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
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 walruses 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 walruses with hogmarking dye (Ketchum Mfg. Co., Ottawa, Ontario).

Dispersion patterns of walruses on land were much affected by beach topography, tide, and thermal conditions (Figs. 1–3). I sampled relationships of the locations of walruses in herds to various measures only for large herds on fairly smooth beaches. I recognized locations of walruses as follows. A walrus was defined as a group member if he was in body contact with one or more other walruses. Walruses 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 walruses, containing up to 20 members, often formed peripheral to main herds, especially in warm weather (Fig. 1). Walruses peripheral to main herds and small groups, and not in body contact with any other walrus, were classed as lone; this applied even to walruses very close to their fellows. The classification of locations was not exhaustive. In addition to their location, walruses were classified for body size and tusk fractures (body size and length of unbroken tusks are positively correlated; see Miller 1975a). Statistical symbols and methods of testing follow Sokal and Rohlf (1969). To test significance of differences between percentages, I computed r, 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

Walruses hauled out on all available kinds of beach habitat: cobbles 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 cobbles 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. Walruses seemed to prefer beaches sheltered from strong
Fig. 1. Part of an extensive herd of male walruses in warm weather (compare Fig. 1 of Miller 1975a).

Fig. 2. Male walruses scattered along a rugged boulder beach, in cool weather. Fig. 3. Part of a large herd of male walruses during early stages of haulout on rugged boulder beach, and coincident with high water. Fig. 4. Contagion of an agonistic interaction. Five walruses are directly involved (central submissive walrus and four larger walruses 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 walruses 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 walruses or more were recorded there on 22 of 31 census days.
Herds formed rapidly and often declined precipitously. At 0615 hours, 15 July 1973, no walruses were present on a beach that later that day (1900 hours) held more than 1000 walruses. 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 walruses had been present since 20 June. Similarly, in 1973 more than 400 walruses 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 walruses 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 walruses 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), walruses of various body sizes and tusk characteristics were distributed non-randomly (Fig. 5). Small walruses were more numerous than predicted in the seaward periphery and at a deficit elsewhere, while large walruses with unbroken or slightly broken tusks showed the opposite trend. Each of these three classes showed significant deviations of observed from expected frequencies ($\chi^2$ estimates, $P < 0.001$ in each case). Large walruses with severely broken tusks exhibited insignificant departures from a random distribution. However, such walruses were at deficits centrally and at the inland periphery, and in excess at the seaward periphery, relative to other large walruses; trends in their distribution paralleled those for small walruses.

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

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

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

Animals in herds commonly rested tusks and faces against other walruses. Thus, 58.2% of 335
recumbent walruses rested tusks and 68.3% of 463 rested mystacial pads against a neighbor.

The location of walruses in herds affected not only the extent of body contact, but also modified the manner in which walruses lay relative to the slope of the beach. Walruses located centrally typically lay parallel to one another and directed upslope, whereas peripheral walruses 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 walruses 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 walruses that attempted to enter the seaward periphery, 5.4% were forced back to the sea by threats; of 66 small walruses trying to enter, 34.8% were forced back ($P < 0.001$). Forty-five (80.4%) large walruses attempted to displace resident walruses, compared with 14 (21.2%) small walruses ($P < 0.001$). Whereas 71.6% of 74 attempted displacements of residents by large walruses were partially or entirely successful, only 26.7% of 15 by small animals were so ($P < 0.001$) (Fig. 8). Large walruses that attempted to displace resident walruses showed a mean frequency of attempted displacements of 1.69, compared with 1.07 for small walruses (for unequal variances, $t = 3.48, P < 0.01$).

For large walruses 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 walruses revealed an insignificant negative correlation. Overall, the number of ranks through which small walruses moved differed insignificantly from that for large walruses (by $t$ estimate) (Fig. 8). These trends reflect the tendency of small walruses to sometimes move quickly inland over the top of residents, and without attempting to displace any. Large walruses, 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 walruses often settled there. Small walruses 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 walruses 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 walruses)\*  

<table>
<thead>
<tr>
<th>Location</th>
<th>Seaward periphery</th>
<th>Central</th>
<th>Inland periphery</th>
<th>Inland small groups and lone</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of walruses (N)</td>
<td>2002</td>
<td>3373</td>
<td>1570</td>
<td>470</td>
</tr>
<tr>
<td>Upslope</td>
<td>80.0</td>
<td>93.7</td>
<td>88.3</td>
<td>68.6</td>
</tr>
<tr>
<td>Cross-slope</td>
<td>11.0</td>
<td>4.7</td>
<td>8.4</td>
<td>23.8</td>
</tr>
<tr>
<td>Downslope</td>
<td>9.0</td>
<td>1.7</td>
<td>3.3</td>
<td>7.6</td>
</tr>
</tbody>
</table>

\*%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. Walruses that engaged in agonistic activity in a 5-min observation period made up 41.5% of 224 walruses in the seaward periphery, 35.0% of 214 walruses in the center, and 21.9% of 219 walruses 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 walruses 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 walruses 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 behavioral differences between large and small walruses upon joining the seaward periphery (preceding section); however, the small sample (N = 22 observation periods) of medium–large walruses 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 walruses interacted more frequently than did small ones (Fig. 9) (see also section below on activity budgets).

