

Walrus ethology. II. Herd structure and activity budgets of summering males

EDWARD H. MILLER¹

College of Biological Sciences, University of Alaska, Fairbanks, Alaska 99701

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Male walruses, *Odobenus rosmarus* (L.), summering (outside the breeding season) at an Alaskan hauling ground, use all available kinds of beach habitat: cobble and boulder beaches, rock benches, and large boulders. Formation and dissolution of large herds on land can occur rapidly. Walruses are very gregarious and positively thigmotactic. In cool weather about 98% of walruses on land lie in passive body contact with other walruses. Dominant walruses (large, with long unbroken tusks) are most successful in entering herds on land, and in keeping positions in them. This results in overrepresentation of subordinates in the periphery of herds. Agonistic interactions occupy 5-10% of the time of walruses in large herds on land, and cause local disturbances that lead to agonistic involvement of up to 20 animals. Fewer kinds of social activity occur on land than in water. On land and in shallow water, small walruses are generally more active than large ones. Extensive body contact while they are hauled out is chiefly an adaptation for heat conservation and may also facilitate molting. The extreme gregariousness of walruses may have evolved because individuals joining large herds have a greater probability of achieving extensive body contact than have those joining small herds.

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Les morses mâles, *Odobenus rosmarus* (L.) qui passent l'été (en dehors de la saison de reproduction) dans une roukerie, en Alaska, utilisent tous les habitats disponibles de la plage: cailloux et rochers, bancs de roche, gros rochers. La formation et la dissolution de grands troupeaux, à terre, peuvent se faire rapidement. Les morses sont très grégaires et à thigmotaxie positive. A température fraîche, environ 98% des morses restent étendus passivement par terre, leur corps en contact avec celui d'autres morses. Les morses dominants (gros et portant des défenses longues et intactes) sont ceux qui ont le plus de facilité à s'introduire au sein d'un troupeau et à y garder leur position. Il s'ensuit que les morses dominés sont sur-représentés en périphérie des troupeaux. Dans les grands troupeaux, les morses passent 5 à 10% de leur temps en interactions agonistiques et produisent des bagarres locales impliquant l'activité agonistique de plusieurs animaux (jusqu'à 20). L'activité sociale des morses est moins variée sur terre que dans l'eau. Sur terre et en eau peu profonde, les petits morses sont généralement plus actifs que les gros. Les contacts corporels prolongés et fréquents à la sortie de l'eau sont une adaptation propre à conserver la chaleur et à favoriser la mue. Le gréganisme exceptionnel des morses s'est probablement développé parce que, chez les individus qui se mêlent aux grands troupeaux, les chances de contacts corporels intenses sont supérieures à celles des individus appartenant à de petits troupeaux.

[Traduit par le journal]

Introduction

Walruses, *Odobenus rosmarus* (L.), are virtually inaccessible to man during critical periods (mating, parturition) of their annual cycle. This has hindered understanding of the social biology of the species. Pacific walruses mate in late winter (February or March) in the Bering Sea pack ice south of St. Lawrence Island, and females give birth in the spring (April-June) of the

next calendar year, as they move north with the receding ice. In the summer and fall, however, and in the absence of ice, walrus herds form on traditional terrestrial hauling grounds, and then offer an opportunity for prolonged and detailed study. In 1972 I initiated a study of walrus behavior at a major Alaskan hauling ground that is used during the ice-free part of the year by about 3000 male walruses. The purposes of the study were to assess the social role of tusks, to investigate social organization of herds on land, and to evaluate the social and thermoregulatory

¹Present address: Department of Biology, Dalhousie University, Halifax, Nova Scotia.

significance of body contact on land. In the first paper of this series (Miller 1975a) I presented evidence pointing to important rank-influencing effects of body size and of tusk length and intactness. In the third paper I will discuss thermoregulatory behavior. Here, I present data on relationships of social dominance (as manifested in tusk intactness and body size) to dispersion in herds on land, on body contact, and on general activities of summering males.

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 (58°36' N, 159°58' W; the coordinates were incorrectly specified in Miller 1975a, p. 591), to observe male walrus summering there. We approached herds from downwind to within 10–50 m, from where we made observations.

This study was chiefly observational in scope, so when herds formed on beaches favorable for observation we spent much time there. This precluded daily censuses of all beaches. However, we daily censused herds under observation, and examined other beaches when possible. In 1972 I temporarily marked eight walrus with hog-marking dye (Ketchum Mfg. Co., Ottawa, Ontario).

Dispersion patterns of walrus on land were much affected by beach topography, tide, and thermal conditions (Figs. 1–3). I sampled relationships of the locations of walrus in herds to various measures only for large herds on fairly smooth beaches. I recognized locations of walrus as follows. A walrus was defined as a group member if he was in body contact with one or more other walrus. Walrus in the large, (usually) densely packed *main herds* were classed as being in the *seaward periphery*, the *center*, or the *inland periphery*. In the simplest herd configurations the depth of each periphery was one rank. *Small groups* of walrus, containing up to 20 members, often formed peripheral to main herds, especially in warm weather (Fig. 1). Walrus peripheral to main herds and small groups, and not in body contact with any other walrus, were classed as *lone*; this applied even to walrus very close to their fellows. The classification of locations was not exhaustive. In addition to their location, walrus were classified for body size and tusk fractures (body size and length of unbroken tusks are positively correlated; I classified by body size because it was easier and less prone to error).

