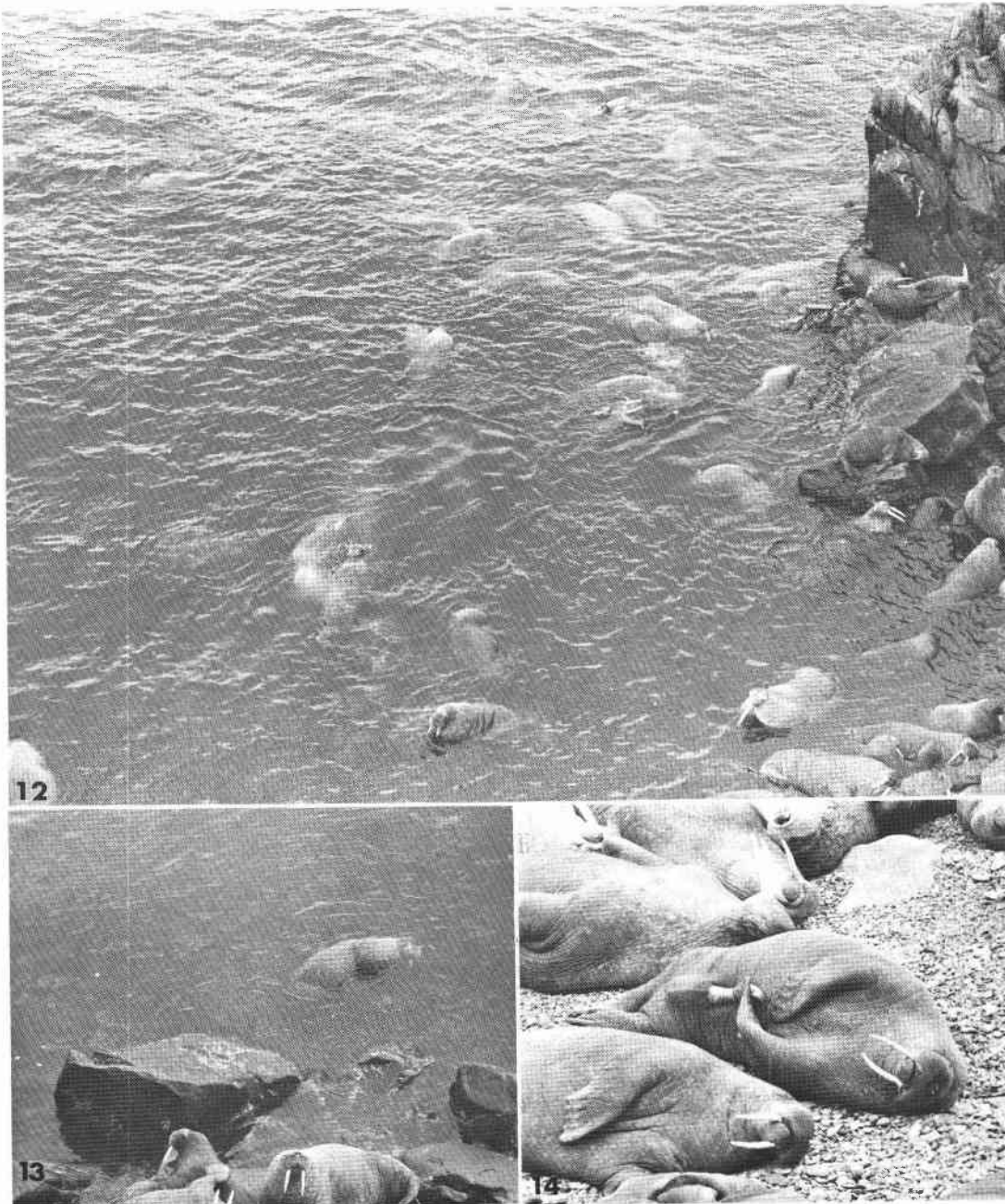


FIG. 12. Male walrus paired off while engaged in pouch inflation, body contactual behavior, etc. (see text). FIG. 13. Medium-sized male walrus engaged in pouch inflation and associated behaviors near large boulder next to beach. He is facing to the right with his right pharyngeal pouch inflated. FIG. 14. Medium-small or medium-sized male walrus stroking his extruded penis with a foreflipper, a context in which knocks are sometimes produced.

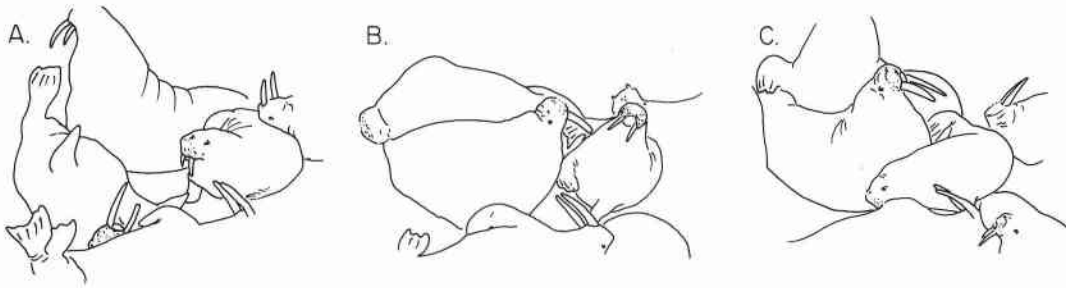


FIG. 15. (A) Small male walrus (on right) approaching large male walrus (on left). (B) The small male's approach evokes rising and leaning visual tusk threat from the large male. Concurrently, the small male starts to flipper with his palmar surface while stretching obliquely backwards and lifting his tusks defensively. (C) As the large male maintains an upright threat posture the small male walks around him, head low.

Round Island, lone subadult walruses often float in shallow water with one or both pharyngeal pouches inflated and with the foreflipper on the side of the inflated pouch brought toward the ventral midline, close to the body proximally but flexed distally (F. H. Fay and G. C. Ray, personal communication, suggest that the flipper is handling the extruded penis; cf. Fig. 14 and Schevill *et al.* 1966). The head is bowed down so that the tusks rest against the chest, and bell tones are emitted (Fig. 13). Walruses can inflate the pouches while the head is underwater by exhaling air from the lungs, and often precede inflation by a series of 'head bows,' with the tusks brought close to the chest on each bow. They can also alternately fill and empty the pouches with the face underwater, and without release of air. Lone walruses behaving thus normally situate themselves near a rock outcrop, cliff face, overhang, or boulder (Fig. 13). From there they often swim rapidly underwater to engage in mock attacks upon walruses that swim nearby, then return. On 24 July 1973 at Round Island, about 50 males were paired and engaged in pouch inflation while floating at the surface. Within pairs, one walrus commonly held the other with a foreflipper or showed suggestions of mounting (Fig. 12). Pair members rubbed against one another and occasionally dove singly or together. I could not determine whether any walrus had the penis extruded. Occasional whistles were given and, although I heard no knocks during the observations, they are given in such situations by summering males at Round Island (F. H. Fay, personal communication). Walruses on land give knocks infrequently (Fig. 14), but I saw no such animals there with

pouches inflated (walruses hauled out on ice sometimes inflate pouches: J. J. Burns, personal communication).

A diversity of social interactions occurs in and near herds on Round Island, but tusk display is a conspicuous feature only of agonistic ones. Only agonistic interactions occurring on land, where their details could be clearly seen, are used in the following analyses.

