UNIVERSITY OF CALIFORNIA
SANTA CRUZ

GROUPING BEHAVIOR OF PACIFIC WALRUSES (*ODOBENUS ROSMARUS DIVERGENS* ILLIGER), AN EVOLUTIONARY PERSPECTIVE

A Dissertation Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Spencer James Taggart

December 1987

The dissertation of Spencer J. Taggart is approved:

James C. Estes

Kenneth S. Norris

Adrienne Zihlman

John Pearse

Dean of Graduate Studies and Research

GROUPING BEHAVIOR OF PACIFIC WALRUSES, *ODOBENUS ROSMARUS DIVERGENS* ILLIGER, AN EVOLUTIONARY PERSPECTIVE

By

Spencer James Taggart

ABSTRACT

Walruses form large groups (maximum size > 10,000 animals) in which adjacent animals make extensive body contact. They are the only ice breeding pinniped that forms large dense groups; all other highly gregarious pinnipeds live in lower latitude ice-free habitats. Among these species, the extreme degree of gregariousness has been explained by limited breeding space on islands, post-partum estrus and terrestrial copulation. These factors are not applicable for explaining large, dense walrus groups because: 1) walruses do not breed on islands, 2) they do not have post-partum estrus, and 3) they copulate in the water.

The following aspects of walrus grouping behavior are discussed: 1) I studied the thermoregulatory costs and benefits of making contact with neighbors. From behavioral data that I collected it appears that a hot microclimate exists in the dense groups. I argue that such a hot microclimate is unlikely to have a thermoregulatory advantage. 2) The aggressive behavior of male and female walruses is compared. Both sexes have tusks and jab opponents during aggressive encounters. I found that female walruses are equally as aggressive as males, and females accompanying calves are more aggressive than males or lone females. 3) My telemetry studies demonstrated that the land-sea movements of walruses are highly synchronized. Based on these data, I hypothesize that walruses may travel at sea in large herds. Evidence for pinniped groups at sea suggests that selective factors in the marine environment may be important in the evolution of walrus grouping behavior. This is considerably different from Bartholomew's (1970) model for the evolution of pinniped polygyny which suggests that environmental factors interact with terrestrial copulation through sexual selection feedback loops to result in extreme gregariousness, and thus extreme polygyny. For walruses, rather than being simply a reproductive adaptation, grouping behavior may have to be viewed in a broader context of selective factors operating throughout the year. 4) I describe methods for attaching radio-tags to the tusks of sleeping walruses.

ACKNOWLEDGEMENTS

The work at Round Island would not have been possible without the permission and financial support of the Alaska Department of Fish and Game, Anchorage, Ak. and the U. S. Fish and Wildlife Research Laboratory, Anchorage, Ak. Jim Estes (U.S. Fish &. Wildl. Res. Lab.) and Jim Faro (Ak. Dept. Fish. & Game) initiated a jointly funded project for walrus studies at Round Island. The following people were subsequently involved in the continuation of the project: Steve Amstrup, Jim Baker, Bob Brownell, Doug DeMaster, J. Estes, J. Faro, Ancel Johnson, Lou Pamplin, Chris Smith, Dale Taylor, Ken Taylor, and Dan Timm. On several occasions, transportation was provided by NOAA and U. S. Coast Guard helicopters. At different stages in the project our only link with civilization was provided by Jim Faro, Chris Smith, Nick Stein, and Ken Taylor.

Collaboration between Francis Fay, Brendan Kelley, Cindy Zabel and myself resulted in synergistic enthusiasm for conceiving and carrying out the Punuk Island expedition. The studies at Punuk Island were funded by a NOAA (OCESP) grant awarded to Francis Fay and Brendan Kelley. Additional equipment and funding was provided by the U. S. Fish and Wildl. Res. Lab, Anchorage, Ak. Permission to set up a camp on Punuk Island was granted by the Saint Lawrence Island Native Corporation. Transportation from Nome to Punuk Island was provided by a NOAA research vessel, *Oceanographer*. Bob Nelson provided logistic support in Nome and while we were on Punuk Island he contacted us daily by radio.

The work at Cape Peirce was made possible by funding from Dave Fisher, U. S. Fish and Wildlife Service.

I thank the members of my thesis committee: J. Estes, K. Norris, J. Pearse, and A. Zihlman for encouragement and valuable comments on the manuscripts.

My advisor, Jim Estes, deserves special thanks. He helped me obtain funding throughout this project, read numerous drafts of manuscripts as ideas developed, and was my most valuable source of critical review.

I thank G. Barlow, F. H. Fay, J. Francis, S. Greene, C. Heath, R. Hinegardner, K. Holecamp, R. Pierotti, F. Pitelka, T. Rowell, J Stamps, G. Van Blaricom and B. Wursig for comments on earlier versions of chapter V.

My wife, Cindy Zabel was my co-worker during all phases of this research, and without her support this project would not have been possible. Her sense of adventure and enthusiasm were undaunted by difficult and adverse field conditions. The ease with which she adapted to living in the field and her appreciation of the wilderness made camp feel like home. She was my major critic and editor during the writing stages of this thesis.

Numerous friends have been supportive during various stages of this dissertation. David Brook, Lydia Marshall, Bob Nelson, and Chow and Ken Taylor provided us with homes in route to our research in Alaska. John Francis, Mike Haley, Carolyn Heath, Philip Hooge, Brendan Kelley, and Chris Otis are important friends with whom I have had numerous heated but always friendly discussions. Sara Taber, Peter Thomas, Dennie and Cindy VanTassel, and Tom Walker provided moral support during various difficult phases of graduate school. Finally I would like to thank my parents Spencer

Taggart and Ila Taggart for the encouragement they have given me.

Table of Contents

List of Figures

List of Tables

CHAPTER I

INTRODUCTION

Taxonomy. Walruses (*Odobenus rosmarus*) are an arctic pinniped with circumpolar distribution. The species may either be divided into two or three subspecies: 1) Pacific walruses (*Odobenus rosmarus divergens* Illiger), 2) Atlantic walruses (*Odobenus rosmarus rosmarus* Linnaeus), and 3) perhaps Laptev walruses. The latter may be either *O. r. divergens* or *O. r. rosmarus* or a third subspecies (*O. r. laptevi* Chapskii; Fay 1982). The modern walrus evolved in the Atlantic and apparently colonized the north Pacific by way of the Arctic Ocean less than one million years ago (Repenning 1976).

Phylogeny. The evolutionary relationship of walruses among other pinnipeds and carnivores is uncertain. A monophyletic or biphyletic origin of pinnipeds (from a terrestrial carnivore ancestor) has been debated from 1885 to present. Evidence for a biphyletic origin is provided by Mivart 1885; McLaren 1967; Tedford 1976; Repenning and Tedford 1977; Repenning et al. 1979; and Arnason 1981. Evidence for a monophyletic origin is from Kellogg 1922; Howell 1929; Howell 1930; Winge 1941; Simpson 1946; Sarich 1969; Arnason 1974; Sarich 1975; Arnason 1977; Arnason and Widegren 1986; and Wyss 1987. Walruses have been considered a member of the superfamily Otarioidea (Sarich 1969, 1975; Tedford 1976; Repenning and Tedford 1977; Repenning et al. 1979; Arnason 1981) but recent evidence indicates they may be more closely related to the Phocoidea superfamily (Wyss 1987).

Life history. Among Pacific walruses, the majority of males and females segregate during summer. Females (and their attendant young) and some males associate with the southern edge of the pack ice during summer. These animals migrate considerable distances (approximately 1700 km) as the pack ice expands and contracts seasonally (Fay 1982). In autumn, they migrate from the Chukchi Sea south through Bering Strait, and spend winter in the Bering Sea. In spring the reverse movement occurs. Most mature males utilize shore locations along the Siberian and Alaskan coasts during summer months (Fay 1982). Mating occurs from January to March (Fay 1982). Pregnancy lasts 15 to 16 months, including four to five months of delayed implantation (Fay 1982; Fay et al. 1984). Thus females reproduce biannually or less frequently. Calves are weaned at about two years of age (Fay 1982).

Extant models for pinniped grouping. Pinniped groups are generally considered to be reproductive aggregations or colonies (Wittenberger 1981; Wilson 1975; Crook et al. 1976; Bartholomew 1970). Thus sexual selection and other selective forces that occur during the breeding season have been emphasized to explain the evolution of the extreme gregariousness of pinnipeds (Nutting 1891; McLaren 1967; Bartholomew 1970; Le Boeuf 1974; Stirling 1975, 1983; Cox and Le Boeuf 1977; Pierotti and Pierotti 1980). By this view, terrestrial parturition and limited terrestrial mobility resulted in pinnipeds utilizing predator free islands where space was limited. Breeding on islands resulted in an initial degree of clumping (Bartholomew 1970), but some pinnipeds clump closer than limited space alone would dictate. Females are thought to form dense groups because single females are likely to mate with marginal males who are not successful at male-male competition and hence may be genetically inferior. The benefits of mating with dominant males may outweigh costs, such as trampled pups, which are correlated with the dense groups (Le Boeuf and Briggs 1977).

Feeding habits may also have had "marked effect on breeding behavior" of pinnipeds (Repenning 1976: p. 388). Repenning noted a distinction between coastal and pelagic feeders. Otariids became pelagic feeders after they developed homodont dentition, while phocids continued the ancestral trait of feeding along coasts or ice fronts. Locating conspecifics in order to mate was simple for phocids, but required "homing instincts" for otariids that were widely dispersed at sea. Dispersed pelagic otariids were able to locate other members of their species by returning to place of birth, which resulted in the evolution of rookery breeding (Repenning 1976).

This argument was countered by Stirling (1983: p.510): "Because pinnipeds evolved from terrestrial mammals, the distribution and availability of habitat for parturition and breeding would be more likely to influence the way in which the different species evolved to obtain maximum utility of the marine habitat, rather than the other way around." Thus, parturition habitat may explain why otariids are more highly polygynous than are phocids (Stirling 1975, 1983). Since the pack ice is an unstable and unpredictable habitat, polar pinnipeds generally do not form dense groups. In contrast, temperate pinnipeds breed on islands (which are stable and predictable) and thus form groups.

Phylogeny may also affect pinniped mating systems (Stirling 1975, 1983). Most phocids copulate in the water like their presumed lutrine ancestors, while most otariids copulate terrestrially as did their ursine ancestors[1]. Stirling suggested that without terrestrial copulation, polygyny would not evolve because it would be too difficult for males to defend females in a three dimensional (aquatic) territory. As Stirling pointed out, however, several species copulate both terrestrially and aquatically, indicating that the copulation site is not obligatory (see also Allen 1985). A monophyletic pinniped phylogeny of course suggests that the differences in copulation between Otarioidea and Phocoidea are probably derived.

Walrus groups. Walruses form large dense herds (often exceeding 10,000 animals). The existence of large walrus groups is important because extant hypotheses for the evolution of pinniped groups are not applicable for walruses (see Chapter V). This is difficult to explain because: 1) walruses do not breed on islands, they breed on the unlimited drifting pack ice. Walruses are the only ice breeding seal that forms large dense groups (Stirling 1975, 1983); 2) walruses do not copulate on ice, but apparently in the water (Fay 1982); 3) walruses do not have post-partum estrus (Fay 1982); and 4) walruses are coastal feeders. One explanation for this disparity is that the gregariousness of walruses may be a "phylogenetic relict" (Stirling 1983: p. 517). Based on paleontological evidence, 12 to 9 million years ago an ancestral walrus species (*Imagotaria downsi*) was "sexually

---

[1] This idea is based on the assumption that pinnipeds are biphyletic.

dimorphic to an extreme degree" and thus was probably a rookery breeder (Repenning 1976: p. 381).

I will examine three aspects of walrus grouping behavior: 1) the thermoregulatory function of dense walrus groups (Chapters II and III); 2) the aggressive behavior of male and female walruses that haul out during the autumn southward migration (Chapter IV); 3) I present data on the land-sea movements of walruses (Chapter V) and propose a new hypothesis for walrus social organization; and 4) I explore the possible application of this hypothesis to other pinnipeds.

CHAPTER I, BIBLIOGRAPHY

Allen S. 1985. Mating behavior in the harbor seal. *Mar. Mamm. Sci.* 1:84-87.

Arnason, U. 1974. Comparative chromosome studies in Pinnipedia. *Hereditas* 76:179-226.

Arnason, U. 1977. The relationship between the four principal pinniped karyotypes. *Hereditas* 87:227-242.

Arnason, U. 1981. Localization of nucleolar organizing regions in pinniped karyotypes. *Hereditas* 94:29-34.

Arnason, U. and Widegren, B. 1986. Pinniped phylogeny enlightened by molecular hybridizations using highly repetitive DNA. *Mol. Biol. Evol.* 3:1-10.

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.

Cox, C. and Le Boeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.* 111:317-335.

Crook, J. H., Ellis, J. E. and Gross-Custard, J. D. 1976. Mammalian social systems: structure and function. *Anim. Behav.* 24:261-274.

Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.

Fay, F. H., Ecology and Biology of the Pacific Walrus. *Odobenus rosmarus divergens* Illiger. 1982. U.S. Dept. Int., Fish & Wildl. Serv., Wash. D.C. N. Amer. Fauna, no. 74. 279 pp.

Fay, F. H., Ray, C. and Kibal'chich, A. A. 1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. Pages 81-88 in F. H.