In studying the extent and nature of body contact, I (a) classified walrus for location, body size, and fraction of body surface in contact with other walrus (0, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{1}{4}$, $\frac{1}{5}$), and (b) observed jostling of recumbent, large, dry, central walrus in $\frac{1}{4}$ or $\frac{1}{3}$ body contact (focal walrus). For the latter, I used a small battery-operated event recorder that used paper tape with a running speed of 25 mm per 10 s. I recorded jostling when a focal walrus was even slightly jostled. Walrus sometimes started even when pipits (*Anthus spinoletta*) landed upon them to feed on flies, so I assumed that they could sense jostling visible to me. Records were as long as possible up to 5 min. I terminated a record if the focal walrus engaged in vigorous activity

(any activity involving major postural changes, such as in locomotion or agonistic interaction).

I classified walrus in herds on smooth beaches for location and for orientation of the long body axis to beach slope: upslope ($\pm 45^\circ$), downslope ($\pm 45^\circ$), or cross-slope ($\pm 45^\circ$).

For large and small walrus newly arrived at the seaward periphery of herds I noted number of resident walrus that each attempted to displace, number of resident walrus each displaced, and number of ranks moved into the herd.

I assessed contagion of agonistic interactions (described in Miller 1975a) occurring centrally in densely packed herds by counting the number of dyadic agonistic interactions and the number of individual walrus eventually involved, resulting from initial dyadic interactions. The lowest value obtainable was one interaction per two walrus.

I watched, for 5 min each, walrus in different locations in herds, and noted the number of agonistic interactions in which each took part.

For recumbent, large, dry, central walrus in $\frac{1}{4}$ or $\frac{1}{3}$ body contact, I assessed 'sleep' duration and incidence; sleep was defined as recumbent with eyes closed. I used the event recorder described above, and terminated prematurely (before 5 min) the record of any focal walrus that did more than lift its head.

I scan-sampled (Altmann 1974) activities of walrus on land and in 'shallow' and 'deep' water. I defined shallow water as the region just seaward of large herds, extending from the water's edge to a depth in which walrus were just able to swim and dive (i.e. about 2 m). I defined deep water as the region beyond about 30–40 m from the beach. I also watched, for as long as possible up to 5 min, walrus in shallow water, and recorded the kinds and frequencies of their overt social interactions and tactual encounters.

For the body size classification used here, see Miller (1975a). Statistical symbols and methods of testing follow Sokal and Rohlf (1969). I consulted statistical tables of Rohlf and Sokal (1969). To test significance of differences between percentages, I computed t_s values for unequal sample sizes (Sokal and Rohlf 1969, p. 607 and following pages); for such tests P estimates only are listed. I accept a significance level of 0.10.

Results

Habitat and Population Trends

Walrus hauled out on all available kinds of beach habitat: cobble and boulder beaches, rock benches, and exposed flat boulders (Figs. 1–3). The largest and most densely packed herds occurred on smooth beaches (compare Figs. 1 and 2) and in cool weather (compare Fig. 1 with Fig. 1 in Miller 1975a). The available area on gently sloping cobble beaches varied much more with the state of the tide than did that on steeper boulder beaches, but no beaches afforded areas great enough for large herds to form when high winds and high water coincided. Walrus seemed to prefer beaches sheltered from strong