#### *The Use of Tusks in Threat*

Visual and tactual threats with tusks occur commonly. Of 1585 agonistic encounters, 79.1% involved visual tusk threats by at least one interactant, 58.2% involved striking, 40.8% involved visual threat and striking, and only 3.5% involved neither. Of the 3170 walruses involved in the interactions, 45.4% visually threatened only, 12.6% struck only, 19.0% visually threatened and struck, and 23.1% did neither. Thus 64.4% of the walruses visually threatened and 31.6% struck. The association of these behaviors between members of an interacting pair is not random (Table 2). The combinations 'strike - no strike' and 'visual tusk threat - visual tusk threat' occur more frequently than predicted, whereas 'strike-strike' and 'visual tusk threat - no visual tusk threat' occur less frequently than predicted. Only 8.3% of interactions with strikes featured strikes by both animals, but 62.7% of interactions with visual tusk threat featured visual tusk threat by both animals.

Similar trends for striking appear when the frequencies of strikes dealt out by each interactant are considered. If records of interactants receiving greater or equal numbers of strikes are summed and compared with those of interactants



TABLE 1  
Characterization of classes of agonistic social encounters  
for which behavioral profiles were analyzed

Interaction class No.	Body sizes of <i>subject walrus</i> (a), other walrus (b) <sup>a</sup>	Relative tusk lengths (a - b) <sup>b</sup>
Set A		
1	<i>L, L</i>	+
2	<i>L, L</i>	0
3	<i>L, L</i>	-
4	<i>L, L*</i> <sup>c</sup>	any (+)
5	<i>L, ML</i>	+
6	<i>L, M</i>	+
7	<i>L, &lt; M</i> <sup>d</sup>	+1
8	<i>L, &lt; M</i> <sup>d</sup>	+2
Set B		
1	<i>M, ML; ML, L</i>	-
2	<i>M, L</i>	-
3	<i>&lt; M</i> <sup>d</sup> , <i>ML</i> or <i>L</i>	-1
4	<i>&lt; M</i> <sup>d</sup> , <i>ML</i> or <i>L</i>	-2
5	<i>ML*</i> <sup>c</sup> or <i>L*</i> <sup>c</sup> , <i>ML</i> or <i>L</i>	any (-)
6	<i>ML, ML; L, L</i>	+
7	<i>ML, ML; L, L</i>	0
8	<i>ML, ML; L, L</i>	-
9	<i>ML, &lt; M</i> <sup>d</sup> ; <i>L, &lt; ML</i> <sup>e</sup>	+2
10	<i>ML, &lt; M</i> <sup>d</sup> ; <i>L, &lt; ML</i> <sup>e</sup>	+1
11	<i>ML</i> or <i>L, ML*</i> <sup>c</sup> or <i>L*</i> <sup>c</sup>	any (+)
12	<i>ML, M; L, ML</i>	+1

<sup>a</sup>Body size of the subject walrus, whose behavior profile is under consideration, is *italicized* and is separated from that of the other interactant by a comma. Where more than one body size is indicated, data were lumped.

<sup>b</sup>Tusk length of subject walrus relative to that of the other interactant. Scores > 0 indicate that subject walrus has tusks longer than those of the other interactant, etc.

<sup>c</sup>Asterisk (\*) indicates tusks broken to an extent greater than 'tip chipped' or 'tip broken.'

<sup>d</sup>All walruses of size smaller than M.

<sup>e</sup>All walruses of size smaller than ML.

TABLE 2  
Frequencies of occurrence of visual and tactual tusk threats<sup>a</sup>

Walrus I		Walrus II		$f^b$	$(f - \hat{f})^c$
Strike	Visual tusk threat	Strike	Visual tusk threat		
-	-	+	-	256	+163.8
-	+	+	+	388	+115.4
-	+	-	+	356	+29.9
+	-	+	-	20	-5.1
+	+	+	+	42	-15.0
-	-	+	+	114	-24.8
-	-	-	-	56	-28.5
+	-	+	+	15	-60.6
-	-	-	+	250	-82.0
-	+	+	-	88	-93.0

<sup>a</sup>Positive (+) indicates presence in agonistic encounter; (-) indicates absence.

<sup>b</sup>Observed frequency.

<sup>c</sup>Deviation of expected from observed frequency ( $\chi^2 = 478.3$ ,  $P < 0.001$ ,  $df = 9$ ).

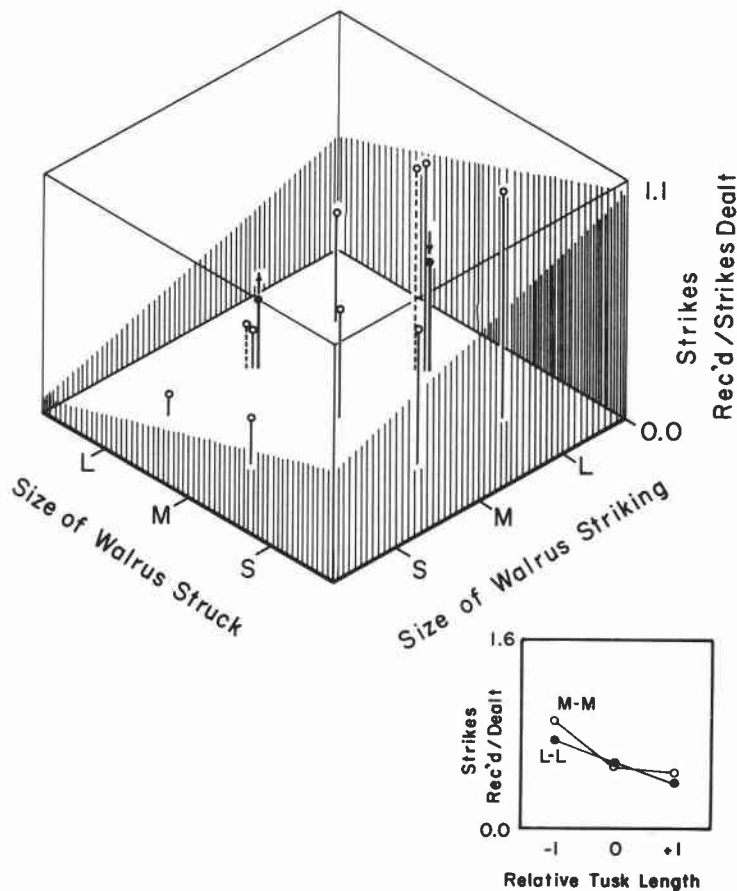


FIG. 16. Relationship of body size of interactants to the fraction (no. strikes received/no. strikes dealt out). The shading on the walls of the box emphasizes the trend of lowest values in the left corner with increases along the sides of the box in moving, city-block fashion, to highest values in the right corner. *Empty balls on solid sticks*, tusk lengths concordant with body sizes; *empty balls on broken sticks*, tusk lengths equal but body sizes unequal; *solid balls on solid sticks*, tusk lengths discordant with body sizes (e.g. in M-L interaction, M having longer tusks). *Arrows* over the solid balls indicate the direction of change of the measure relative to the situation where tusk lengths and body sizes are concordant. (S, small; M, medium; and L, large; in general terminology for data of both years.) **INSET**: Relationship of the fraction (no. strikes received/no. strikes dealt out) to relative tusk lengths of M and L walrus engaged in M-M and L-L agonistic interactions. The axes refer to the subject walrus. Thus, M and L walrus at tusk length disadvantage (-1) received proportionately more strikes than did those with tusk lengths equal to those of the other interactants (0), etc.