Fay, & G. A. Fedoseev eds. Soviet-American Cooperative Research on Marine Mammals. Volume I Pinnipeds. U. S. Dept. of Commerce, NOAA, Wash. D. C.

Gentry, R. L. 1981. Northern fur seal - *Callorhinus ursinus* (Linnaeus, 1758) Pages 143-160 in S. H. Ridgway and R. J. Harrison, eds. Handbook of Marine Mammals. Volume I: the Walrus, Sea Lions, Fur Seals and Sea Otter. Academic Press, London.

Howell, A. B. 1929. Contributions to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). Proc. U.S. Nation. Mus. 73(15), 142 pp.

Howell, A. B. 1930. Aquatic mammals, their adaptations to life in the water. Charles C. Thomas, Baltimore, 338 pp.

Kellogg, R. 1922. Pinnipeds from Miocene and Pleistocene deposits of California. A description and a resume of current theories regarding the origin of the Pinnipedia. Bull. Dept. Geol. Univ. California 13:23-132.

Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *Amer. Zool.* 14:163-176.

Le Boeuf, B. J., and Briggs, K. T. 1977. The cost of living in a seal harem. *Mammalia*. 41: 167-195.

McLaren, I. A. 1967. Seals and group selection. *Ecology* 48:104-110.

Mivart, G. 1885. Notes on the Pinnipedia. *Proc. Zool. Soc.* Lond.:484-500

Nutting, C. C. 1891. Some of the causes and results of polygamy among the Pinnipedia. *Am. Nat.* 25:103-112.

Pierotti, R., and Pierotti, D. 1980. Effects of cold climate on the evolution of pinniped breeding systems. *Evolution* 34: 494-507.

Repenning, C. A. 1976. Adaptive evolution of sea lions and walruses. *Syst. Zool.* 25:375-390.

Repenning, C. A. and Tedford, R. H. 1977. Otarioid seals of the Neogene. U.S. Geol. Survey Prof. paper 992.

Repenning, C. A., Ray, C. E., and Grigorescue, D. 1979. Pinniped Biogeography. Pages 357-369 in J. Gray and A. J. Boucot, eds. Historical Biogeography, Plate Tectonics, and the Changing Environment. Oregon State Univ. Press, Newport.

Sarich, V. M. 1969. Pinniped phylogeny. *Syst. Zool.* 18:416-422.

Sarich, V. M. 1975. Pinniped systematics: immunological comparisons of their albumins and transferrins. *Am. Zool.* 15:826.

Simpson, G. G. 1946. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Natur. Hist.* 85, 350 pp.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* 169:205-212

Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489-527 in J. Eisenberg and D. Kleiman, eds. Advances in the Study of Mammalian Behavior. Am. Soc. Mammal., Spec. Publ. 7.

Stirling, I. 1984. A group threat display given by walruses to a polar bear. *J. Mamm.* 65:352-353.

Tedford, R. H. 1976. Relationship of pinnipeds to other carnivores (Mammalia). *Syst. Zool.* 25:363-374.

Wilson, E. O. 1975. Sociobiology: the New Synthesis. Beklnap Press, Cambridge, Mass.

Winge, H. 1941. The interrelationships of the mammalian genera.

Transl. from Danish by E. Deichman and G. M. Allen. C. A. Reitzels, Copenhagen, vol. 2, 376 pp.

Wittenberger, J. F. 1980. Group size and polygamy in social mammals. *Am. Nat.* 115:197-222.

Wittenberger, J. F. 1981. Animal Social Behavior. Duxbury, Boston.

Wyss, A. R. 1987. The walrus auditory region and the monophyly of pinnipeds. *Am. Mus. Novit.* 2871:1-31.

CHAPTER II

DENSE WALRUS GROUPS. I. WALRUSES LIKE IT HOT.

Pinnipeds alternate between aquatic and terrestrial environments which are thermally very different. At most temperatures the cooling capacity of water is about ten times greater than air (Irving and Hart 1957). Thus the change in thermal environment that occurs when pinnipeds leave the aquatic environment is probably greater than most temperate mammals experience between winter and summer.

Acclimation to extreme temperatures has been demonstrated in many mammals (e.g., pigs, humans, and mice; Folk 1974). Simultaneously, however, such animals become less tolerant of opposite thermal environments (Fregley 1970; Ingram 1977; Macari et al. 1983). Young pigs that were raised in 10^0 C cold chambers experienced severe hyperthermia when transferred to 35^0 C chambers where their siblings were raised (Ingram 1977). Increased tolerance to low temperatures and concordant intolerance to hot temperatures demonstrates that individuals can acclimate but that there are constraints.

This type of thinking has been extended to evolutionary arguments of generalist versus specialist phenotypes (Huey and Hertz 1984), or the Principal of Allocation (Levins 1968). Consistent with this idea, many morphological and physiological features of pinnipeds are specialized aquatic adaptations, including the thermal mechanisms for preventing heat loss (Bartholomew 1970). A layer of blubber effectively prevents heat loss in cold water, allowing arctic pinnipeds to maintain thermoneutrality in 0° C water at basal metabolic rate (Irving and Hart 1957; Hart and Irving 1959). However, blubber has disadvantages in air: 1) Blubber is heavy compared to fur. 2) Blubber is a poor insulator in subfreezing air because the relatively bare skin of a pinniped must be maintained at approximately 0° C, unlike fur. Thus maintaining a skin temperature of 0° C when ambient temperature is below zero can result in high convective and radiant heat loss (Pierotti and Pierotti 1980). 3) At warm air temperatures pinnipeds are so well insulated that they may have trouble loosing enough heat. When northern fur seals (*Callorhinus ursinus*) are forced to locomote on land (even at cool temperatures), their core temperature increases dramatically and some individuals die of heat prostration (Bartholomew and Wilke 1956). The specialized mechanisms that pinnipeds have evolved for minimizing heat loss in cold water simultaneously constrain the thermal environment that they can tolerate on shore.

Walruses (*Odobenus rosmarus divergens*) haul out on land or sea ice where they form dense groups in which individuals have extensive body contact with neighbors. Body contact among walruses may be a thermoregulatory adaptation to conserve heat in the cold polar environment (Fay and Ray 1968; Ray and Fay 1968). This suggestion is consistent with findings from laboratory studies of young pigs (Mount 1960; Holmes and Mount 1967) and mice (see Contreras 1984 for review) which demonstrate that at cool temperatures metabolic rate is substantially reduced if the young animals are allowed to make contact with one another.

Similarly, incubating Emperor penguins (*Aptenodytes forsteri*) reduce metabolic rate during winter by huddling (Pinshow et al. 1976). Due to the high potential heat loss in cold arctic air, the heat conservation hypothesis for the formation of dense walrus groups seems plausible. Thus, the evolution of walrus groups might be viewed as the result of individuals attempting to minimize heat loss. It would be advantageous for individuals to move from the edge of a group toward the center (where contact is greater), and to join larger groups where the probability of being on an edge is lower. This argument is similar to the "selfish herd" model that suggests herding behavior reduces each individual's probability of being preyed upon (Hamilton 1971), except the cost being minimized for walruses is heat loss.

Models for the evolution of group living suggest three selective forces: predator avoidance, increased foraging efficiency, and utilization of limited resources (Alexander 1974; West-Eberhard 1979, 1983). Grouping behavior of pinnipeds is thought to be primarily the result of utilizing a limited resource: islands or other safe habitats for breeding and parturition. All pinnipeds leave the marine environment to bear their young (or give birth) (Stirling 1975, 1983). An interesting aspect of many island breeding pinnipeds (and walruses) is that they form dense groups even when there is additional space available (Stirling 1975, 1983). The tendency to form dense groups is thought to be the result of a sexual selection factor called the "marginal male effect" (Nutting 1891; McLaren 1967; Bartholomew 1970; Stirling 1975, 1983). Thus, the heat conservation hypothesis is important because it is an alternative rarely suggested for group living in pinnipeds, or mammals in general.

The advantages of grouping have to overcome "automatic detriments" before grouping will evolve (Alexander 1974: pp.328; West-Eberhard 1979, 1983). Walruses' contact behavior might have considerable costs. Fay and Ray (1968; Ray and Fay 1968) concluded that walruses' huddling behavior is temperature independent, and therefore walruses are prevented from moving into warmer climates due to heat stress.

In this paper I examine the relationships among walrus herd density, thermoregulatory behaviors and a range of thermal conditions. I also estimate the insulative effects of dense groups by comparing the thermoregulatory behavior between individuals in dense groups and individuals that are not in contact with neighbors. I discuss whether current views of pinniped thermoregulation are adequate explanations for the behavior that is described in this paper.

Methods

From 16 August through 21 September 1979 I studied thermoregulation of walruses at Round Island, Alaska (56°02'N160°50'W) in the southeastern Bering Sea. Observations were made from a blind located on a cliff 30 meters above a 325 m long beach. This was the beach used most frequently by walruses, often occupied by up to 3500 animals. Directly below the blind a cove partially separated a 42 m section of the beach. My studies were conducted on this 42 m section of beach.

Walrus density was estimated by visually superimposing a string grid on the study beach. When walruses were away from the island, I laid out a grid of six m by six m plots on the beach using surveyors tape as temporary markers. The grid divided the small beach into five rows that were parallel to the ocean and seven columns that were perpendicular to the ocean. I then built a 5 X 3 m square with 2"X4" lumber and mounted it approximately three m in front of the blind. The gridded section of beach was enclosed within this square when observing the beach through binoculars mounted on a fixed tripod. Strings were then attached to the square so that they were visually superimposed onto the gridded beach when observed through the binoculars.

Density and behavior of walruses, and weather data were collected for each of the 35 plots throughout the day for 15 sample days. A walrus was operationally classified as occurring in a plot if his tusks fell within the string grid. The individual walruses in each plot were scan sampled (Altmann 1972) for thermoregulatory behaviors. Two thermoregulatory postures were recorded: 1) Extended flipper. A walrus was classified as having a flipper in the air if one or both flippers were not contacting its body, the beach, or a neighbor. 2) Reclining on the back. The following weather parameters were recorded after each sample: air temperature (measurement was taken in the shade with a *Weather Measure* mercury thermometer), blackbulb temperature [measurement was taken in the direct sunlight with a *Weather Measure* thermometer (bulb was painted black)], wind direction and velocity, sea state, percent of cloud cover, precipitation (yes or no), tide state (falling, rising, high, or low), and the distance from the cliff to the water (width of the beach).

Five to 7 samples were taken between 0730 and 2000 h each day of the study.

Results

General description of density changes. Walrus density varied considerably between observation days, among rows, and from hour to hour on warm days (Figs II.1e-II.1o). On cool days, the density remained constant through time (Figs. II.1a-II.1d; especially next to the cliff, rows 1 and 2). On hot days there was a reduction in density near the cliff in rows 1 and 2 and sometimes in row 3 (Figs. II.1e-II.1o). The reduction in density near the cliff did not appear to be caused by members of the group spreading out; rather individuals apparently became overheated and climbed over other walruses in the group to reach the water or intertidal substrate. Thus there was an increase in the number of walruses adjacent to the sea periphery on hot days (rows 4 and 5; Figs. II.1e-II.1o). The departing walruses moved quickly, characteristically ignoring threats or jabs dealt by other walruses. Departing walruses moved at an average rate of 14 m/min. (n=39) while walruses entering herds from the sea traveled at an average rate of 5 m/min. (n=81).

Relationship between temperature and density. The density measurements are interrupted time series data. Therefore the data cannot be pooled and analyzed with regression because the observations are not independent. However, one sample from each observation day is an independent sample. For this analysis I used data collected at the maximum temperature of the day and restricted the analysis to row 1 (which eliminates the overriding effects of the cool sea periphery). Density is plotted against blackbulb and ambient temperature (Figs. II.2a and II.2b respectively). Correlations between density and both blackbulb ($r=.94$, $p<.0001$) and ambient temperature ($r=.66$, $p<.003$) are significant, however, blackbulb provides a better fit.

Relationship between posture and temperature. The percentage of walruses laying on their backs and extending flippers was calculated for all of the walruses in row 1 when ten or more walruses were present in that row. Only data from the hottest time of each day were used in this analysis. The data were transformed to arcsin-squareroot percent values for regression analyses. The percentage of walruses laying on their backs, and the percent with flippers extended, were regressed against blackbulb (Figs. II.3a and II.4a) and ambient temperature (Figs. II.3b and II.4b). Neither posture was significantly correlated to blackbulb (backs: $r^2=.08$, $p<.79$; flippers: $r^2=.20$, $p<.47$) or ambient temperature (backs: $r^2=.12$, $p<.55$; flippers: $r^2=.04$, $p<.89$). I also plotted the percentage of walruses resting on their backs as time series so the data can be visually inspected (Figs. II.1a-II.1o).

Visual inspection of the time series figures suggests several patterns. Consistent with the regression analyses, there does not appear to be a simple linear relationship between temperature and percentage of thermoregulatory postures. On the four coldest days, density and temperature remained relatively constant throughout time, but the percentage of walruses on their backs varied considerably both within and among days. Even though temperatures were cool, the percentage of walruses on their back was often above 50 percent. Rain combined with cool temperatures seemed to reduce the percentage of walruses laying on their backs (Figs.II.1a, II.1b, and II.1c respectively). Excluding the four coolest days, density in row 1 declined with increasing temperature. However, since decreasing contact with neighbors decreased the temperature of the thermal microenvironment, the relationship between postures and temperature is confounded by changes in density. The percentage of thermoregulatory postures was high during high temperatures, but similar to the percentage observed at low temperatures.