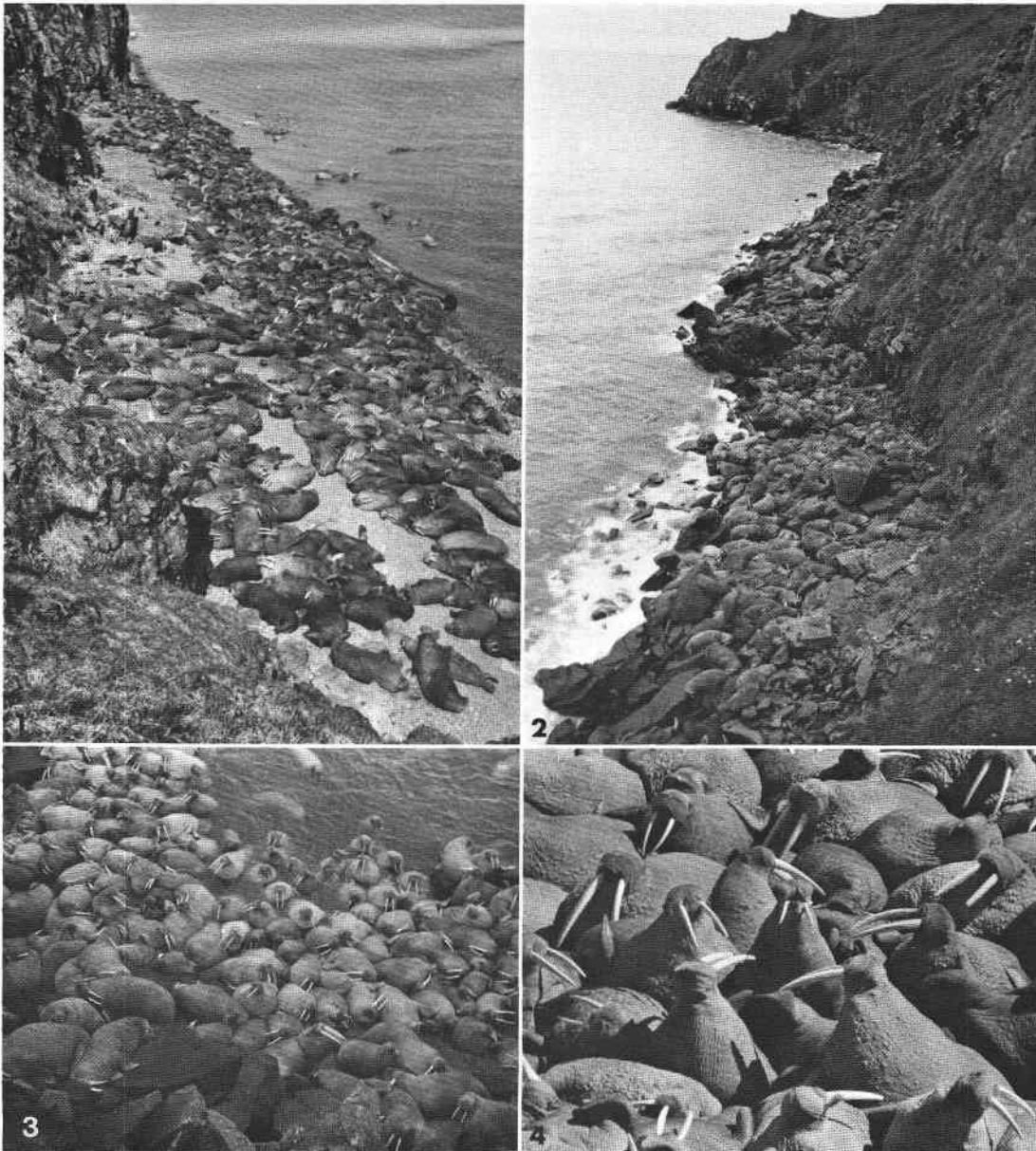


FIG. 1. Part of an extensive herd of male walrus in warm weather (compare Fig. 1 of Miller 1975*a*). FIG. 2. Male walrus scattered along a rugged boulder beach, in cool weather. FIG. 3. Part of a large herd of male walrus during early stages of haulout on rugged boulder beach, and coincident with high water. FIG. 4. Contagion of an agonistic interaction. Five walrus are directly involved (central submissive walrus and four larger walrus surrounding him). The threat by the broken-tusked walrus (right foreground) also resulted from the initial interaction, through jostling.

winds in any case (cf. Tomilin and Kibal'chich 1975). Beaches favored by walrus differed between years. In 1972, herds occupied one beach (Fig. 1) on 26 of 33 census days there, but in 1973, herds of comparable size (700–1000) were

there on only 2 of 24 census days for that beach. In 1972 no herds were seen along the south-eastern side of the island (e.g. Fig. 2) in 10 census days there, but in 1973, herds of 85 walrus or more were recorded there on 22 of 31 census days.

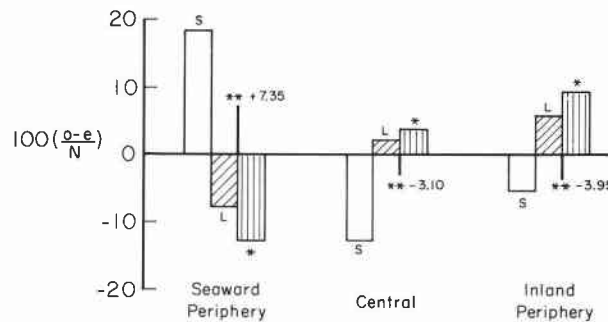


FIG. 5. Deviations (in %) of expected (e) from observed (o) frequencies of walrus of different body sizes and tusk characteristics, in different locations in herds. S, small ($N = 777$); L, large ($N = 2750$); *large with slightly broken tusks ($N = 251$); **large with severely broken tusks ($N = 57$). For the latter class, the magnitude of each deviation is indicated.

Herds formed rapidly and often declined precipitously. At 0615 hours, 15 July 1973, no walrus were present on a beach that later that day (1900 hours) held more than 1000 walrus. None remained by 0600 hours of the next day, though the weather had changed little. The longest period that any beach was continuously occupied was 14 days (29 June to 12 July 1972). The period probably would have been longer, but visitors on June 28 caused a disturbance; 100 or more walrus had been present since 20 June. Similarly, in 1973 more than 400 walrus occupied one beach from at least 26 June to 5 July, but on 5 July visitors landed there and caused the animals to abandon it.