receiving fewer or equal numbers, the ratio of strikes received by the former to those received by the latter is 2.17:1.0 ( $N = 944$  interactions). The ratio is affected by body size and tusk length of the interactants. The ratio of strikes received by small walrus to those received by medium walrus in small-medium interactions is 3.27:1.00 ( $N = 64$ ), that for small to large in small-large interactions is 5.95:1.00 ( $N = 153$ ), and that for medium to large in medium-large interactions is 3.48:1.00 ( $N = 363$ ). Overall, the

ratio (strikes received : strikes dealt out) is 2.70:1.00 for interactants with shorter tusks ( $N = 503$ ), is 2.17:1.00 for interactants with tusks of equal length (records compared as above) ( $N = 187$ ), and is 0.37:1.00 for interactants with longer tusks ( $N = 445$ ). Body size and tusk length interact, resulting in small interactants with shorter tusks receiving most and dealing out fewest strikes, and large interactants with longer tusks receiving fewest and dealing out most strikes (Fig. 16). Where relative tusk

TABLE 3  
Deviations in excess of predicted, for frequencies of  
agonistic interaction of walrus in subgroups<sup>a</sup>

Body size of receiver	Body size of initiator			Totals
	Small	Medium	Large	
Small	+17	+14	+59	+90
Medium	-50	+29	+70	+49
Large	-81	-84	+27	-138
Totals	-114	-41	+156	

<sup>a</sup>I computed expected interaction frequencies on the assumption that agonistic interactions occur randomly with respect to body size, and with knowledge of the number of small, medium, and large walrus in the sample. Each cell entry is the appropriate (observed - expected) interaction frequency. I counted 984 agonistic interactions involving 836 individual walrus; ( $G \gg \chi^2_{.005(7)} = 20.3$ ).

length is discordant with relative body size (e.g. where medium has longer tusks than does large), the ratio is reduced but remains in favor of larger interactants (thick lines in Fig. 16).

Tusk length and body size tend to vary together, so walrus that initiate agonistic interactions with larger animals usually find themselves confronted by walrus with longer tusks, and so on (Fig. 17). Initiators of agonistic interactions are generally larger than are receivers of them; large walrus initiate more interactions than do small or medium, and small walrus receive a disproportionately high number of threats (Table 3). Data on walrus moving through herds reveal complementary trends. Of those walrus that were passed, a greater percentage threatened small animals than they did large ( $P < 0.001$ ). There was a significantly greater percentage of threats with strikes toward small than toward large walrus ( $P < 0.02$ ), and a significantly greater percentage of those walrus passed by small walrus responded by striking, than did those passed by large animals ( $P < 0.002$ ) (preceding  $P$ -estimates derived from  $t_s$  values). Small walrus showed significantly greater values than did large on number of strikes received per walrus passed ( $P < 0.002$ ); number of strikes received per threat ( $P < 0.05$ ); and number of strikes received per threat with strikes ( $P < 0.10$ ) (preceding  $P$ -estimates derived from  $F_s$  values).

The relationships of relative tusk length and body size to loss and gain of space can be appraised through data on 'displacement.' In this context, walrus attempt, through strikes and visual threats, to displace another walrus from his position in the herd. A total of 671 such inter-

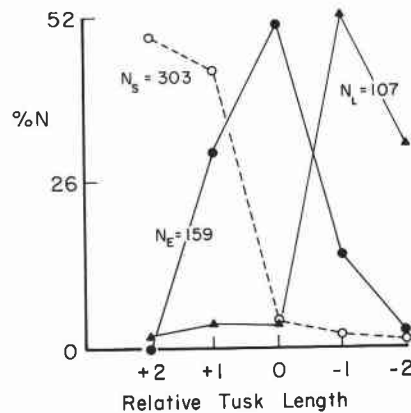


FIG. 17. Relationship between the percentage of agonistic encounters which behavioral acts of subject walrus initiated with smaller (S), larger (L), and equally sized (E) walrus, and the relative tusk lengths of the interactants. Values < 0 indicate that subject walrus were under a tusk length disadvantage, etc.

actions was examined (Table 4). The following generalizations can be made: (a) larger walrus with longer tusks gained space more often and lost space less often than did walrus lacking size advantage, regardless of tusk length; and (b) walrus lacking advantages of larger size and longer tusks lost space more often than did walrus lacking only one of these advantages. Of the walrus without advantage of larger size, those with longer tusks showed a suggestion of a higher rate of gain of space than did those without longer tusks (15.7% vs. 10.2%, for which  $t_s = 1.55$ ,  $P = 0.121$ ). That the trend is probably real is suggested by point (b); longer tusks impart an advantage in retaining space (Table 4B), so the suggestion that they also bestow an ad-

TABLE 4  
Relationship of body size and relative tusk length to gain and loss of space

A. Space gain. <sup>a</sup> Displacing walrus, <sup>b</sup> relative to other interactant:				
	Body larger		Body not larger	
	Tusks longer	Tusks not longer	Tusks longer	Tusks not longer
$n_{\text{gain}}$	46	5	19	34
$N$	184	32	121	334
$(n_{\text{gain}}/N)\%$	25.0	15.6	15.7	10.2
B. Space loss. <sup>c</sup> Displaced walrus, <sup>d</sup> relative to other interactant:				
	Body larger		Body not larger	
	Tusks longer	Tusks not longer	Tusks longer	Tusks not longer
$n_{\text{loss}}$	11	2	19	153
$N$	116	26	112	417
$(n_{\text{loss}}/N)\%$	9.5	7.7	17.0	36.7

<sup>a</sup>'Gain' and 'loss' need not cooccur. A walrus that insinuated himself beside the other interactant without actually displacing him was considered to have gained space, but the other to have lost none.

<sup>b</sup>Interactant that gained space, with other interactant not gaining space. Only two encounters occurred in which both interactants gained space, and they are excluded from consideration.

<sup>c</sup>Significant differences ( $P < 0.01$ ) exist between percentage values underlain by the ends of any line. For broken line,  $P = 0.121$ .

<sup>d</sup>Interactant that lost space, with other interactant not losing space. Only two encounters occurred in which both interactants lost space, and they are excluded from consideration.

vantage in *gaining* space seems reasonable (I will present related data on this subject in a separate paper). Walruses often did not fill vacated spaces of displaced walruses, though they could have, which probably biased the data conservatively.

#### MINISSA: R-technique

Sixteen behavior groupings were chosen during early stages of data analysis. Inclusion of certain groupings, those deemed to be fairly independent of agonistic behavior and dominance status, increased measures of stress and difficulty of interpretation. They were therefore dropped from further analysis: *visual orientation* (without display of tusks, or defensive orientation); *move offending part* (e.g. movement of a flipper away after being touched there); and *splay* (rolling onto the back and stretching out the foreflippers in response to disturbance). Groupings retained for analysis are (original numbering scheme retained) (1) static visual tusk threat (Figs. 2-10); (2) kinesic visual tusk threat; (3) strike forequarters with tusks (from the shoulder area forward); (4) strike hind-

quarters with tusks (posterior to the shoulders); (5) head-low/face-away (Figs. 5, 15); (7) protectively cover up (head-tucking and its variants) (Fig. 9); (8) lean laterally away (Figs. 5-7, 15, suggestion in Fig. 10); (9) neck stretch (Fig. 8, suggestion in Fig. 10); (10) bellowing and (or) vibrissae erection (photographs in Miller 1975b); (11) lean protectively against (Fig. 10); (12) move away; (15) flipper (Figs. 4, 7, 15); (16) redirected strike (to nearby animal). I determined the presence or absence of each of these groupings in the behavioral profile of each interacting walrus, and computed their pairwise association (see Appendix).