Upper critical temperature for walruses in dense herds. If one assumes that walruses escape to the cool sea periphery when the maximum critical temperature is reached, then the upper critical temperature of individuals in dense groups can be estimated by observing the temperature at which movement to the sea begins. Since the cliff rows were free from the cooling effects of the sea periphery, I used only those rows for this estimate (rows 1 and 2). The best estimate of maximum critical temperature for a walrus in a dense herd is the warmest temperature at which there was no decline in density. During all heavy overcast days (Fig. II.1a, ambient=blackbulb=11^{0} C; Fig.II.1b, ambient=11.5^{0} C, blackbulb=12^{0} C; Fig. II.1c, ambient=blackbulb=13^{0} C; and Fig. II.1d, ambient=14^{0} C, blackbulb=14.5^{0} C) there was little reduction in density along the cliff rows. The coolest sunny day (Fig. II.1e, ambient=11.5^{0} C, blackbulb=18.5^{0} C) was characterized by a moderate reduction in density in rows 1 and 2, suggesting that maximum critical temperature had been exceeded for a walrus in a dense herd. Thus, the maximum critical temperature for walruses in dense groups appears to be greater than 14^0 C ambient (simultaneous blackbulb =14.5^0 C) and less than 18.5^0 C blackbulb (simultaneous ambient=11.5^0 C).

Upper critical temperature for individuals not in dense herds. After the critical temperature for walruses in dense groups is reached, density declines and thus spacing increases. The temperature that the remaining walruses can tolerate therefore increases because they are making contact with fewer neighbors. At high temperatures, numerous walruses move to the sea periphery, and the remaining walruses have little contact with one another. Thus the upper critical temperature of walruses who are not making contact with neighbors can be estimated by observing the temperature at which no walruses remain along the cliff rows. At 34^0 C blackbulb (the highest temperature I observed) only one walrus remained in the cliff row (Fig.II.1o). Walruses did remain in the cliff rows during the peak temperature of the second warmest day (maximum temperature = 31^0 C blackbulb; Fig.II.1n; 1500 h). After maximum temperature had been reached, walruses in the cliff rows continued to depart; two hours later one walrus remained in row 2. At a maximum temperature of 29^0 C blackbulb (Fig.II.1m) walruses remained in the cliff rows and the number did not continue to decline following maximum temperature. Thus the maximum critical blackbulb temperature for a lone walrus is between 29^0 and 31^0 C blackbulb.

Discussion

Density. Inter-individual distance is maintained in most fur seals (except Northern fur seals and Cape fur seals, *Arctocephalus pusillus,* Stirling 1975) and in all phocids (except elephant seals, *Mirounga angustirostris,* Bartholomew 1952, 1970; Stirling 1975). In contrast, walruses (Fay and Ray 1968; Ray and Fay 1968), sea lions (*Zalophus californianus*, Peterson & Bartholomew 1967; *Otaria flavescens*, Vaz-Ferreira 1975; *Neophoca cinerea* and *Eumetopias jubatus,* Gentry 1973), Northern fur seals and Cape fur seals make body contact.

The relationship between temperature and density has not been quantitatively measured in other pinniped groups. It subjectively appears that walruses consistently form denser groups than California sea lions, Steller sea lions, or elephant seals (pers. obs.). Steller sea lions have been measured at a maximum density of .77 females/m^2 (average weight=365 kg; Gentry 1970). The maximum density I measured for walruses in this study was .73 males/m^2, and they have an adult body weight of approximately 1200 kg (Fay 1982). Thus, mass per area is approximately 876 kg/m^2 and 281 kg/m^2 for walruses and Steller sea lions respectively. In a Steller sea lion study (Gentry 1973), individuals were scored as "huddling" if 75 percent of their length on one or both sides was in contact with a neighboring sea lion. No more than one third of the population ever huddled. If this same definition of huddling is applied to walruses, maximum number of walruses huddling would be 100 percent of the population (on cool days or early in the morning on sunny days).

Relationship between temperature and density. Huddling behavior was found to be negatively correlated with temperature in Steller sea lions (Gentry 1973). Previous studies of walrus thermoregulatory behavior suggested that huddling behavior was independent of temperature (Fay and Ray 1968). In this study I observed walruses at higher temperatures than Fay and Ray (1968) and I was able to quantify density. I found a highly significant negative correlation between density and temperature, which leads me to reject the hypothesis that density of walrus herds is independent of temperature.

Correlations between behavior and environmental variables are commonly used as evidence for adaptive explanations (Brown and Orians 1970). Thus, one could argue that the correlation between temperature and density is evidence that dense walrus groups are an adaptation for heat conservation; at cool temperatures density is high to facilitate heat conservation, and at high temperatures density is low because heat conservation is not necessary. This argument is probably incorrect for walruses. Changes in density of walrus herds do not appear to be the result of individuals gradually increasing their individual distance relative to their neighbors. Instead these changes appear to be the result of individuals (who have presumably reached the upper limit of thermoneutrality) climbing over the herd to reach the cooling effects of the sea periphery. The space created by the departing walruses results in a reduction in density. Lower density reduces body contact that remaining walruses have with neighbors, which increases their surface area available for dissipating heat, and hence the ambient temperature that they can tolerate.

Although it seems reasonable to view behaviors such as sand flipping, extending flippers into the air, sprawling on the back and escaping to the water as behavioral responses (exaptation in the terminology of Gould and Vrba 1982) for dissipating heat, the reduction in density of walrus groups would probably be better viewed as an effect (Gould and Vrba 1982) of one of these responses, i.e., escaping to the water. This distinction is important when considering evolutionary explanations for traits. Although there was a highly significant negative correlation between temperature and density in walruses, the correlation is apparently the result of a correlation between individuals escaping to the water and temperature. Since escaping to the sea periphery is a response to overheating, it is inappropriate to use the correlation between temperature and density as supporting evidence for the view that walrus groups evolved to conserve heat. The correlation between temperature and density does not explain why groups form; only why they disperse.

Regardless of the cause of group formation, density reduction appears to be flexible, allowing walruses to tolerate a wide range of temperatures. This observation suggests that the dense grouping behavior of walruses is unlikely to limit the southern latitude of their range (see Fay and Ray 1968; Ray and Fay 1968 for details of hypotheses that walruses are limited to cool climates by their grouping behavior).

Relationship between posture and temperature. I found no correlation between posture and temperature over the temperature range that I studied. In contrast, thermoregulatory postures have been correlated to temperature in Steller sea lions, Australian fur seals, *Arctocephalus forsteri* (Gentry 1973) and elephant seals (White & Odell 1971). One interpretation is that reclining on their back and extending flippers are not thermoregulatory behaviors for walruses. This interpretation contradicts observations of young captive walruses that were exposed to incremental temperature increases. At cool temperatures these individuals pressed their flippers next to their bodies and at high temperatures they extended flippers and reclined on their backs (Fay and Ray 1968).

The insignificant correlation between temperature and posture that I found is probably due to the confounding effect of density declining with increasing temperature. That is, a reduction in density (which accompanies increasing temperature) results in a similar thermal environment for the remaining walruses even when temperature is increasing. This suggests that walruses within dense groups at low air temperatures may be as hot as lone walruses at high temperatures. Although 30^0 C (blackbulb) is a surprisingly high temperature for a walrus to tolerate, it appears that dense walrus herds may create a similar microclimate even on cool days.

Upper critical temperature for individuals in dense groups. Walruses in dense groups began escaping to the water at low temperatures. The temperature at which individuals began leaving was between 14^0 C ambient (a cloudy day so blackbulb was also 14^0 C) and 18^0 C blackbulb. In contrast, elephant seals began escaping to the water at much higher temperatures, 30^0 to

32^0 C blackbulb (White and Odell 1971)[1].

Upper critical temperature of individuals not making contact with other walruses. Walruses tolerated maximum temperatures that were similar to those tolerated by elephant seals. On four observation days, all elephant seals had migrated to the surf at blackbulb temperatures of 30^0, 36^0, 33^0 and 34^0 C (White and Odell 1971). I found that all but one walrus left the cliff rows at 34^0 C, but some walruses remained in cliff rows at 29^0 to 31^0 C blackbulb. The wide range of temperatures between the onset of movement to the sea periphery and the maximum temperature tolerated by some walruses is probably the result of the density reduction which greatly changes the microclimate for the remaining walruses.

I made observations on one warm but moderately overcast day (Fig.II.1n); thus the ambient and blackbulb temperatures were close. Data from this day are important for comparison to captive studies of pinnipeds where experiments are conducted in shaded rooms. During observations on this overcast day, walruses remained on shore at 27^0 C ambient. Since blackbulb was simultaneously 31^0 C, this is a conservative estimate of shaded temperature that walruses can tolerate. Adult walruses apparently remain ashore beyond temperatures at which smaller captive sea lions and captive walrus calves exceed their upper

---

[1] Steller sea lions began escaping to the water between 10^0 and 15^0 C rock temperature and Australian fur seals began escaping between 15^0 and 20^0 C rock temperature (Gentry 1973). Rock temperatures are not comparable to blackbulb so I cannot rank walruses with respect to these species.

critical temperature:

1) Four recently captured walrus calves were progressively exposed to a 3^0 or 4^0 C increase (starting at 1^0) in temperature every 15 minutes. The behavior of the calves progressively changed as the temperature increased:

> "At the lowest temperature, about 1^0 C, each animal assumed a fetal position with occasional violent shivering. As the temperature was raised, each became more relaxed and paid less attention to keeping its appendages against the body. At 10^0 C, the animals became fully relaxed and lay either on the back or side; at 15^0 they began to sprawl and extend their appendages; at 18^0 C they became restless and began fanning intermittently with their flippers; at 20^0 C they were so restless that the experiment was terminated." (Fay and Ray 1968: pp.4-5).

When compared to my data, these observations suggest that immature walruses may have a lower upper critical temperature than adults.

2) Like walrus calves, California sea lions may also have a lower upper critical temperature than adult walruses. a) Experimental data show increasing deep body temperature at an air temperature of 25^0 C (Luecke et al. 1975; South et al. 1976). b) A theoretical biothermal mathematical model predicts a rise in deep body temperature at an air temperature of 25^0 C (Luecke et al. 1975; South et al. 1976). c) Elevation in rectal temperature and oxygen consumption was demonstrated in two captive California sea lions (weighing 54 and 69 kg) at temperatures between 21-27^0 C (Matsuura and Whittow 1973). This indicates that the sea lions were hyperthermic at these temperatures and had exceeded their upper critical temperature.

3) Compared to the adult walruses I studied in the field, the

captive walruses and sea lions were much smaller and had a higher surface to body weight ratio. Thus I would expect the smaller captive animals to have a higher upper critical temperature than the adult wild walruses. This suggestion is supported by empirical data. In Matsuura and Whittow's (1973) studies, a smaller younger California sea lion (weighing 32 kg) had a higher upper critical temperature of approximately 30^{0} C, compared to 21-27^{0} for the two larger sea lions.

Thus walruses are surprizingly heat tolerant: they are a large arctic species with similar heat tolerance as elephant seals inhabiting low latitudes (White and Odell's study was done at Guadalupe Island, Mexico) and smaller California sea lions. Pinnipeds may utilize several physiological mechanisms to increase their upper critical temperature:

1) Heat sequestering. There is evidence that California sea lions exposed to warm thermal conditions are able to sequester heat. This may be done by pooling blood in hepatic and splenic portions of the splanchnic circulation (South et al. 1976).

2) Reduced metabolism. Matsuura and Whittow (1973) pointed out the physiological analogies between how some desert rodents divert blood away from heat producing tissues and the way that marine mammals shunt blood away from oxygen consuming tissues during diving. Given that blood redistribution mechanisms have already evolved for diving, it seems reasonable to hypothesize that pinnipeds might be able to utilize these mechanisms for diverting blood away from heat producing tissues. However, no evidence was found that sea lions could reduce metabolic rate below basal when they were hyperthermic

(Matsuura and Whittow 1973).

3) Variable body temperature. Camels have a variable body temperature (34^0 to 40^0 C; Schmidt-Nielsen et al. 1957). This mechanism makes it possible for camels to store heat during the day and then dump it during cooler nights (Schmidt-Nielsen et al. 1957). The body temperature of elephant seals varies diurnally (McGinnis and Southworth 1967), suggesting that they may also store heat. Labile body temperatures have been reported in other pinniped species including walruses (34^0 to 39^0 C, Ray and Fay 1968), Monk seals (*Monachus schauinslandi*, 35.9^0 to 38.8^0 C, Kridler et al. 1971), elephant seals (33^0 to 37.5^0 C, Bartholomew 1954; 35^0 to 40.5^0 C, McGinnis and Southworth 1967; 33^0 to36^0 C, White and Odell 1971), and California sea lions (36.5^0 to 39.5^0 C, Matsuura and Whittow 1973).