Because walrus gather in such large dense herds it is difficult to obtain complete records of individual attendance. The longest definitely unbroken period spent ashore by any dye-marked walrus was about 36 h, a figure also given by Freuchen (1935, p. 248). This estimate is surely too small. One other walrus was identified on 4 consecutive days, another on 3 consecutive days, and yet another was seen for 2, disappeared for 2, reappeared for 3, disappeared for 2, and reappeared again for 1 day. Four others were each seen on 2 consecutive days. However, between days all of these walrus changed location on the beach, so I could not be certain that they had remained ashore continuously between sightings.

Description of Herd Structure

Relationship of In-herd Location to Tusk Breakage and Body Size

In densely packed herds (e.g. Fig. 1 in Miller 1975a), walrus of various body sizes and tusk characteristics were distributed non-randomly

(Fig. 5). Small walrus were more numerous than predicted in the seaward periphery and at a deficit elsewhere, while large walrus with unbroken or slightly broken tusks showed the opposite trend. Each of these three classes showed significant deviations of observed from expected frequencies (χ^2 estimates, $P < 0.001$ in each case). Large walrus with severely broken tusks exhibited insignificant departures from a random distribution. However, such walrus were at deficits centrally and at the inland periphery, and in excess at the seaward periphery, relative to other large walrus; trends in their distribution paralleled those for small walrus.

The presence of large boulders within herds apparently afforded some protection to socially subordinate walrus. Small walrus represented 20.3% of 241 animals adjacent to large boulders within herds, compared with 9.8% of 164 walrus on nearby smooth beach ($P < 0.01$).

Relationship of In-herd Location to Body Contact and Resting Orientation

The non-random distribution of walrus in herds resulted in small individuals resting in less body contact with other walrus than did larger ones (Fig. 6). In addition, the predominantly seaward peripheral distribution of small walrus resulted in their resting in contact with fewer individuals than central walrus did (Fig. 7). Overall, in cool weather (black bulb temperature below 10°C), the mean number of individuals contacted by walrus resting in large herds was 4.6 (computed from data in Fig. 7), and more than 98% of walrus resting on land contacted at least one other walrus.

Animals in herds commonly rested tusks and faces against other walrus. Thus, 58.2% of 335

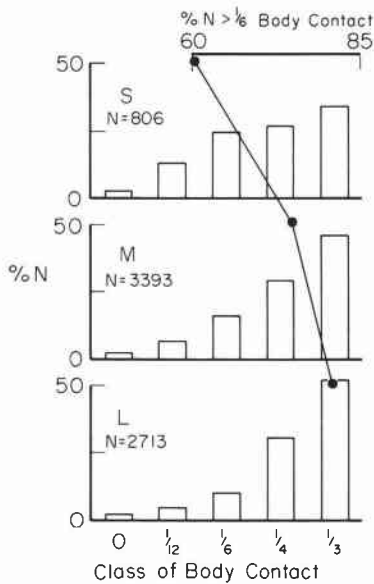


FIG. 6. Relationship of body size to degree of body contact achieved in cool weather and in large herds by small (S), medium (M), and large (L) walrus.

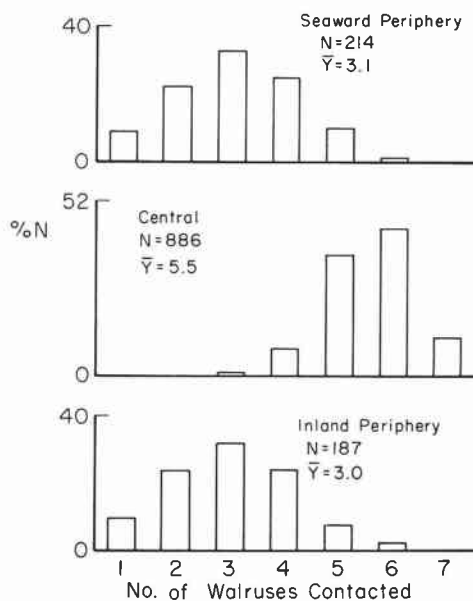


FIG. 7. Relationship of location to number of walrus contacted in cool weather.

recumbent walrus rested tusks and 68.3% of 463 rested mystacial pads against a neighbor.

The location of walrus in herds affected not only the extent of body contact, but also modified the manner in which walrus lay relative to the slope of the beach. Walrus located central-

ly typically lay parallel to one another and directed upslope, whereas peripheral walrus were less constrained by neighbors and showed greater variation (Table 1; Fig. 1).

Dynamics of Herd Structure

Relationship of Body Size to Success in Entering Herds

Dominant walrus preferentially threatened and often displaced subordinate ones (Miller 1975a), and were generally more assertive than were subordinates upon joining a herd. Of 56 newly arrived large walrus that attempted to enter the seaward periphery, 5.4% were forced back to the sea by threats; of 66 small walrus trying to enter, 34.8% were forced back ($P < 0.001$). Forty-five (80.4%) large walrus attempted to displace resident walrus, compared with 14 (21.2%) small walrus ($P < 0.001$). Whereas 71.6% of 74 attempted displacements of residents by large walrus were partially or entirely successful, only 26.7% of 15 by small animals were so ($P < 0.001$) (Fig. 8). Large walrus that attempted to displace resident walrus showed a mean frequency of attempted displacements of 1.69, compared with 1.07 for small walrus (for unequal variances, $t_s' = 3.48$, $P < 0.01$).