Two loose clusters are suggested by a three-dimensional representation (Fig. 18): set I, {5, 7, 8, 9, 10, 11, 12}, and set II, {1, 2, 3}. There is also a suggestion of polarity within set I. Higher-dimensional plots support the reality of distinguishing between sets I and II (Fig. 19A), and indicate strong similarities between some elements of set I (Fig. 20). The suggestion of polarity within set I is supported by the finding that removal of the six-dimensional plots of

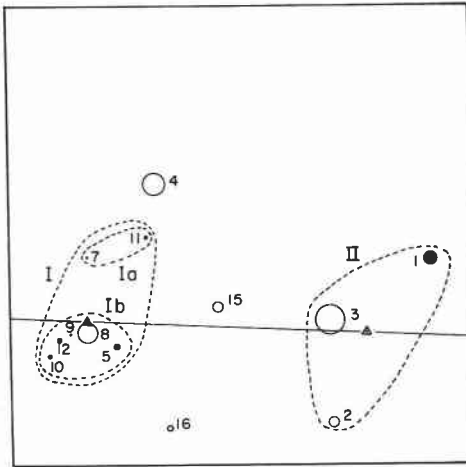


FIG. 18. MINISSA vector plot (three dimensions, vectors for the first and third being in the plane of the page). Numbers represent behavior groupings mentioned in the text. The coordinate values for the second dimension are represented by circle diameters, hollow for negative values and solid for positive values. The centroids for sets I and II are located at the centers of the small triangles, and the *centroid axis* passes through them. ( $K = 0.120$ ,  $S = 0.083$ , weak monotonicity.)

groupings 7 and 11 from set I results in the largest decrease in overlap between I and II that can be achieved through discarding *any* single pair of components from it (Fig. 19B). One can further decrease overlap (in increasingly smaller steps) between I and II by discarding, in order, {5}, {8, 9}, and {10, 12} (Fig. 19B). The correspondence between positioning along the *centroid axis* (Fig. 18) in two dimensions, and overlap in six dimensions, was evaluated by the following procedure. I scored ( $R = 0$  to 3) each member curve of I for the amount of overlap with each of the member curves of II, then weighted ( $w$ ) the overlap according to how much each curve of II was overlapped overall. For example, a curve of II that was crossed a total of eight times by member curves of I imparted  $w = 8$  to each of them. I computed a *score*  $T$  for each curve of I as  $T = \sum R_i w_i$  for the  $i$  curves of II. High  $T$  values indicate much overlap with little-overlapped curves of II, some overlap with much-overlapped curves, or both; low  $T$  values indicate little overlap with little-overlapped curves or, at a minimum, no overlap at all.  $T$  values and rank position along the centroid axis are strongly associated ( $0.01 < P < 0.05$ , Kendall's rank correlation coefficient). I conclude that the order {10, 12}, {8, 9}, {5}, {7, 11} has significance. One

can describe the ordering in terms of defensive/tactical and submissive/avoidance/subordinance qualities (Fig. 21). Head-low/face-away (grouping {5}) often seemed to be precautionary behavior grading into higher intensity covering-up, and its positioning in Fig. 21 is consistent with that subjective evaluation.

I applied the scoring system of the preceding paragraph to member curves of II, and determined that 1 is least similar, 2 is more similar, and 3 is most similar to set I. These findings accord with Fig. 18, and support the suggestion that ordering along the centroid axis has interpretive significance. Set II is internally heterogeneous in three dimensions (Fig. 18), and even in six dimensions no apparent associations between components appear. The reasons for this heterogeneity, and the finding that striking fore-quarters (grouping 3) and feinting (grouping 2) are closer to set I than is static visual tusk threat (grouping 1), may be due to errors in classification of behaviors. Consider two examples: (a) small subordinate walrus commonly strike larger animals that are moving through herds, when the moving walrus cannot or do not bother to respond; and (b) kinesic visual tusk threat is often used in a seemingly frustrated manner, as when a walrus submissive in an encounter makes rapid downward intention movements of striking, but from a distance; such movements seem to be not so much threats as inhibited strikes. By including such different contextual uses of groupings 2 and 3, it would be expected that set II's internal homogeneity would decrease and dispersion would increase, in the observed manner. Overall, though, set II is reasonably discrete from set I and it seems fair to consider the II pole as representing aggression/threat. Description of members of set I in other terms (Fig. 21) does not necessarily invalidate the grosser descriptors; set II may embrace tactical/defensive qualities not readily apparent because they are overridden, in the observer's eyes at least, by aggressive/threatening qualities.

In the first and third dimensions, groupings 4, 15, and 16 show no clear alliance with other groupings (Fig. 18). Flipping (grouping 15) has the lowest centrality index (= greatest centrality) of the 13 groupings, indicating similar affinities with each of I, II, 4, and 16. This agrees with the subjective impression that flipping is primarily tactical, and supports the choice of descriptors in Fig. 21. Redirected striking (grouping 16) and



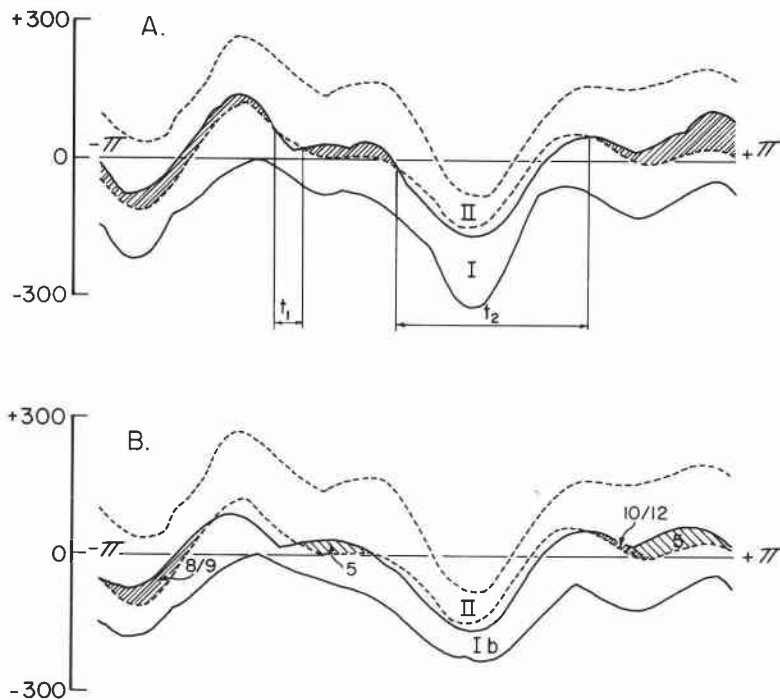


FIG. 19. (A) Members of sets I and II of Fig. 18 plotted in six dimensions using MINISSA coordinates. The areal limits represent the outermost curve segments of curves plotted for each set member, according to a general formula for high-dimensional data,

$$f_x(t) = x_1/\sqrt{2} + x_2 \sin(t) + x_3 \cos(t) + x_4 \sin(2t) + x_5 \cos(2t) + \dots$$

plotted on the range  $-\pi < t < \pi$  (Andrews 1972, 1973; see also Goodchild and Vijayan 1974). Parts of the range where I and II are completely non-overlapping are indicated ( $t_1, t_2$ ). In six dimensions,  $K = 0.027$ ,  $S = 0.017$ , with weak monotonicity. (B) As for preceding, but with the curves for behavior groupings 7 and 11 deleted. Overlap due to each of {5}, {8, 9}, and {10, 12} is indicated.

strike hindquarters (grouping 4) are outliers, but along the centroid axis both fall closer to I than to II. To explore the possibility that 4 and 16 have affinities with I or II not apparent in three dimensions, I examined the courses of six-dimensional plots of the two groupings. I felt that if some subtle alignment was present, it should be detectable for those parts of the range of  $t$  where the areas of I and II are non-overlapping ( $t_1$  and  $t_2$  in Fig. 19A). Such is not the case: 4 is aligned with II over  $t_1$  and with I over  $t_2$ , and 16 is aligned with I over  $t_1$  and with II over  $t_2$ . Redirected striking and strike hindquarters thus show no clear alliance with either of sets I or II in six dimensions. As above, errors in the classification of behaviors may be responsible for the ambivalence. Redirected striking sometimes appears to be an expression of general aggressive arousal, for large males just terminating agonistic encounters often strike nearby animals. On

the other hand, small subordinates struck or threatened by dominants sometimes repeatedly strike neighbors that are smaller or unprotected. The ambivalent position of 4 surely reflects the previously mentioned tendency of subordinates to strike dominants moving through the herd; striking of hindquarters is common in such situations.