Regardless of the mechanism, it is surprising that walruses have similar heat tolerance as low latitude pinnipeds. Walruses live in cold arctic water but simultaneously do not appear to be constrained in their ability to withstand high temperatures. I propose that walruses have this ability because they spend time in a "tropical" microclimate created by their dense groups. Social behavior may effect the evolution of a species. It has been hypothesized that social behavior may allow an animal to occupy new habitats which result in new selective forces that eventually lead to physiological or morphological adaptations (Mayr 1978; Huntingford 1984). Walrus groups may be an example. The formation of dense walrus groups is obviously mediated by social behavior. Within dense groups a hot microclimate is created, perhaps resulting in a new set of selective forces for preventing heat stress.

BIBLIOGRAPHY, CHAPTER II

Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5:325-383.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.

Bartholomew, G. A. 1952. Reproductive and social behavior of the northern elephant seal. *Univ. of Calif. Publ. Zool.* 47:369-472.

Bartholomew, G. A. 1954. Body temperature and respiratory and heart rates in the northern elephant seal. *J. Mamm.* 35:211-217.

Bartholomew, G. A and Wilke, F. 1956. Body temperature of fur seal. *J. Mamm.* 37:327-337.

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.

Brown, J. L. and Orians, G. H. 1970. Spacing pattern of mobile animals. *Ann. Rev. Evol. Syst.* 1:239-263.

Contreras, L. C. 1984. Bioenergetics of huddling: test of a psycho-physiological hypothesis. *J. Mamm.* 65:256-262.

Fay, F. H. 1982. Ecology and Biology of the Pacific Walrus. *Odobenus rosmarus divergens* Illiger. U.S. Dept. Int., Fish & Wildl. Serv., Wash. D.C. N. Amer. Fauna, no. 74. 279 pp.

Fay, F. H. and Ray, C. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). *Zoologica* 53:19-32.

Folk, G. E. 1974. Textbook of Environmental Physiology. Lea and Febiger, Philadelphia.

Fregley, M. J. 1970. Cross-adaptation. Pages 170-179. in D. H. K. Les and D. Minard, eds. Physiology, Environment, and Man. Academic Press, New York.

Gentry, R. L. 1970. Social behavior of the Steller sea lion. Ph.D. diss., Univ. California, Santa Cruz.

Gentry, R. L. 1973. Thermoregulatory behavior of eared seals. *Behaviour* 46:73-93.

Gould, S. J. and Vrba, E. S. 1982. Exaptation-a missing term in the science of form. *Paleobiol.* 8:4-15.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Ther. Biol.* 31:295-311.

Hart, J. S., Irving, L. 1959. The energetics of harbor seals in air and in water with special consideration of seasonal changes. *Can. J. Zool.* 37:447-457.

Holmes, C. W. and Mount, L. E. 1967. Heat loss from groups of growing pigs under various conditions of environmental temperatures and air movement. *Anim. Prod.* 9:435-452.

Huey, R. B and Hertz, P. 1984. Is a jack-of-all-temperatures a master of none? *Evolution* 38:441-444.

Huntingford, F. 1984. The Study of Animal Behaviour. Chapman and Hall, London, New York.

Ingram, D. L. 1977. Adaptation to ambient temperature in growing pigs. *Pflügers Arch. ges. Physiol.* 367:257-264.

Irving, L. and Hart, J. S. 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. *Can. J. Zool.* 35:497-511.

Kridler, E., Olsen, D. L. and Whittow, G. C. 1971. Body temperature of the Hawaiian monk seal. *J. Mamm.* 1. 52:476.

Levins, R. 1968. Evolution in Changing Environments. Princeton Univ. Press, Princeton.

Luecke, R. H., Natarajan, V. and South, F. E. 1975. A mathematical biothermal model of the California sea lion. *J. Therm. Biol.* 1:35-45.

Macari, M., D., Ingram, D. L. and Dauncey M. J. 1983. Influence of thermal and nutritional acclimatization on body temperatures and metabolic rate. *Comp. Biochem. Physiol.* 74:549-553.

Matsuura, D. T. and Whittow, G. C. 1973. Oxygen uptake of the California sea lion and harbor seal during exposure to heat. *Am. J. Physiol.* 225:711-715.

Mayr, E. 1978. Evolution. *Sci. Amer.* 239:38-47.

McGinnis, S. M. and Southworth, T. P. 1967. Body temperature fluctuations in the northern elephant seal. *J. Mamm.* 48:484-485.

McLaren, I. A. 1967. Seals and group selection. *Ecology* 48:104-110.

Mount, L. E. 1960. The influence of huddling and body size on the metabolic rate of the young pig. *J. Agric. Sci.* 55:101-105.

Nutting, C. C. 1891. Some of the causes and results of polygamy among the Pinnipedia. *Am. Nat.* 25:103-112.

Peterson, R. S. and Bartholomew, G. A. 1967. The natural history and behavior of the California sea lion. *Amer. Soc. Mammal. Spec. Publ.* 1:1-79.

Pierotti, R., and Pierotti, D. 1980. Effects of cold climate on the evolution of pinniped breeding systems. *Evolution* 34: 494-

507.

Pinshow, B., Fedak, M. A., Battles, D. R. and Schmidt-Nielsen, K. 1976. Energy expenditure for thermoregulation and locomotion in emperor penguins. *Am. J. Physiol.* 231:903-912.

Ray, G. C. and Fay, F. H. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). *Zoologica* 53:19-32.

Schmidt-Nielsen, K., Schmidt-Nielsen, B., Jarnum, S. A., and Houpt, T. R. 1957. Body temperature of the camel and its relation to water economy. *Am. J. Physiol.* 188:103-112.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* 169:205-212.

Stirling, I 1983. The evolution of mating systems in pinipeds. Pages 489-527 in J. Eisenberg and D. Kleiman, eds. Advances in the Study of Mammalian Behavior. Am. Soc. Mammal., Spec. Publ. 7.

South, F. E., Luecke, R. H., Zatzman M. L., and Shanklin, M. D. 1976. Air temperature and direct partitional calorimetry of the California sea lion (*Zalophus californianus*). *Comp. Biochem. Physiol.* 54:27-30.

Vaz-Ferreira, R. 1975. Behavior of the southern sea lion, *Otaria flavescens* (Shaw) in the Uruguayan Islands. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* 169:219-227.

West-Eberhard, M. J. 1979. Sexual selection, social competition and evolution. *Proc. Amer. Phil. Soc.* 123:222-234.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 58:155-183.

White, F. N. and Odell, D. K. 1971. Thermoregulatory behavior of the northern elephant seal, *Mirounga angustirostris*. *J. Mamm.* 52:758-774.

Figures II.1a-II.1o. Daily changes in the density of walrus herds and temperature. Walrus density is plotted against temperature for each sample day in a series of six plots. In the first graph at the top of the page, blackbulb temperature and ambient temperature are overlaid as bar charts and plotted against time. The percentage of walruses resting on their back (in row 1) is overlaid as a line graph. The two temperature plots converge when the sun is obscured by clouds or when the rock cliffs cast a shadow over the study area. Blackbulb temperature is above ambient temperature on sunny days. The five graphs below the temperature graph represent the density of walruses in each row (row 1 was next to the cliff; row 5 was the row closest to the sea). The density for each row is depicted by lines (5 or 6 depending on the row), each representing one 6 meter by 6 meter section of the row. Sample days are displayed in order of increasing blackbulb temperature (maximum for the day).