For large walrus attempting to enter herds there was a significant positive correlation between the number of residents they attempted to displace and the number of ranks through which they moved into the herd ($r = 0.40$, $P < 0.10$). Comparable data for small walrus revealed an insignificant negative correlation. Overall, the number of ranks through which small walrus moved differed insignificantly from that for large walrus (by t estimate) (Fig. 8). These trends reflect the tendency of small walrus to sometimes move quickly inland over the top of residents, and without attempting to displace any. Large walrus, trying to enter herds in such a manner, responded to threats in kind more often than did small animals, and when residents moved aside or relinquished space the large walrus often settled there. Small walrus readily exhibited submissive behavior, which often evoked threats (Miller 1975a), and consequently were often obliged to keep moving once they were within the herd.

Relationship of Location and Body Size to Frequency of Agonistic Interaction; Contagion

Most walrus joined herds from the seaward side and tried to move inland. This resulted in

TABLE 1. Orientation of the long body axis to slope of beach, in relation to location in the herd (for large walrus)*

	Seaward periphery	Central	Inland periphery	Inland-small groups and lone
No. of walrus (<i>N</i>)	2002	3373	1570	470
Upslope	80.0	93.7	88.3	68.6
Cross-slope	11.0	4.7	8.4	23.8
Downslope	9.0	1.7	3.3	7.6

*%*N* in each location.

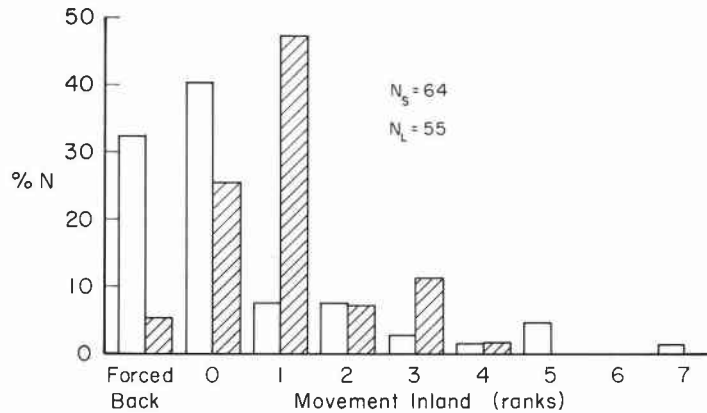


FIG. 8. Relationship of body size (small (S), open bars) and large (L, hatched bars) to movement inland after attempt to join herds from the seaward side. 'Forced back' indicates that the focal walrus neither penetrated nor lay against the herd, but instead moved away (seaward usually) upon being threatened; '0' indicates that the focal walrus lay against the seaward rank; '1' indicates that the focal walrus penetrated and lay in the first rank; and so on.

high levels of agonistic activity at the seaward periphery and lower levels inland. Walrus that engaged in agonistic activity in a 5-min observation period made up 41.5% of 224 walrus in the seaward periphery, 35.0% of 214 walrus in the center, and 21.9% of 219 walrus in the inland periphery. All but the first and second of these percentages differ significantly from one another. This same trend is seen in the mean frequency of agonistic interactions per focal walrus (0.97, 0.71, and 0.34, respectively) and per interacting walrus (2.3, 2.0, and 1.5, respectively). Location and body size of walrus exerted a direct influence on frequency of interaction, but did not operate independently (Table 2). The interdependence of the two factors occurred because the smallest walrus had highest rates of agonistic interaction centrally, rather than in the seaward periphery ($N = 69$ observation periods) (Fig. 9). This result seems to agree with be-

havioral differences between large and small walrus upon joining the seaward periphery (preceding section); however, the small sample ($N = 22$ observation periods) of medium-large walrus shows a similar trend. More data are required before the interaction term in Table 2 can be accepted as having major importance. In summary, frequencies of agonistic interaction were highest in the seaward periphery and decreased to a minimum in the inland periphery, and large walrus interacted more frequently than did small ones (Fig. 9) (see also section below on activity budgets).

The number of walrus that became involved in agonistic interactions as a consequence of initial dyadic interactions, ranged from 2 to 20 (Fig. 4). The maximal number of threats recorded was 62. The number of threats per walrus regressed significantly and positively on the number of walrus involved (1972 and 1973

TABLE 2. Analysis of variance table, computed from 1973 data on frequency of agonistic interaction per 5-min observation period

Source of variation	SS	df	MS	F	P
Mean	302.8	1	302.8	108.2	
Body size (BS) ^a	42.0	5	8.4	3.0	<0.025
Location (L)	59.7	2	29.9	10.7	<0.001
BS × L	51.2	10	5.1	1.8	<0.10
Error	601.4	215	2.8		

^aBody size in six classes, from very small to large (see Miller 1975a).