As defined in this study, groupings 1, 2, 4, and 16 probably subsume important motivational diversity. This has obscured the contributions of aggression and submission (in general terms) to 4 and 16, and probably misplaced the locations in Fig. 18, of true kinesic visual tusk threat and aggressive use of striking forequarters. Based on subjective impressions and vector plots, Figs. 18–20, I feel that the following statements are valid: indicators of submission (bellowing and vibrissae erection) form part of a discrete group of behaviors functioning in avoidance, protec-

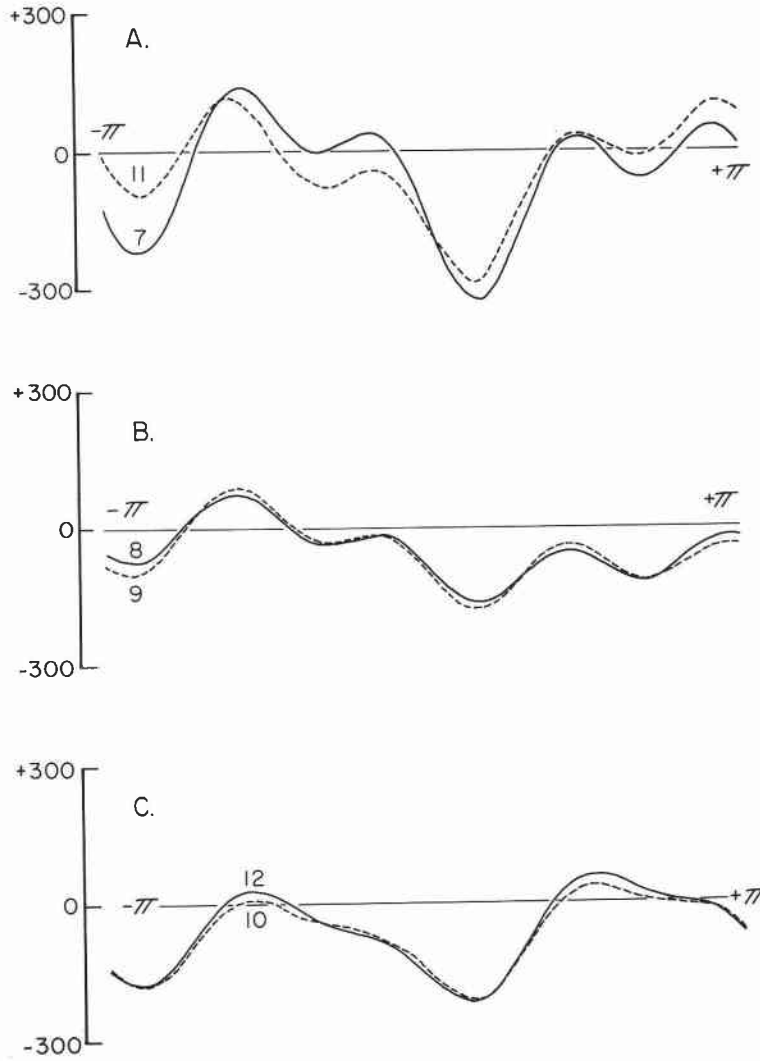


FIG. 20. Curves for members of each of {7, 11} (A), {8, 9} (B), and {10, 12} (C), plotted as described in legend to Fig. 19.

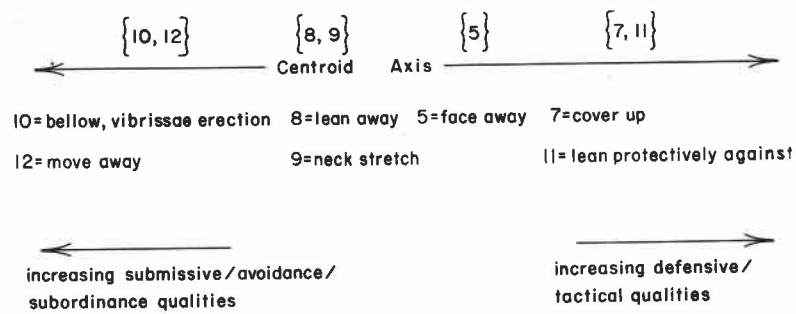


FIG. 21. Interpretable qualities for components of set I (Fig. 18) along the centroid axis.

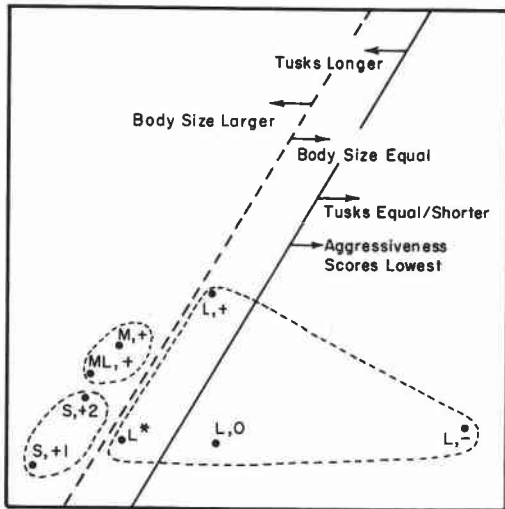


FIG. 22. Two-dimensional MINISSA vector plot of behavior profiles of L walruses (Table 1, set A). Body size of the other interactant, and relative tusk lengths of the interactants, are indicated (values  $< 0$  indicate that subject walruses had shorter tusks, and so on; \* indicates that the other interactant had fractured tusks). Verbal descriptions refer to subject walruses. ( $K = 0.049$ ,  $S = 0.025$ , weak monotonicity.)

tion, and defence; behaviors related to tusk presentation and striking are most completely opposed to those of the preceding group; flipping is tactical and may accompany opposing motivational states; and conflict tendencies and frustration may be manifest through inhibited and redirected striking. I think that striking hindquarters is primarily aggressive, despite its equivocal position in Fig. 18, and have combined it with striking forequarters (grouping 3) for Q-technique.

#### MINISSA: Q-technique

Behavior of large walruses varies systematically with the body size and tusk length of the other interactant (Fig. 22). I constructed 'aggressiveness' scores for behavior profiles, on the assumption that visual and tactual tusk threats carry aggressive/threatening overtones absent from other groupings. The score was computed as the sum of the reverse ranks of values of mean occurrence per encounter of the groupings strike, static visual tusk threat, and kinesic visual tusk threat, plus the sum of the ranks of the other groupings. Large walruses interacting with other large walruses, and with tusks equal in length to or shorter than those of the other interactant, have the lowest aggressiveness scores (Fig. 22).

This trend can be illustrated with reference to the frequency of strikes dealt out in large-large agonistic interactions. Subject walruses with shorter tusks dealt out a mean number of strikes per encounter of 0.208; those with tusks of equal length dealt out 0.688; those with longer tusks than intact-tusked animals dealt out 1.042; and those with longer tusks by virtue of the other interactant having fractured tusks dealt out 0.739 (cf. inset, Fig. 16). The basic differentiating factor across the vector plot, Fig. 22, is thus one related to aggression/threat on the left and its complex converse on the right.