Figure II.1a. September 20

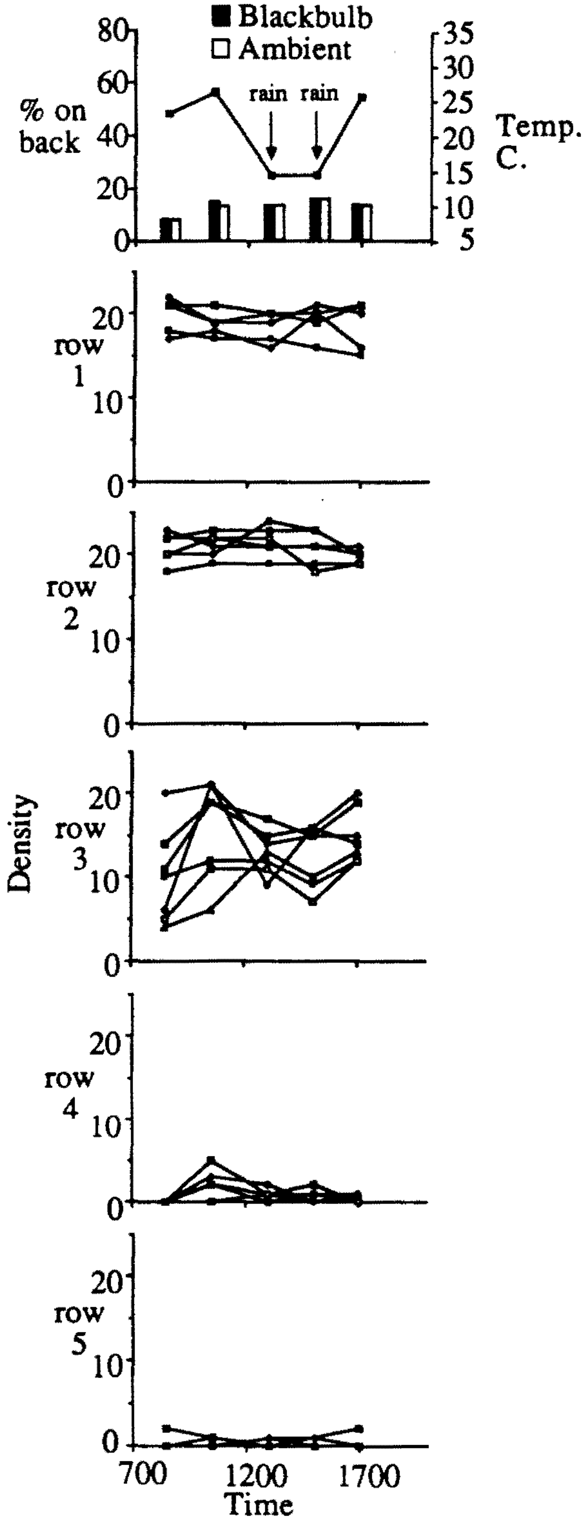


Figure II.1b. September 16

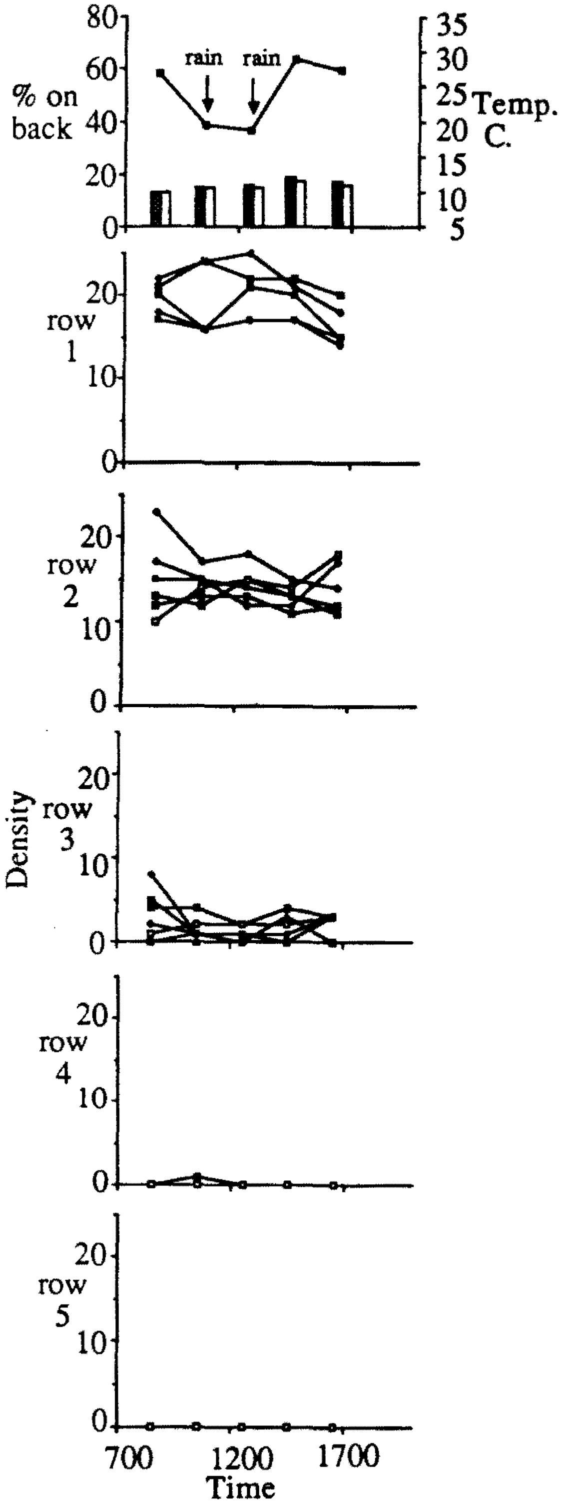


Figure II.1c. September 15

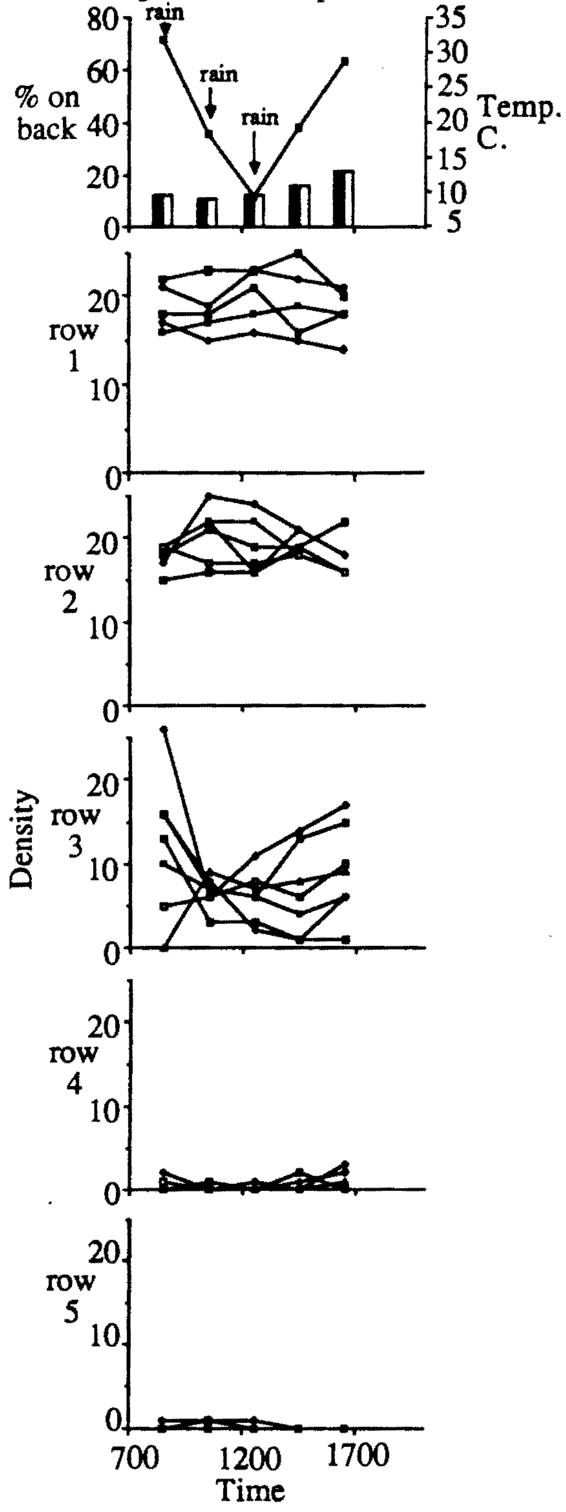


Figure II.1d. September 19

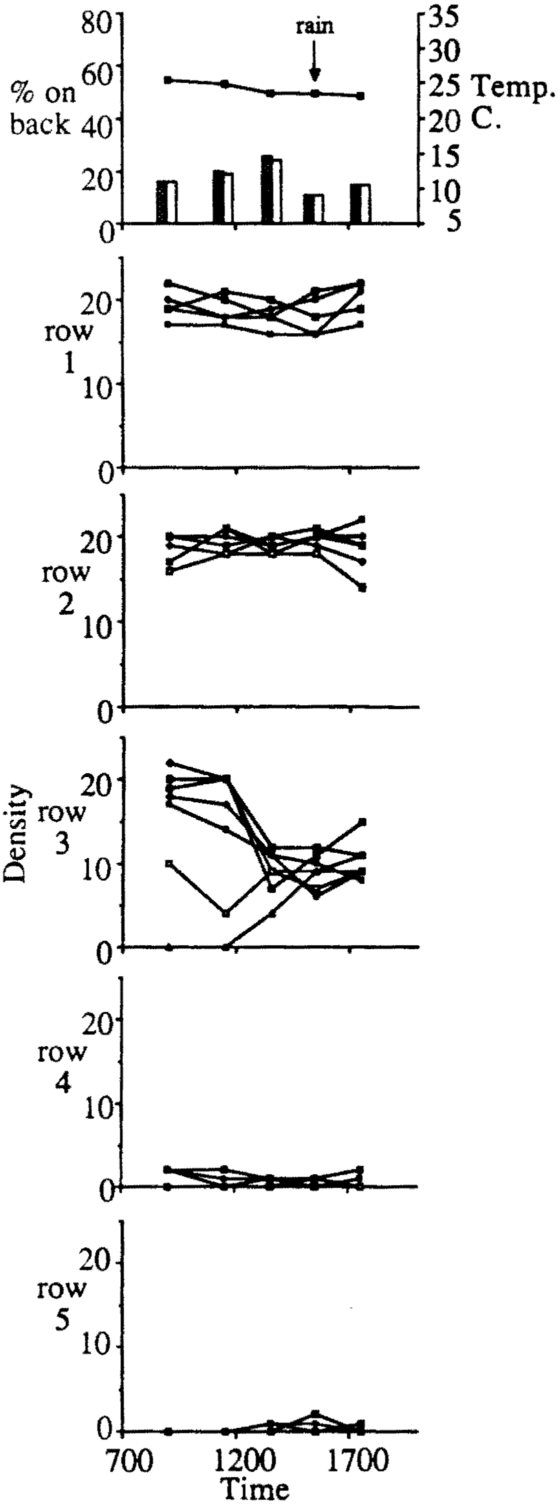


Figure II.1e. September 3

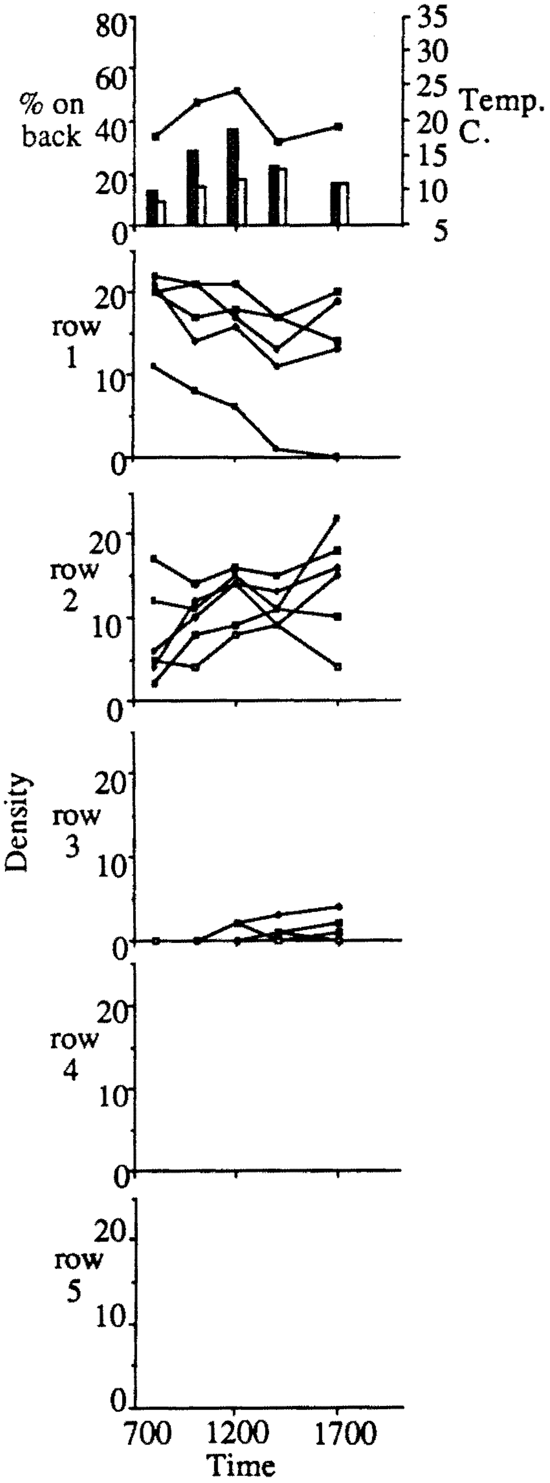


Figure II.1f. September 2

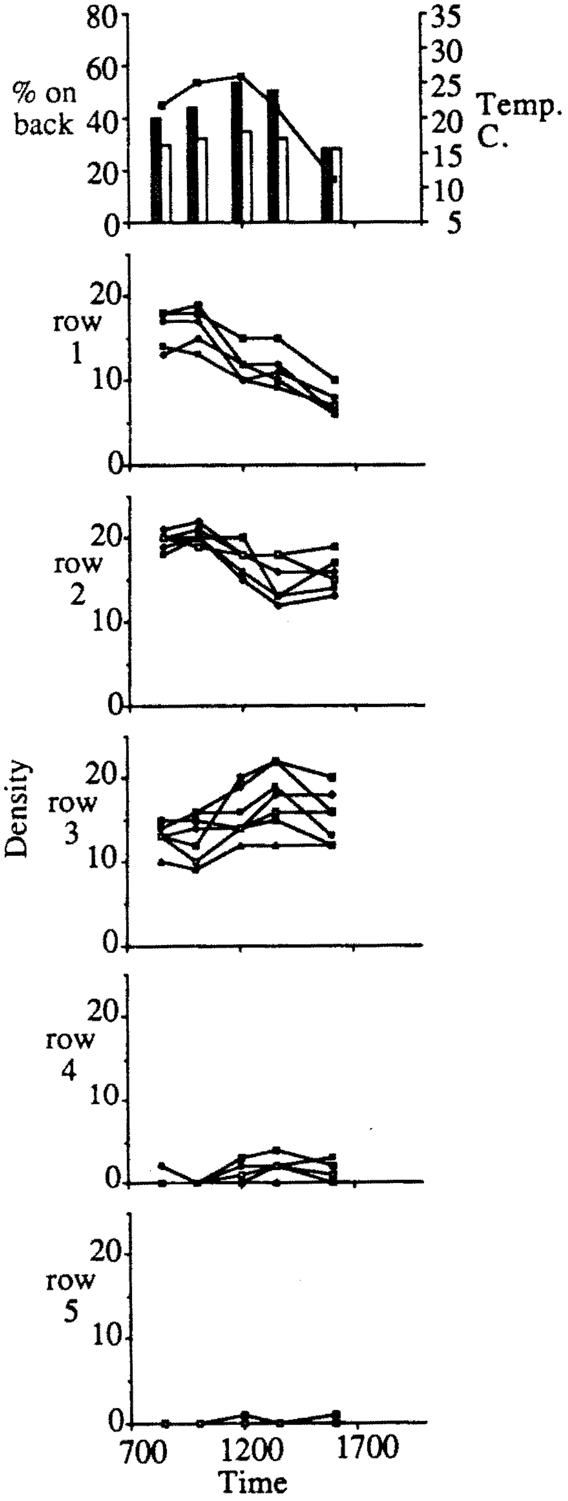


Figure II.1g. August 22

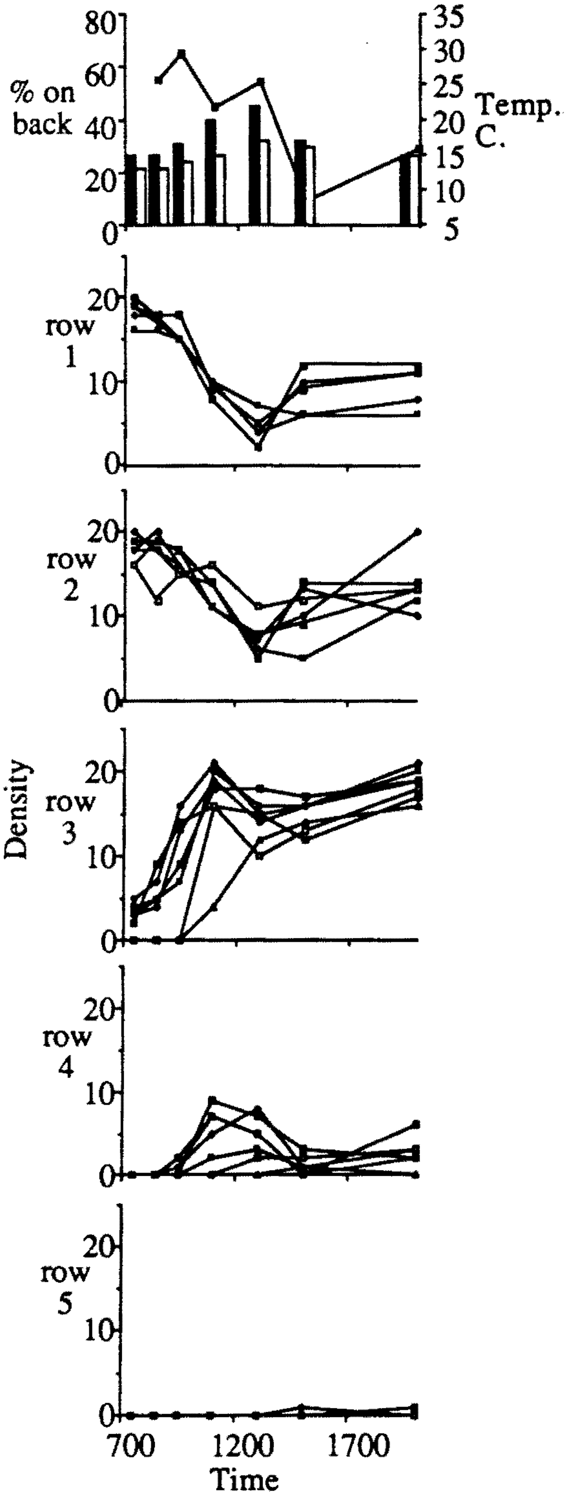


Figure II.1h. September 10

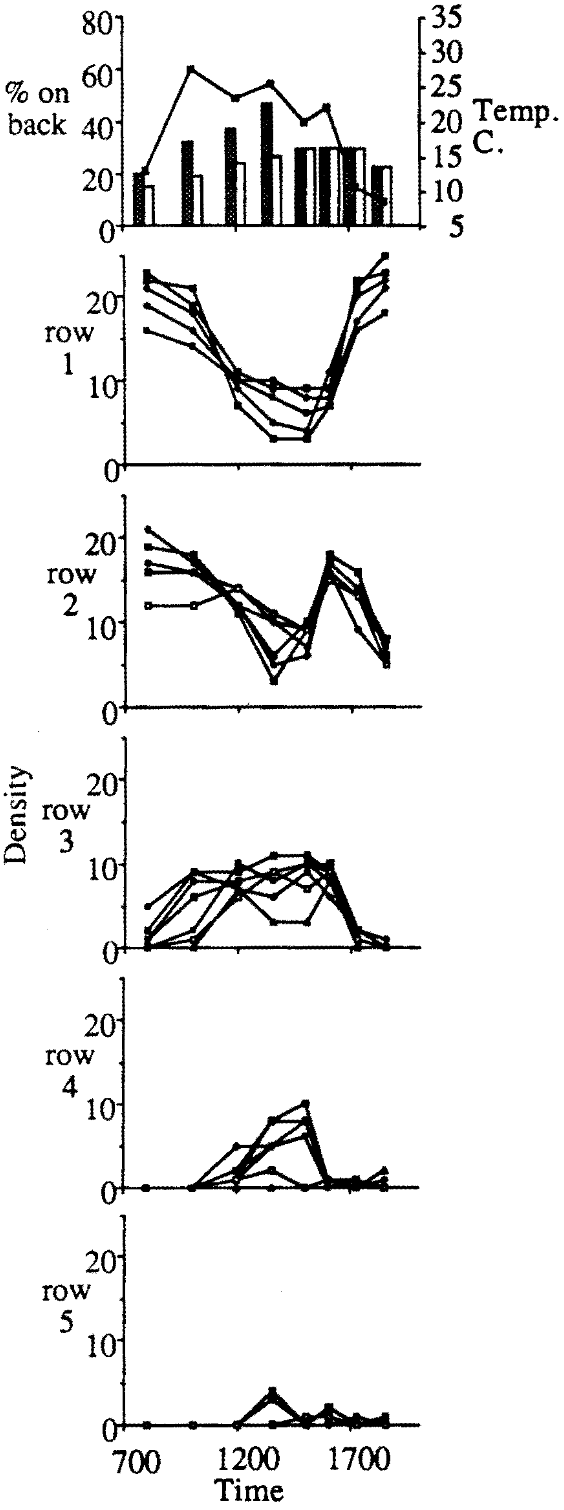


Figure II.1i.September 4