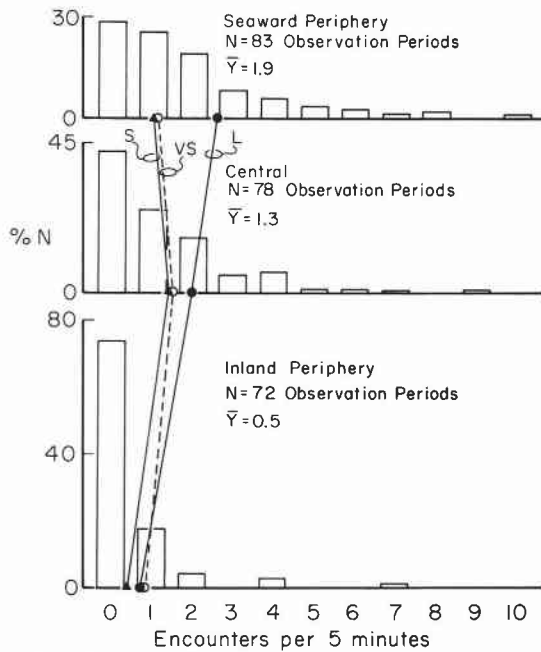


FIG. 9. Relationship of location and body size to frequency of agonistic interaction (VS, very small; S, small; L, large).

data are treated separately because of different sampling techniques between years: $t_s = 6.8$ and 10.0 , respectively, for each of which $P < 0.001$.

Activities of Walrus in Herds

Activities At and Near the Seaward Periphery, and Upon Joining a Herd

Walrus in the seaward periphery and in the shallow water just beyond tended to be most active. Agonistic communication was common but formed a smaller fraction of overt social encounters there than in other locations. For example, of 87 walrus arriving at the seaward periphery, 31.0% investigated (tactually or olfactorily, or both) other walrus, 3.4% in-

vestigated rocks, and the rest (65.5%) engaged in other activities, including agonistic interactions. Nostrils were open and mystacial vibrissae erect in most investigations (Table 3; cf. Miller 1975b).

Walrus around the seaward periphery of herds commonly engaged in mutual greetings. Small walrus showed the greatest propensity for this: 32.7% of walrus noted in mutual greetings were of small size. This figure is substantially greater than the incidence of small walrus in the seaward periphery ($P < 0.001$). Also, walrus tended to engage in mutual greetings most often with walrus of similar size (χ^2 estimate, $P < 0.005$). Assortment by body size in 33 one-way investigations was also non-random (χ^2 estimate, $P < 0.05$) because of much investigating by small walrus of small (observed = 8, expected = 5.2) and of large (observed = 10, expected = 7.9) animals.

Sleep Soundness and Jostling

Walrus resting on land appear to spend much time asleep (Figs. 1-3). Indeed, central walrus were recumbent for about 88% of the time that they were either recumbent or with head raised. Nevertheless, recumbent walrus had their eyes open surprisingly often: about 23% of the time. Overall, central walrus were recumbent with eyes closed for about 68% of the time. The mean durations ($\pm s_y$) of periods with eyes closed and open were 13.8 ± 1.26 s ($N = 348$) and 4.7 ± 0.35 s ($N = 397$), respectively. Walrus lying in the seaward periphery had their eyes open more of the time than did walrus elsewhere, and walrus lying alone inland of large herds had eyes closed more of the time than did walrus anywhere in the main herd (Table 4).

Large central walrus were jostled by others 41.2% of the time. The mean durations ($\pm s_y$) of

TABLE 3. Characteristics of one-way olfactory-tactual investigations by walrus entering the seaward periphery of herds^a

Characteristic	Nostrils open ^b	Nostrils closed ^b	Totals
No mystacial pad contact	5 (1)	—	5
Mystacial pad contact			
Vibrissae erect	23 (3)	2 (1) ^c	25
Vibrissae not erect	10 (1)	5 (1)	15

^aFor full description, see Miller (1975b).

^bTotal number of investigations of rocks shown parenthetically.

^cFour additional investigations that occurred underwater are not included.

TABLE 4. 'Sleep soundness' on land, in relation to location in the herd^a

	Seaward periphery	Central	Inland periphery	Inland	
				Small groups	Lone
Total sample (<i>N</i>)	348	326	235	80	199
No. with eyes closed (<i>n</i>)	192	234	168	60	159
(<i>n/N</i>) × 100	55.2	71.8	71.5	75.0	79.9

^aScan-sampled data. Percentage figures underlain by the opposite ends of any horizontal line differ significantly ($P < 0.10$).

periods with and without jostling were 27.4 ± 2.53 s ($N = 300$) and 40.6 ± 2.87 s ($N = 292$), respectively.

Activity Budgets

Lone walrus spent more time than did central walrus in grooming and locomoting (4.9% vs. 3.5%, $P < 0.10$; Table 5). Of 678 grooming acts, 77.3% were performed by walrus in small groups and in lone and peripheral locations, and the rest was performed by the more numerous central walrus (χ^2 estimate, $P < 0.001$, even assuming equal numbers of walrus in the two locations). Lone walrus spent less time involved in agonistic interactions than did central ones, principally as a result of the high frequency of short-range threats and virtual absence of long-range ones (Table 5; Miller 1975a).

Walrus in shallow water engaged in overt social behavior (including contact-seeking behavior such as rubbing against another walrus, lolling with other walrus, investigations, mutual greetings, and agonistic interactions) 11.3% of the time (vs. 8.9% in herds on land, $P < 0.01$).