To explore further the relationships of size and tusk length to behavior, I defined a greater number of classes (Table 1B). Clear polarity exists in a three-dimensional plot (Fig. 23), with behavior profiles of smaller interactants with shorter tusks positioned far to the left (Fig. 23, set Ia), interactants of smaller size or with shorter tusks positioned to the left of center (Fig. 23, set Ib), walruses of larger size or with longer tusks positioned to the right of center (Fig. 23, set IIb), and larger interactants with longer tusks positioned far to the right (Fig. 23, set IIa).

Polarity suggested on the basis of relative tusk length and relative body size is also reflected in the distribution of high and low ranks of frequency of occurrence of behavior groupings (Fig. 24). Those groupings I considered as non-aggressive/non-threatening tend to show highest ranks to the left and lowest to the right (broken lines in Fig. 24), while aggressive/threatening behaviors show a reverse trend (solid lines in Fig. 24) (for identification of classes see Fig. 25). Kinesic visual tusk threat shows some ambiguity and is not illustrated (see below). Based on the distribution of highest and lowest ranks for groupings of behavior, excluding kinesic visual tusk threat, flipping, and redirected striking, two sets can be characterized (Fig. 25): set I, lowest ranks for frequency of striking and frequency of visual static tusk threat, highest ranks for frequencies of all other components, body size less than or equal to that of the other interactant, tusk length less than that of the other interactant; and set II, highest ranks for frequency of striking and frequency of visual static tusk threat, lowest ranks for frequencies of all other components, body size equal to or greater than that of the other interactant, tusk length equal to or greater than that of the other interactant. Kinesic visual tusk threat is more weakly

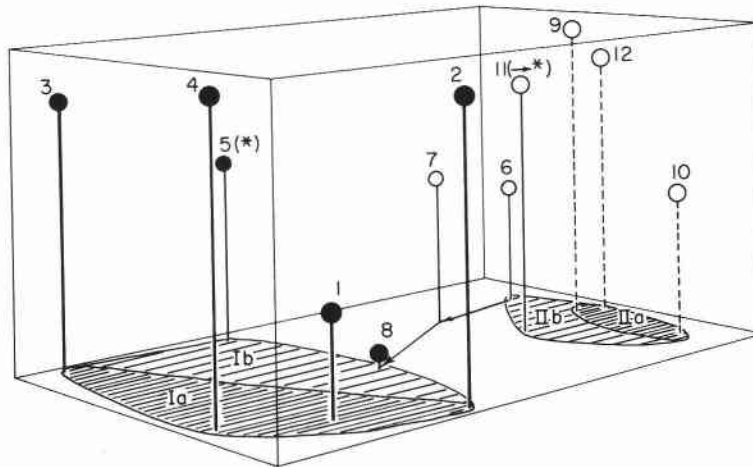


FIG. 23. Three-dimensional MINISSA vector plot of behavior profiles (Table 1, set B). *Solid balls*, subject walrus with tusks shorter than those of the other interactant (set I); *empty balls*, subject walrus with tusks longer than (set II) or equal in length to (No. 7 only) those of the other interactant; *thin solid sticks*, subject walrus of same size as the other interactant; *broken sticks*, subject walrus larger than the other interactant (set IIa); *thick solid sticks*, subject walrus smaller than the other interactant (set Ia). Subject walrus with body size equal to and tusks shorter than those of the other interactant fall in set Ib. Subject walrus with body size equal to and tusks longer than those of the other interactant fall in set IIb. The arrows join, sequentially, points for subject walrus with body size equal to and tusks longer than (6), equal in length to (7), and shorter than (8), those of the other interactant. ( $K = 0.064$ ,  $S = 0.045$ , weak monotonicity.)

This figure was traced from a CALCOMP plot programmed and run by A. R. Gibson, University of Toronto.

TABLE 5

Relationship of tusk breakage and relative tusk length to the prevalence of aggressive/threatening behavior in the behavior profiles of large walrus

Characterization <sup>a</sup>	Mean rank of:		Set membership, Fig. 22
	agg./threat. behavior	non-agg./non-threat. behavior <sup>b</sup>	
L, L (+), set B-6	2.3	8.3	II
L, L (0), set B-7	6.0	7.4	II
L, L (-), set B-8	6.0	5.0	I
ML or L, ML* or L* (any), set B-11	3.7	8.8	II
ML* or L*, ML or L (any), set B-5	6.0	3.9	I
Fig. 22, set I	8.6	3.9	—
Fig. 22, set II	4.1	9.1	—

<sup>a</sup>Refer to Table 1.

<sup>b</sup>Excluding flipping and redirected striking.

aligned than are other aggressive/threatening groupings, but nevertheless has a mean rank of frequency of occurrence of 4.5 for set II and of 8.5 for set I members. Overall, it matters little whether set-delimiting features are taken as characteristics of behavior groupings or as characteristics of body size and tusk length, in support of earlier interpretations (Table 5; cf. Fig. 22). As expected, the association on a gross

level between aggressive/threatening groupings and others (excluding flipping, redirected striking) is significantly negative ( $P = 0.0016$ , Kendall's rank correlation coefficient).

### Discussion

#### *Tusks as Display Organs*

The importance of striving for dominant social status was probably minimal during this study

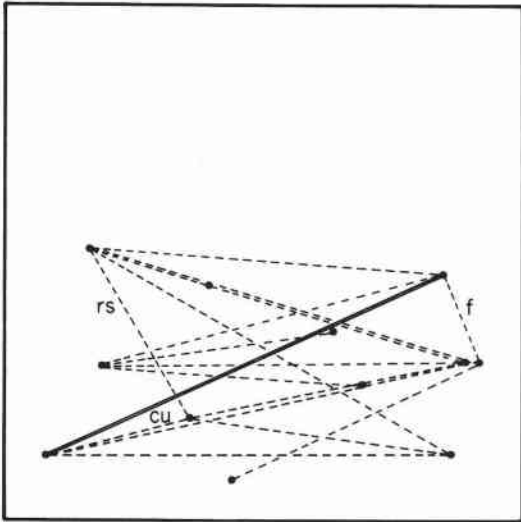


FIG. 24. Two-dimensional MINISSA vector plot of behavior profiles (Table 1, set B). Broken lines join profile classes with highest ranks to the left and lowest ranks to the right, on frequency of occurrence per interaction of the behavior groupings. Solid lines join classes with lowest ranks to the left and highest to the right. Where tied ranks occur, all tied classes are joined by lines to the class of opposite rank. The groupings flipping (*f*), redirected strike (*rs*), and cover-up (*cu*), are indicated. Kinesic visual tusk threat is omitted (see text). For identification of classes, see Fig. 25. ( $K = 0.120$ ,  $S = 0.086$ , weak monotonicity.)

for several reasons: (a) all observations were made in summer, well after the season of oestrus and copulation, when maximal competition for mating rights would be expected to occur; (b) walrus able to obtain a position centrally within a herd during the extreme cold of winter probably achieve significant energy savings (Fay and Ray 1968; cf. Laws 1956, and Le Boeuf *et al.* 1972), but thermal conditions in summer on Round Island are such as to render such savings unimportant; (c) the age structure of the male population frequenting Round Island is under-representative of young age classes, so social interactions featuring mock fighting and the ontogenetic emergence of dominance relations would not be expected to occur there as frequently as in groups of younger walrus; and (d) all analyses reported above pertain to terrestrial behavior, whereas copulation, courtship, and serious intermale fighting probably occur in the sea (cf. Ray and Watkins 1974; Schevill *et al.* 1966).

In this study, I obtained evidence in support of interpretation (d). Subadult males, with pharyn-

geal pouch(es) inflated, often engaged in lone or social play with sexual and agonistic overtones; 'practice' sessions for adult behavior are clearly suggested. Second, scarring is heavier on the forequarters than on the hindquarters, which disagrees with the observed distribution of strikes received in on-land agonistic interactions. This suggests that many important interactions were not observed. The observed pattern of scarring would result from interacting in frontally oriented postures in the water, such as characterize adult males in serious threat (F. H. Fay and G. C. Ray, personal communication; E. H. Miller, unpublished data).