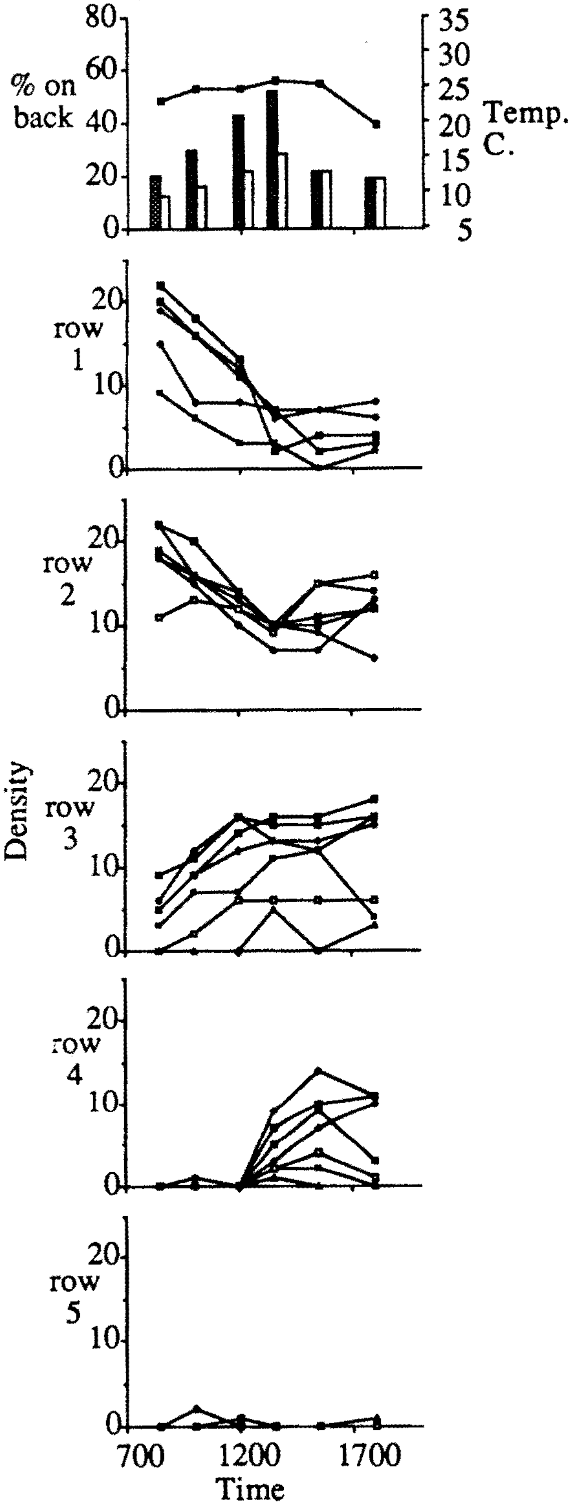


Figure II.1j. September 6

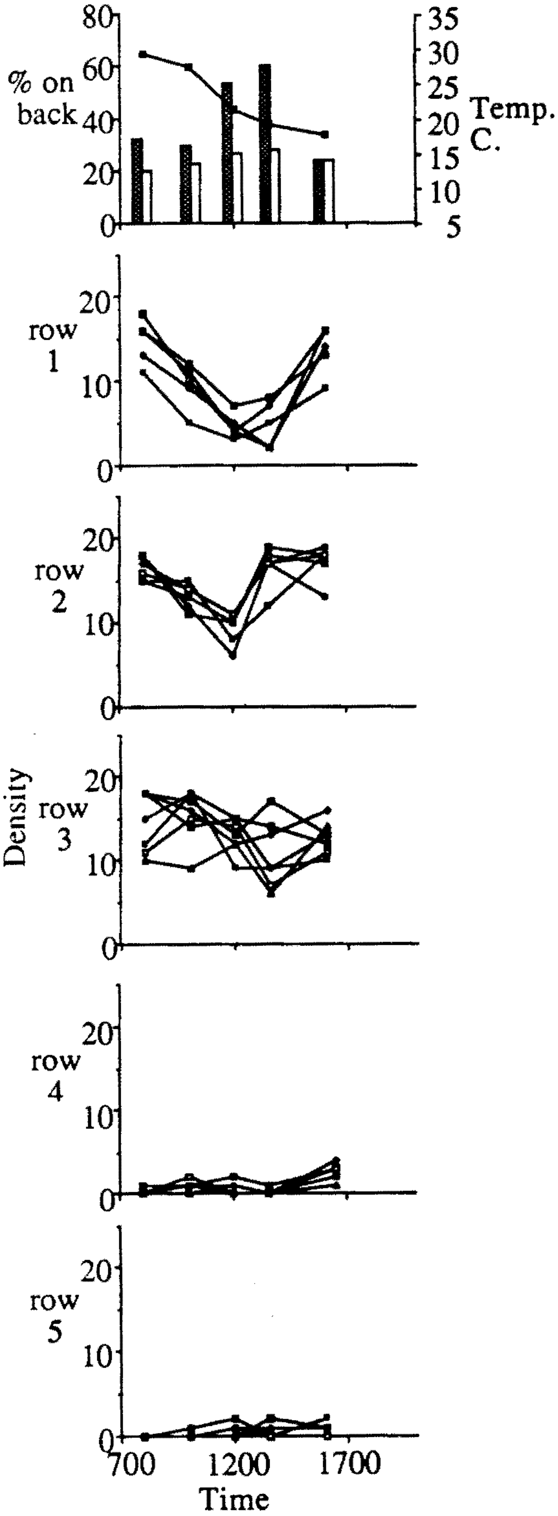


Figure II.1k. September 5

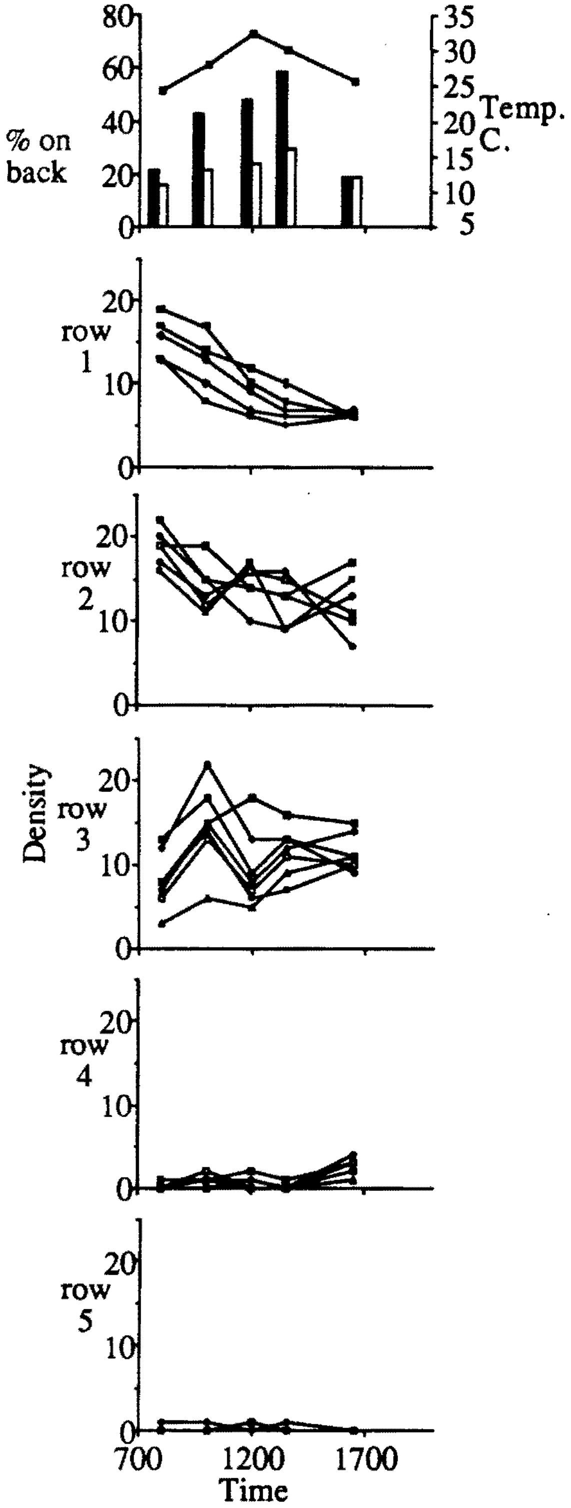


Figure II.1l. September 8

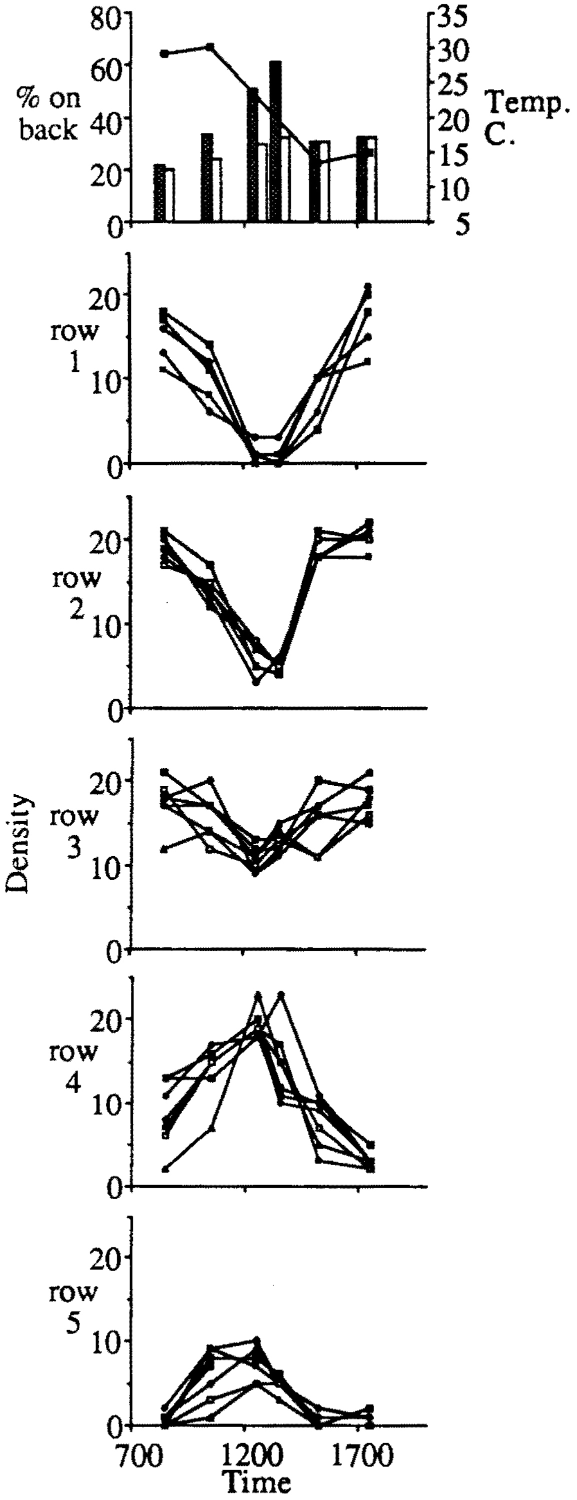


Figure II.1m. August 21

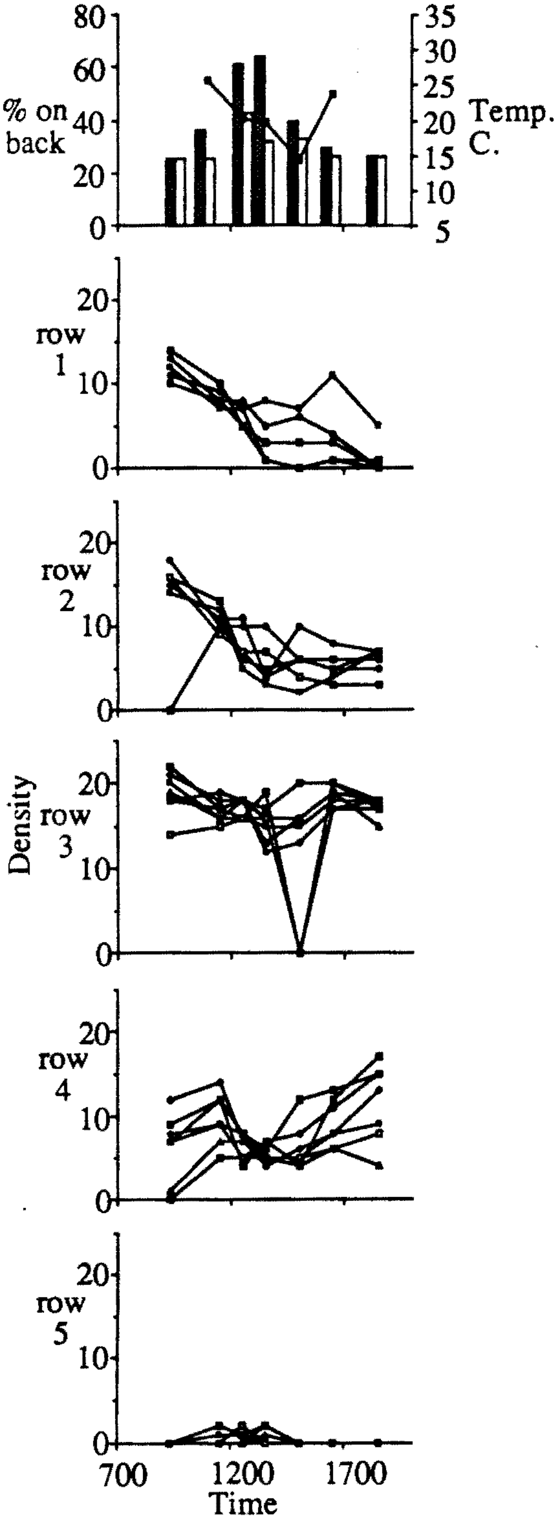


Figure II.1n. August 16

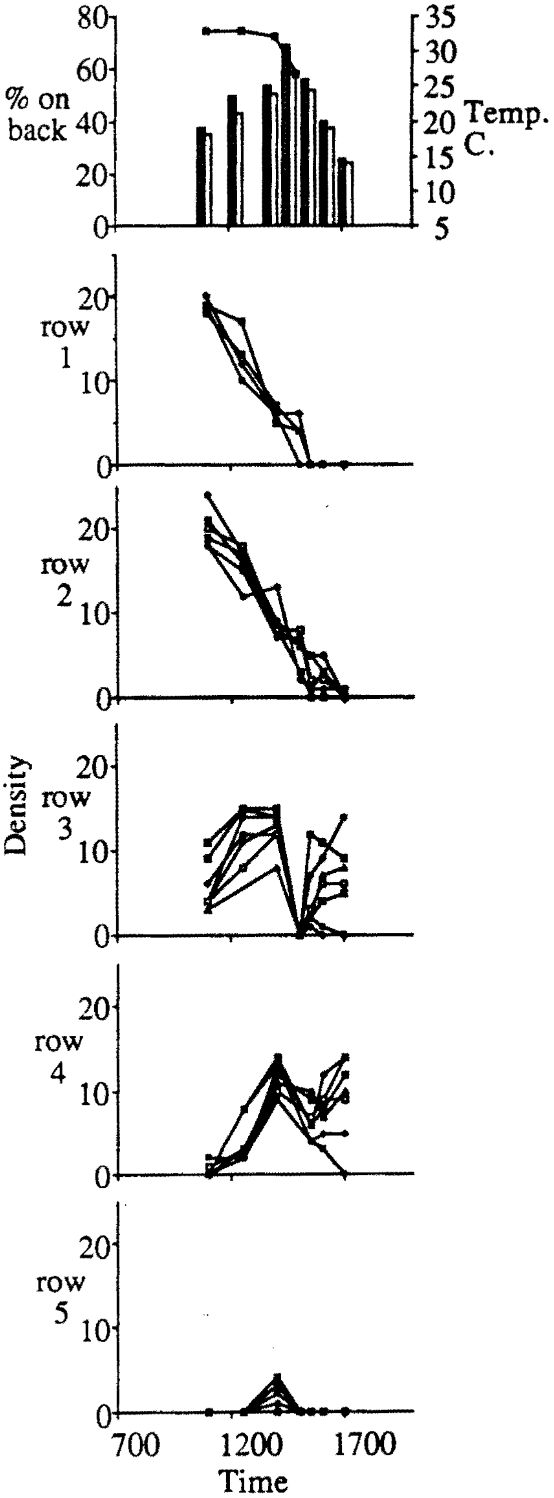


Figure II.1o. August 25

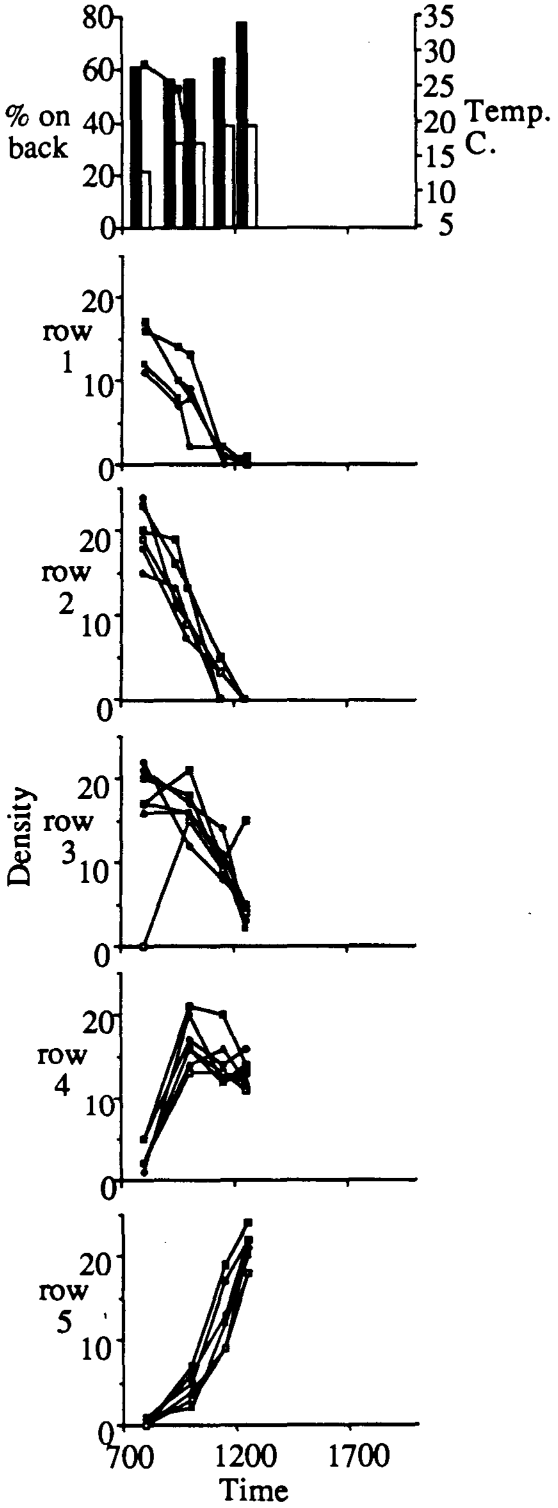


Figure II.2. Relationship between density of walrus groups and temperature. Data presented were collected at the maximum temperature