I sampled no mutual greetings or investigations on land, but observed them outside of sampling periods. Thus the figure of 3.1% for such activities in shallow water, though low, indicates their more frequent occurrence there than on land. Overall, agonistic interactions figured less importantly in shallow water (5.1%) than in terrestrial (8.9%) activity budgets, and they made up only 57.5% of sampled overt social activities in shallow water (vs. 100% in herds on land, $P < 0.001$). Non-social activities constituted 36.6% of the activity budget in shallow water (vs. 3.5% in herds on land, $P < 0.001$). Of these, locomotion by itself accounted for 17.4% of the total activity budget (vs. 3.0% in herds on land, $P < 0.001$), and grooming accounted for 13.4% (vs. 0.5% in herds on land, $P < 0.001$). Walrus in shallow water also groomed more vigorously than did those on land. Small walrus in shallow water were more active than were large ones, and spent less time lying and standing ($P < 0.001$), more time locomoting ($P < 0.10$), and more time floating with pharyngeal pouch(es) inflated and engaging in associated activities ($P < 0.10$) (cf.

TABLE 5. Comparison of activity budgets of walrus on land within large herds, and alone in inland locations^a

Body size	N	Individual activities				Agonistic interactions
		Recumbent non-active	Upright non-active ^b	Groom	Locomotion	
Within large herds						
Small	570	85.4	10.0	1.1	3.5	5.3
Medium	1126	87.4	9.5	0.4	2.8	9.2
Large	1215	89.2	7.4	0.5	3.0	10.2
Means		87.8	8.7	0.5	3.0	8.9
ΣN	2911					
Inland alone						
Small	61	83.6	6.6	3.2	6.6	7.6
Medium	80	82.5	13.8	1.2	2.5	1.2
Large	67	94.0	4.5	0.0	1.5	5.6
Means		86.5	8.7	1.5	3.4	4.6
ΣN	208					

^aData from 1973 only. Certain sampling errors appeared in the 1972 data, and they are referred to in the text only in general terms. Figures for individual activities are percentages of all non-social activities; those for agonistic interactions are of total activities.

^bNon-recumbent rest postures were generally unsteretyped and blended into recumbent postures. However, some individuals assumed a posture strikingly similar to the well-known 'nose-up' rest posture of otariids.

Miller 1975a). Body size bore no apparent relationship to the percentage of time spent in agonistic activities in shallow water. However, small walrus spent more time in overt social activities than did large ones (16.2% vs. 10.6%, $P < 0.05$). Overall, walrus engaged in more kinds of activities in shallow water than on land.

For focal walrus in shallow water I obtained the following data (given as frequency per walrus-hour): agonistic interactions = 10.8 ($N = 116$ walrus), fortuitous body contacts (e.g. touching or being touched in passing) = 14.4 ($N = 116$), sought-out body contacts = 5.4 ($N = 114$), and total times contacted by other walrus = 21.6 ($N = 114$). More small than large walrus actively sought body contact (47.6% of 42 vs. 24.1% of 54, $P < 0.02$).

In the study of walrus herds in deep water I probably oversampled stationary groups because they predominated off beaches occupied by herds. Walrus in stationary groups often slept with one or both pharyngeal pouches inflated. Lines of two or more walrus often formed, with the walrus aligned directly one behind another, all facing one direction and floating vertically, and with each member clasping with foreflippers the one ahead of him. All forms of overt social communication occurred most commonly in small groups, and low activity levels predominated in larger groups.

Levels of social activity in groups of size 2-3 were significantly higher than in all other groupings (viz. 4-5, 6-7, 8-10, and 10+; $P < 0.02$ in each case). Also, groups of sizes 4-5 and 6-7 showed higher levels than did groups of 10+ ($P < 0.05$ for each comparison).

Discussion

Gregariousness and Body Contact

The adaptive significance of gregarious behavior in pinnipeds has been ably discussed by Bartholomew (1970) and McLaren (1967). Much of seal sociality is explicable through reproductive rates, spatial predictability of the environment, and the form and intensity of reproductive competition among males. Ghiselin (1974) overemphasizes the importance of restricted breeding space in directly promoting gregariousness of pinnipeds (but see LeBoeuf and Petrino-vich 1974). Certainly his arguments are inapplicable to walrus, which breed in association with ice. Gregariousness among walrus probably facilitates locating patchily distributed resources such as food and suitable ice conditions (see Jarman 1974; Krebs 1974), the locations of which vary seasonally and between years (Fay 1974). In addition, the structure, distribution, and movements of ice influence herd movements and the locations where mating occurs. By remaining in or near groups, walrus, therefore, also have the maximal opportunity to

compete for mates. Gregariousness is prerequisite to body contact, so it should develop insofar as body contact is selectively advantageous. Extensive body contact during winter months probably affords significant energy savings (Fay and Ray 1968; Ray and Fay 1968) and should be maximal for walrus in central locations in herds. As herd size increases, central locations account for an increasing fraction of total locations, so that walrus joining large herds have a high probability of achieving extensive body contact, i.e. centrally. This necessary result may by itself largely account for the extreme gregariousness of walrus.