The number of walruses 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 walruses involved (1972 and 1973...
TABLE 2. Analysis of variance table, computed from 1973 data on frequency of agonistic interaction per 5-min observation period

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>302.8</td>
<td>1</td>
<td>302.8</td>
<td>108.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body size (BS)*</td>
<td>42.0</td>
<td>5</td>
<td>8.4</td>
<td>3.0</td>
<td>&lt;0.025</td>
</tr>
<tr>
<td>Location (L)</td>
<td>59.7</td>
<td>2</td>
<td>29.9</td>
<td>10.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>BS \times L</td>
<td>51.2</td>
<td>10</td>
<td>5.1</td>
<td>1.8</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>Error</td>
<td>601.4</td>
<td>215</td>
<td>2.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

Activities of Walruses in Herds
Activities At and Near the Seaward Periphery, and Upon Joining a Herd

Walruses 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 walruses arriving at the seaward periphery, 31.0% investigated (tactually or olfactorily, or both) other walruses, 3.4% investigated 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).

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

Sleep Soundness and Jostling

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

Large central walruses were jostled by others 41.2% of the time. The mean durations ($\pm s_d$) of
TABLE 3. Characteristics of one-way olfactory-tactual investigations by walruses entering the seaward periphery of herds

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Nostrils open¹</th>
<th>Nostrils closed¹</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>No mystacial pad contact</td>
<td>5 (1)</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>Mystacial pad contact</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vibrissae erect</td>
<td>23 (3)</td>
<td>2 (1)</td>
<td>25</td>
</tr>
<tr>
<td>Vibrissae not erect</td>
<td>10 (1)</td>
<td>5 (1)</td>
<td>15</td>
</tr>
</tbody>
</table>

¹For full description, see Miller (1975a).
²Total number of investigations (number of investigations of rocks shown parenthetically).
³Four additional investigations that occurred underwater are not included.

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

<table>
<thead>
<tr>
<th>Inland</th>
<th>Inland</th>
<th>Small</th>
<th>Lone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total sample (N)</td>
<td>348</td>
<td>235</td>
<td>199</td>
</tr>
<tr>
<td>No. with eyes closed (n)</td>
<td>192</td>
<td>60</td>
<td>159</td>
</tr>
<tr>
<td>(n/N) x 100</td>
<td>55.2</td>
<td>71.5</td>
<td>79.9</td>
</tr>
</tbody>
</table>

²Scan-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 walruses spent more time than did central walruses in grooming and locomoting (4.9% vs. 3.5%, P < 0.10; Table 5). Of 678 grooming acts, 77.3% were performed by walruses in small groups and in lone and peripheral locations, and the rest was performed by the more numerous central walruses (χ² estimate, P < 0.001, even assuming equal numbers of walruses in the two locations). Lone walruses 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).

Walruses in shallow water engaged in overt social behavior (including contact-seeking behavior such as rubbing against another walrus, lolling with other walruses, 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). Walruses in shallow water also groomed more vigorously than did those on land. Small walruses 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 walruses on land within large herds, and alone in inland locations

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

*Data 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.

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

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 walruses, which breed in association with ice. Gregariousness among walruses 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, walruses, 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 walruses in central locations in herds. As herd size increases, central locations account for an increasing fraction of total locations, so that walruses 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 walruses.

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; Repenning et al. 1971), so thigmotactic behavior may have developed, in parallel with increased size, to compensate for the decreased importance of pelage in thermoregulation. Walruses are more thigmotactic than sea lions, presumably because of their sparser pelage and much colder habitat; energetic advantages to social thermoregulation among walruses must be especially great during the winter and for young calves. Extensive body contact among large summering walruses 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 walruses 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 walruses.

Because of their extreme gregariousness and positive thigmotaxis, walruses 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, walruses 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 walruses on land exhibit no allogrooming, and very few nasonasal greetings. The reasons for this seem clear. First, active walruses 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, walruses joining herds on land typically approach other walruses from the rear, a direction in which individual distance is less than it is in front. Finally, walruses 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, walruses 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 walruses 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 walruses 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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