Despite evidence pointing to a basically aquatic social system, I assume that determinants of rank and that qualities and outcomes of agonistic interactions resemble, at least, those occurring elsewhere and at different seasons. All else being equal, large body size or long tusks, or both, positively influence the gain and maintenance of space in herds on land. Both characteristics are associated with aggressive and threatening behavior. Subordinate walrus generally are small or have short tusks, or both. They show much submissive, defensive, protective, and avoidance

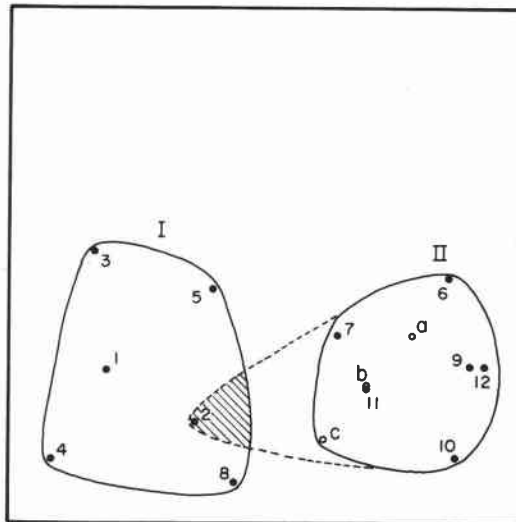


FIG. 25. Two-dimensional MINISSA vector plot of behavior profiles (Table 1, set B), showing set construction suggested by Fig. 24. Centroids for tied classes are represented as hollow circles: *a* for 6, 7, 9 (tied for lowest rank on lean laterally away); *b* for 2, 6, 10 (tied for lowest rank on redirected strikes); and *c* for 2, 10 (tied for lowest rank on covering up). Class 2 ties twice for lowest rank on non-aggressive/non-threatening groupings, and is indicated as not clearly allied with either set. (Stress measures as for Fig. 24.)



behavior, and readily lose space in the herd to superiors. The manner in which tusk length comes to be associated with dominance is probably similar to that proposed for other mammals. Geist (1966a, p. 205) writes: "... in a species with graded horn sizes males learn to associate large horns with superior strength during frequent, minor agonistic encounters outside the rutting season," and further suggests that this learned association can serve as a basis for avoiding serious and potentially injurious competition with physically superior males during the rut (cf. Geist 1971; Michael 1968). The same is probably true of walrus; walrus tusks, despite their large size and visual conspicuousness, function basically as offensive weapons and not as physically inoffensive threat symbols (cf. Geist 1966a; Gould 1973, 1974). Since tusks can inflict serious injuries during battles between adult males in the breeding season (F. H. Fay and G. C. Ray, personal communication), it behooves individuals to be able to discriminate between walruses likely to be dominated and those not likely to be dominated. Natural selection thus favors enhanced powers of discrimination for features related to physical prowess (body size, tusk length, experience). Consequently, walruses that attempt a purely bluffing strategy are selected against (Fisher 1958; Schaffer and Reed 1972; Smith 1972; Smith and Price 1973). The joint operation of these selective pressures maintains within the population the potential to inflict injury, and reserves serious dominance contests for vigorous mature males in the breeding season.

The enlargement of the upper canines as fighting and threat organs has been accompanied by formalization of the manner in which they are visually presented in threat, and high frequency of cooccurrence of visual tusk threats between interactants (Table 2). The manner of presentation is modifiable by the level of aggressive arousal of the sender and by posture, orientation, and distance, so it seems preferable to refer to it as a 'modal action pattern' (MAP: Barlow 1968, p. 230) rather than as a fixed-action pattern. The form is particularly likely to vary at low levels of aggressive arousal, but is relatively invariant over a wide range of higher levels of arousal. It may therefore be considered to have 'typical intensity' (Morris 1957) or 'typical form' (Tinbergen, cited by Cullen 1966, p. 368). Nevertheless, it is difficult to judge whether the MAP is

evolutionarily ritualized. In the related fur seals and sea lions, formalized threat displays between breeding territorial bulls involve raising and tilting up of the head and opening of the mouth, with consequent exposure of the primary fighting weapons, the lower canines (Miller 1975b). This so-called 'boundary ceremony' (Peterson 1968; Peterson and Bartholomew 1967) clearly incorporates elements derived from fighting, and commonly involves unstereotyped biting, lunging, and swinging (Gentry 1970; Miller 1971). Similarly in walruses, the MAP of visual tusk presentation usually occurs with feinting, swinging, and strikes by one or both interactants. There is thus a close relationship throughout the Otarioidea between formalized male-male threat displays and unformalized overt aggression. This initially seems surprising for walruses, because the tusks have evolved to such visually conspicuous proportions, but is explicable by appreciating the high probability that mature males must fight seriously during their reproductive lives. A ceiling may be set on the degree to which the MAP of visual tusk presentation can be motivationally emancipated from natural selectively critical motor patterns necessary in serious intermale strife (cf. Bartholomew 1970; Le Boeuf 1974; and Miller 1975a). The classical concept of ritualization, where there is a "gradual change of a useful action into a symbol and then into a ritual: or, in other words, the change by which the same act which first subserved a definite purpose directly comes later to subserve it only indirectly (symbolically) and then not at all" (Huxley 1968, p. 39) is thus only applicable if one considers the original function to have been 'display of lower canines' rather than 'threat display.'

Tusks function importantly in defence, for example in parrying blows, and defensive orientation is a common response of walruses subordinate in agonistic interactions (Figs. 8, 15). Such posturing is probably optimal for effective defensive use of tusks, in conformity with Geist's theorizing (Geist 1966a, 1971).

Walruses preferentially threaten smaller and equally sized individuals, and subordinates receive many threats despite their non-threatening behavior (Table 3). These findings contrast with those of Geist (1966a, 1966b, 1971) for bighorn sheep (*Ovis canadensis*). His data indicate frequent agonistic interactions between rams of similar dominance status (similar horn size).

His data refer, however, to dominance contests in which the *purpose* of interacting is to establish or reinforce dominance relations. Walruses, living in large anonymous herds, usually need establish only temporary dominance relations as they relate to proximate goals, such as protection of the calf, or maintenance of position in a herd on ice or land. (One expects, of course, that adult male walruses engage frequently in agonistic interactions during the mating season. This parallels the situation in *O. canadensis*, but is restricted in context, space, and time.)

Cephalic display organs of ungulates contribute significantly to social status (Geist 1966a, 1966b, 1971; Espmark 1964; Lincoln 1972; Schaffer and Reed 1972). A comparable situation exists among walruses. No other otarioid pinniped shows such markedly developed social organs, although the massive neck and somewhat long neck hairs of breeding bull fur seals and sea lions are probably important in visual signaling. Sandegren (1974) suggests that the mystacial vibrissae of bull Steller's sea lions, *Eumetopias jubatus*, have visual signal function, but I doubt that their extreme development reflects selection for such function (Miller 1975b). Of the earless seals (Phocidae), adult male elephant seals (*Mirounga* spp.) have an enlargeable snout that is used in visual threat display (Carrick *et al.* 1962; Laws 1956; Sandegren, unpublished data), and adult male hooded seals (*Cystophora cristata*) have an enlargeable snout and evertable bright red nasal septum that may be used similarly (Berland 1965; Mansfield 1964).