Thigmotactic behavior is variously developed in the Pinnipedia, and is not consistently correlated with habitat, geography, body size, development of the pelage, or gregariousness. Within the Otarioidea, however, large species generally have the sparsest pelage and are the most positively thigmotactic (I will deal with this subject at greater length in paper III of this series). Large size and loss of underfur in pinnipeds are probably derived characters (Ling 1974; Mitchell 1966; Reppenning *et al.* 1971), so thigmotactic behavior may have developed, in parallel with increased size, to compensate for the decreased importance of pelage in thermoregulation. Walrus are more thigmotactic than sea lions, presumably because of their sparser pelage and much colder habitat; energetic advantages to social thermoregulation among walrus must be especially great during the winter and for young calves. Extensive body contact among large summering walrus may simply be 'carried over' from the winter, when it is selectively most advantageous (Fay and Ray 1968, p. 10). Because of the cold temperature and high thermal conductivity of the aquatic environment, pinnipeds cannot there achieve the high peripheral temperatures required for molting (Feltz and Fay 1967). It is probably thermally necessary for walrus and other pinnipeds to rest in air in order to molt (Feltz and Fay 1967; Laws 1956; McLaren 1958), and molt may also be thermally facilitated by extensive body contact among summering walrus.

Because of their extreme gregariousness and positive thigmotaxis, walrus inhabit a social environment in which purposeful and incidental tactual interaction occur frequently, at times almost continuously. Nevertheless, no ritualization or marked stereotypy of mechanical signal

patterns occurs. For example, tusk display, which is a relatively stereotyped form of in-air communication, often involves strikes with the tusks, but these vary in vigor, frequency, and location (Miller 1975a). In addition, walrus on land only infrequently engage in certain forms of tactual communication common to many highly social species of mammals, and which promote distance reduction or proximity maintenance between individuals (Eisenberg 1966; Marler 1968). Thus walrus on land exhibit no allogrooming, and very few nasonasal greetings. The reasons for this seem clear. First, active walrus on land maintain a very small individual distance, possibly because of their clumsiness and poor locomotory facilities there, and because of their reputedly poor vision. Second, walrus joining herds on land typically approach other walrus from the rear, a direction in which individual distance is less than it is in front. Finally, walrus at rest in herds on land maintain no individual distance at all among themselves (though they commonly threaten approaching animals, e.g. see Fig. 15 in Miller 1975a). In contrast, walrus in the water seaward of herds are more mobile and easily maintain a greater individual distance, and it is there that nasonasal greetings are most common. If formalization of mechanical signaling occurs at all, it is probably in the water, where the most complex walrus communications occur (Fay 1960; Miller 1975a; Ray and Watkins 1975; Schevill *et al.* 1966).

Structure of Male Herds

Dominance rank affects the spatial ordering of individuals within groups in various vertebrate species, and there is a diversity of adaptive explanations for this (Murton *et al.* 1972; Murton *et al.* 1971; Nursall 1973; Pulliam 1973). Socially subordinate walrus predominate in the seaward ranks of herds on land because dominants are assertive and aggressive, dominants preferentially threaten subordinates, dominants have greater success than have subordinates at displacing residents, and resident dominants are displaced less often than are resident subordinates (for further details, see Miller 1975a). The observed dispersion, therefore, seems to be a straightforward result of numerous agonistic interactions with consequent 'sorting out.' Loughrey (1959, pp. 35, 48) notes that in mixed herds of Atlantic walrus females predominate in seaward ranks. This may be for the

same reason, though no detailed studies of mixed herds have been made.

Elsewhere in the range of Pacific walruses, age and sex classes apparently do not mingle and form herds of random composition. For example, "older animals...tend to occur in much smaller herds which are less concentrated" and frequently are solitary (Burns 1969, p. 11; cf. Belopolsky 1939; Chapskii 1936; Pedersen 1962). Also, full-term and parturient females gather in large nursery herds in the spring (Burns 1965), and in general "females...seldom crowd closely together and do not annoy and agitate each other in the manner of bulls" (Brooks 1954, p. 64). Herds of summering males on land are structured simply and seem to conform to Wilson's (1975, p. 8) definition of aggregation. Current knowledge is too scanty to permit generalization to other parts of the range, population, and annual cycle.

Activity Budgets

The amount of time devoted by animals to various activities is probably finely attuned to local ecological and social circumstances (Brown 1975; King 1974; Wilson 1975). Walruses breed in late winter far from land and, like other pinnipeds, feed at sea. Thus summering males at Round Island need only partition their time among non-reproductive social activities and minor individual activities, and need not accommodate major energy-demanding activities (unlike otariids: cf. Miller 1975c; Stirling 1971), nor must they devote much time to vigilance because of danger from predators, unlike ringed seals, *Phoca hispida* (Stirling 1974; cf. Dimond and Lazarus 1974). Even sleep requirements of walruses on land may be easily met, since most walruses join herds on land in preference to lying alone, yet lone animals are not physically jostled, engage in fewer agonistic interactions, and 'sleep' more. These advantages of lying alone may simply be surpassed by thermal benefits achieved by lying in groups.

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