of each day, and were restricted to row 1. Each point represents the mean number of walruses in six plots during one sample day.

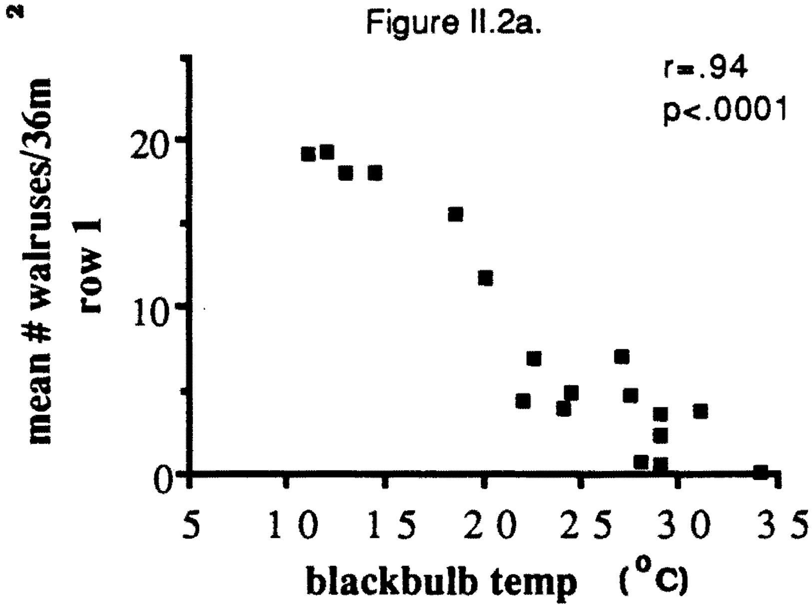


Figure II.2a.

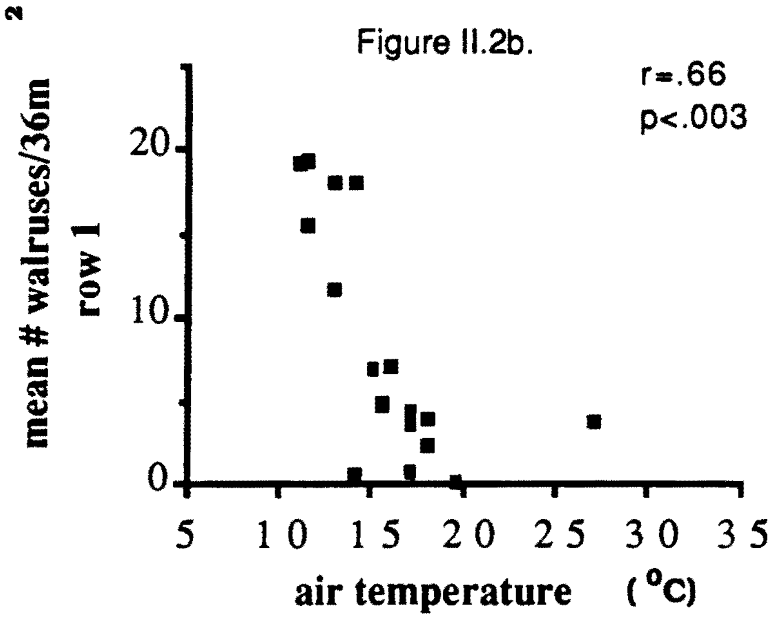


Figure II.2b.

Figure II.3. Relationship between posture and temperature. Data presented were collected at the maximum temperature of each day, and were restricted to row 1. Data were excluded when less than 10 walruses were present in that row. Each point represents one sample day.

Figure 3a.

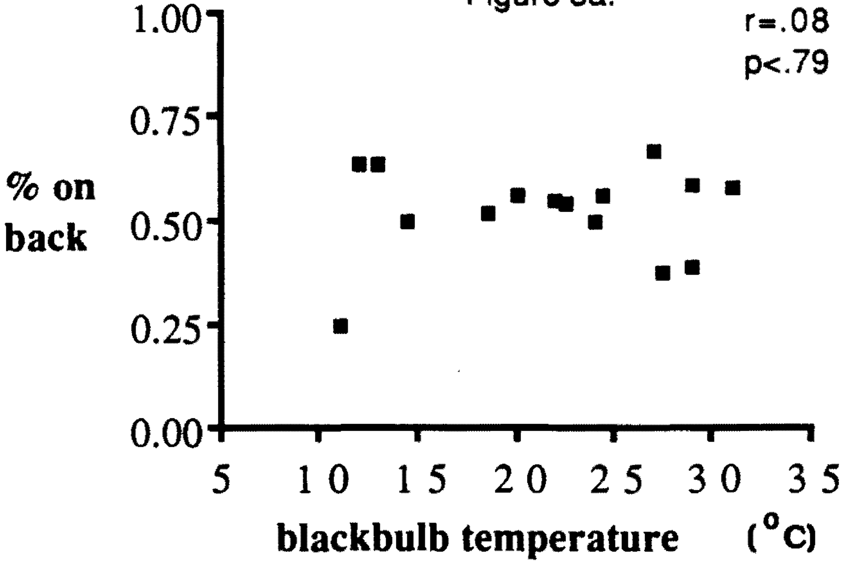


Figure 3b.