#### *Applications of Multidimensional Scaling*

In *R*-technique, MINISSA pointed to basic affinities and polarities among behavior groupings. Separation of groupings (as curves) was achieved in high dimensionality. This was not as marked as in some studies in physical anthropology (Andrews 1972; Oxnard 1973), but was interpretable and consistent with low-dimensional vector plots. MINISSA was clearly sensitive to methodological errors in my behavioral taxonomy, and must be applied to more detailed and carefully specified data in order to assess its utility for similar studies.

In *Q*-technique, MINISSA vector plots strongly and consistently supported the reality of partitioning behavior profiles on the basis of tusk length, tusk intactness, and body size. Vector plots were partitioned by previously interpreted

behavior groupings (on the basis of *R*-technique), and provided insight into the factors differentiating agonistic behavior of the walrus classes.

Multidimensional scaling techniques can be applied to many kinds of data and to data in numerous forms (Shepard 1972b provides a useful review; see also Green and Rao 1972). These techniques hold promise for data analysis in ethological studies because many of them can handle qualitative, *n*-chotomous, and mixed-mode data, and because interpretation of axes is generally possible. Fully non-metric techniques, which require no assumptions about the nature of the quantitative factors underlying the subject classes, may prove especially valuable. These generate a metric space from a non-metric one and provide to the ethologist a conceptually fruitful means for interpreting complex data.

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#### **Appendix**

Multidimensional scaling techniques have potentially great value for ethological analyses. Because these techniques are at present used little in ethology, and because a number of distinctly different algorithms is likely to be employed in the future, it is necessary to specify the nature of the algorithm and program setup used in this study. The following description outlines the functioning of the program as used in this study;

numerous other data options are available (see Lingoes 1973).

Data input was in the form of off-diagonal, symmetric proximity matrices. In Q-technique, Gower's similarity coefficient for quantitative data,  $S_G$ , was used (Gower 1971). A value of  $S_G$  was computed for each of the  $\binom{n}{2}$  combinations among the  $n$  walrus classes in each of sets A and B (Table 1), and the resulting measures ordered into the appropriate matrices. For R-technique,  $S_G$  for dichotomous data seemed less desirable because it does not take account of relative frequencies of occurrence of the behavior groupings in the sample as a whole. A coefficient ( $V$ ) useful for data in the form of  $2 \times 2$  contingency tables was chosen (Pielou 1969).  $V$  values were computed for contingency tables, each table summarizing the frequencies of cooccurrence and non-cooccurrence over all behavioral profiles for a pair of behavior groupings. There were 13 behavior groupings used (see text), hence 78  $V$  values were obtained.

MINISSA rank-orders the  $r$  proximity coefficients of the off-diagonal symmetric proximity matrix  $P$  (the user can rank-order the coefficients himself without affecting the final configuration), and positions the member subjects of the data set in a configuration in Euclidean space such that the distances between points (corresponding to subjects) correspond as closely as possible to the initial rank-ordering. This objective is achieved subject to the constraint that whenever  $p_{ij} > p_{kl}$  (for similarity data, such as those used here), the elements  $\delta_{ij} = f(p_{ij})$  of the  $r$ -element vector  $\Delta$  fall in the relationship  $\delta_{ij} < \delta_{kl}$  or  $\delta_{ij} \leq \delta_{kl}$  (Lingoes and Roskam 1971, 1973). That is,  $\Delta$  maps into  $P$  monotonically. An intuitively pleasing measure of how well an Euclidean configuration 'resembles'  $P$  is one that estimates how deviant the distances  $d_{ij}$  (of the  $r$ -element vector  $D$ ) between points are relative to the numbers  $\delta_{ij}$ . The latter form a set of numbers "chosen to be as close to their respective  $d_{ij}$  as possible, subject to being monotone with the  $p_{ij}$ " (Green and Carmone 1970, p. 38), and a widely used measure utilizes them to estimate stress:

$$S = \sqrt{\frac{\sum_{i < j} (d_{ij} - \delta_{ij})^2}{\sum_{i < j} d_{ij}^2}}$$

(Kruskal 1964a, 1964b).

In MINISSA, the vector  $\Delta$  acts both to weight iterations in moving toward the final configuration and to assess the 'goodness-of-fit' of a set of spatial coordinates to  $P$  (Lingoes and Roskam 1971, 1973). Lingoes and Roskam (1971, 1973) and Roskam and Lingoes (1970) suggest a measure of stress alternative to Kruskal's  $S$  and with theoretical and practical properties superior to it. This coefficient of alienation,

$$K = \sqrt{1 - \mu^2},$$

where

$$\mu = \frac{\sum_{ij} d_{ij} \cdot d_{ij}^*}{\sum_{ij} d_{ij}^2}$$

and the  $d_{ij}^*$ 's are the 'rank-images' of L. Guttman (1968; a more readable treatment is provided by Lingoes and Roskam 1971, 1973). In general,  $K > S$ , but inasmuch as there is no mathematical relationship between the measures, this does not imply that the 'goodness-of-fit' is any better or worse.  $K$  is adapted to the semistrong/strong monotonicity principle and favors untied distances for untied data;  $S$  is adapted to the semiweak/weak monotonicity principle, and favors tying of untied data (cf. Lingoes and Roskam 1971, 1973). MINISSA provides for minimization of loss functions underlying both  $S$  and  $K$ .

Theoretically, no more than  $n - 2$  dimensions are necessary to fulfill conditions of strict monotonicity between the off-diagonal elements  $\{p_{ij}\}$  of the real symmetric matrix  $P$  of order  $n$ , and the set of interpoint distances  $\{d_{ij}\}$  (L. Guttman 1968; cf. Lingoes 1971). Practically, this means that at any given dimensionality, and all other things being equal, a large set of subjects exhibits higher stress than does a smaller set, and that stress for both decreases as dimensionality increases. The rate of decrease of  $S$  and  $K$  tends to be highest over the first few dimensions. "Ideally, if stress is plotted against number of dimensions, the number of dimensions chosen will correspond to an 'elbow' where this curve first approaches zero and then declines only very slowly thereafter" (Shepard 1972a, p. 9). Working with low dimensionality also facilitates graphical representation and comprehension, and renders interpretations of axes easier (Shepard 1972a).

## NOTE ADDED IN PROOF

Over-reliance upon measures of stress and the 'elbow' criterion (mentioned above) can result in erroneous interpretations based on spurious configurations (Isaac and Poor 1974; Shepard 1974; Wagenaar and Padmos 1971; Young 1970). Inference of underlying structure may be particularly hazardous for only a few points (six or seven) in two or more dimensions (Klahr 1969). However, if appropriate dimensionality is underestimated, recovery of metric information deteriorates sharply (Spence and Graef 1974). Metric recovery is maximal in appropriate dimensionality, and may decline even when dimensionality is overestimated (Spence, cited by Spence and Graef 1974, p. 337).

Interpretations I made based on Figs. 18, 22–25 were unidimensional in nature, even though I depicted two to three dimensions in the figures. Interpretations I based on Figs. 19 and 20 were ancillary to and in agreement with those made in lower dimensionality (Fig. 18), and supported a one-dimensional interpretation (Fig. 21). I have since applied to these data techniques for estimating appropriate dimensionality (Spence and Graef 1973, 1974; Wagenaar and Padmos 1971; cf. Isaac and Poor 1974), and computed it to be one in all cases. My interpretations based on Q-technique remain unaltered. Interpretation in one dimension in R-technique was more difficult, but certainly supported the basic dichotomy between sets I and II (Fig. 18) with components 4, 15, and 16 lying between them. When 1973 data (which were more carefully and consistently collected than were 1972 data) for behavior components were considered alone, appropriate dimensionality of two was indicated. The configuration achieved was very similar to that shown in the plane of the page, Fig. 18. A variety of approaches to the interpretation of configurations in low dimensionality (e.g. Shepard 1974) may prove more enlightening than applying only a few techniques through various dimensionalities.

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