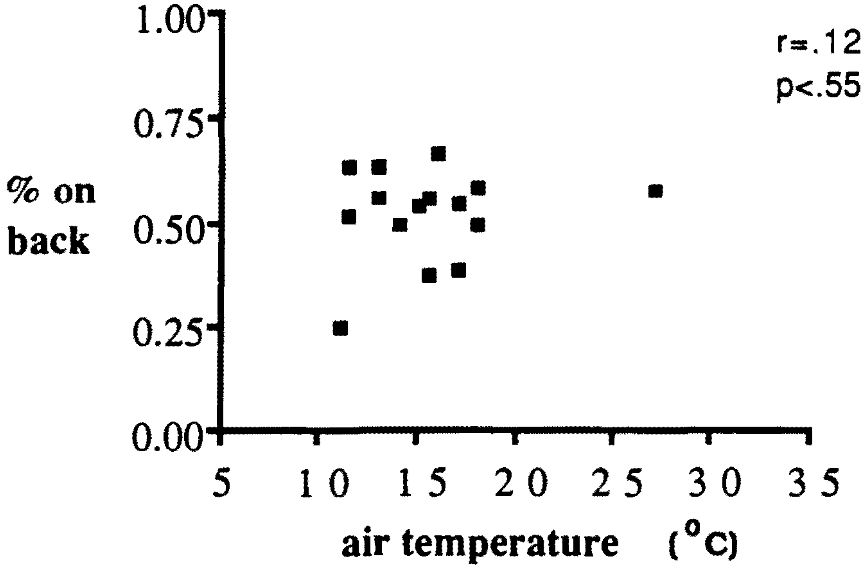


Figure II.4. Relationship between the proportion of walruses extending flippers and temperature. Data presented were collected at the maximum temperature of each day, and were restricted to row 1. Data were excluded when less than 10 walruses were present in that row. Each point represents one sample day.

Figure 4a.

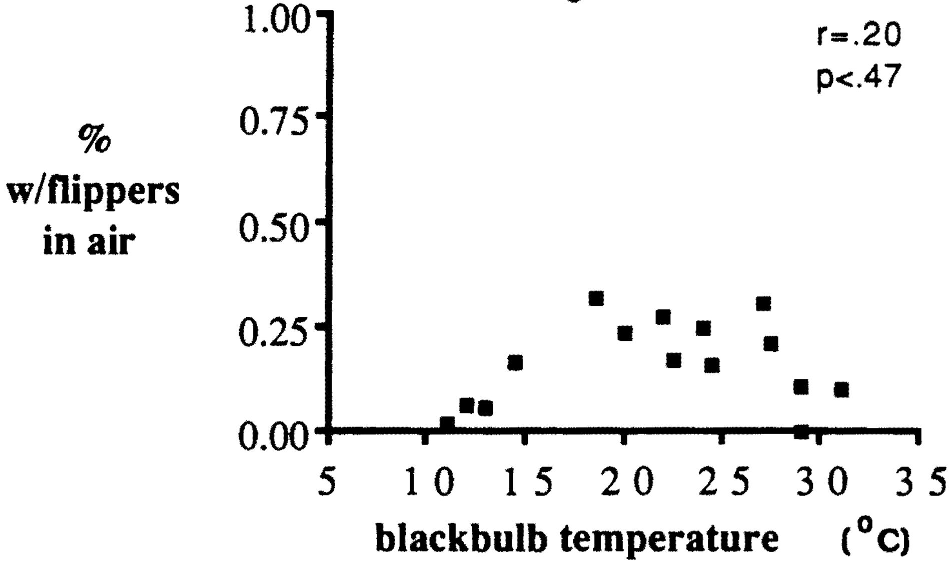
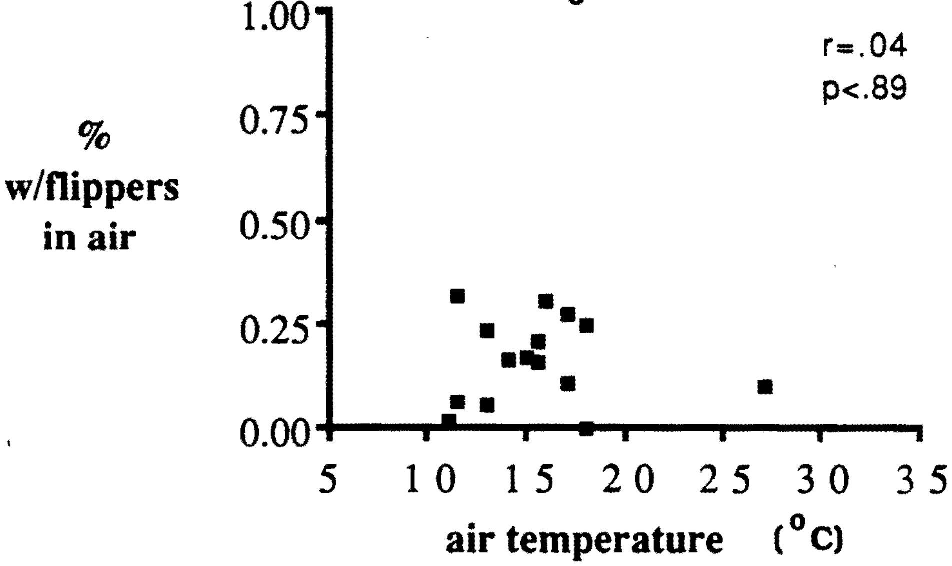


Figure 4b.



CHAPTER III

DENSE WALRUS GROUPS. II.

A THERMOREGULATORY COST OR BENEFIT?

I have presented evidence that walrus (*Odobenus rosmarus divergens*) groups create a hot microclimate (Chapter II). In this chapter I will discuss possible relationships between thermoregulatory behavior and the evolution of walrus groups.

Since the marine environment is where their food resources are located, one might ask why pinnipeds leave the marine environment at all. The amphibious life of pinnipeds is generally viewed as a compromise between two major inflexible aspects of their life history: terrestrial parturition and marine feeding (Bartholomew 1970; Gentry 1973). In comparison to cetaceans, pinnipeds might be viewed as being stuck on a lower adaptive peak (using the terminology of Wright 1932), while cetaceans occupy a higher adaptive peak which emancipates them from the terrestrial environment.

Female otariids, following parturition, alternate between nursing their pups on shore and replenishing energy reserves by foraging at sea. Variations to this general pattern have been correlated to ecological parameters (Gentry and Kooyman 1986). Consistent with other otariids, walruses alternate between the marine and terrestrial (or pack ice) environments (Fay 1982). However, the concept that amphibious life in walruses is caused by an inflexible compromise between marine feeding and terrestrial parturition is not adequate for several reasons: 1)

Walruses are emancipated from the land-sea movements associated with parturition in other otariids. Walruses give birth on the pack ice (and may occasionally give birth in the water; Fay 1982) and the calves are immediately capable of traveling with their mothers (Fay 1982) and nursing aquatically (Miller and Boness 1983). Thus, female walruses do not need to leave the marine environment in order to return to a nursing calf. 2) Amphibious life of walruses is not restricted to the reproductive season or only to females. Male walruses leave the marine environment during the non-breeding season to come ashore at terrestrial locations. If terrestrial parturition is not an adequate explanation for why walruses leave the marine environment, is thermoregulation an alternative explanation?

The energy conservation hypothesis: do walruses reduce their metabolic rate by leaving the marine environment? Water is approximately ten times as heat conductive as air (Irving and Hart 1957); therefore it is reasonable to hypothesize that walruses reduce heat loss by leaving the marine environment to rest in the thermally less demanding terrestrial (ice) environment. For the purposes of discussing this hypothesis, I assume the following: 1) Walruses alternate between periods of feeding and resting. 2) Walruses can rest in either water or air (pers. obs.; Miller and Boness 1983). 3) During time spent resting walruses minimize energetic costs by minimizing metabolic rate. An energetic cost/benefit analysis would predict that walruses leave the feeding grounds and rest on shore when the following is true:

$$K_{travel} + K_{fasting} < (M_{water} - M_{shore}) T_{rest} \qquad (1)$$

Where K_{travel} = costs of traveling from the feeding grounds to shore; $K_{fasting}$ = amount of prey not consumed while traveling; M_{water} = metabolic rate while resting in water; M_{shore} = metabolic rate while resting on shore; and T_{rest} = duration of a rest period.

Travel costs for swimming pinnipeds are low compared to other types of locomotion (i.e., walking or flying; Gold 1973). As the body size of marine organisms increases, the energetic costs of swimming converges on basal metabolic rate (Brodie 1975). Since walruses are large, the cost of travel is probably low. However, pinnipeds with much smaller body size than walruses can maintain thermoneutrality in ice water at basal metabolic rate (Irving and Hart 1957; Hart and Irving 1959; Lavigne et al.1976; Gallivan and Ronald 1979). Thus M_{water} - M_{shore} is always equal to zero and the above inequality is never true. The only instances when M_{water} - M_{shore} may not equal zero are: 1) at extremely low air temperatures when heat loss in air may exceed heat loss in water, in which case M_{water} - M_{air} would actually be negative (Pierotti and Pierotti 1980); and 2) at warm air temperatures when thermoneutrality is exceeded, again resulting in a negative number.

From this simple analysis it seems likely that forming dense walrus groups can be rejected as an energy conservation behavior, since leaving the marine environment does not even save energy (however see discussion below).

The warm skin/energy conservation hypothesis: do walruses need to leave the marine environment to warm the *skin*? The preceding analysis assumes that skin temperature in cold water is close to water temperature. Although pinnipeds are endothermic, this is accomplished to a large degree by vasoconstriction and vasodiolation in the blubber and skin, which makes these tissues heterothermic (Irving and Krog 1955; Irving and Hart 1957). Although the skin of pinnipeds may be cold for long periods of time, it does not appear to have special mechanisms to allow it to regenerate at low temperatures (Feltz and Fay 1966). Tissue cultures of several species of pinnipeds would not undergo mitosis at low temperatures (Feltz and Fay 1966). Regeneration of peripheral tissues may be an explanation for why pinnipeds leave the marine environment (Laws 1956; McLaren 1958; Fay and Ray 1968). If we assume that the skin temperature periodically needs to be warmed for tissue regeneration, the energetic cost/benefit analysis of leaving the marine environment may change considerably. Peripheral vasodiolation is necessary to warm the skin in cold water; this results in a reduction in the insulative properties of blubber, causing immense heat loss. If warming the skin is necessary for walruses, then leaving the marine environment seems reasonable from an energetic standpoint.

Whether forming dense groups might result in additional energetic savings will be addressed under the next hypothesis. First I want to point out several potential problems with the epidermal regeneration hypothesis.

1) Many pinnipeds apparently spend long periods of time at sea without resting in air (Stirling 1983). This demonstrates that frequent hauling out in air is not obligate for all pinnipeds.

2) Cetaceans can apparently regenerate their peripheral tissues in cold water. A prediction for future studies is that there should be physiological differences in the ability of pinniped and cetacean skin to regenerate at low temperatures.

3) Pinniped epidermal cells can remain at cold temperatures for long periods of time (e.g., harbor seal, *Phoca vitulina*--26 weeks, Steller sea lion, *Eumetopias jubata*--8 weeks; Feltz and Fay 1966). A prediction of these observations is that pinnipeds should emerge from the water infrequently, especially if distance to the resting grounds is large (i.e., travel time is costly).

4) Pinnipeds (at least some species) might have mechanisms which allow epidermal growth in cold water, that would not be evident from tissue cultures: a) Since northern fur seals (*Callorhinus ursinus*) are pelagic except during the breeding season (Gentry 1981), they apparently have a mechanism(s) for regeneration of peripheral tissues. Their thick pelage may make it possible for them to achieve high skin temperatures even in cold water. b) Although not previously suggested for a pinniped, warming of the skin might be possible if only small parts of the body are warmed at a time. A well know process associated with vasoconstriction in diverse taxa of mammals is Lewis's Hunting Reaction (Folk 1974). Cooled extremities periodically have bouts of vasodiolation that result in peaks in skin temperature (Folk 1974); this process might function to maintain epidermal growth in pinnipeds.

The warm skin/neighbor contact/energy conservation hypothesis. If walruses can warm their skin for less energetic costs in air than water, does making contact with neighbors save *additional calories?* Laboratory studies of harbor and harp seals (*Pagophilus groenlandicus*) show that both can attain high skin temperatures at low air temperatures, without making contact with other seals and without increasing metabolic rate above basal (Irving and Hart 1957). Harbor seals had skin temperatures of approximately 20^0 C and 20^0-30^0 C at -10^0 and 10^0 C ambient respectively; harp seals had skin temperatures of 20^0 C at 10^0 C ambient (Irving and Hart 1957). Captive juvenile walruses showed similar skin temperatures; a juvenile female (aged one month-two years, weighing between 54-245 kg) had skin temperatures between 13^0-32^0 C at 10^0 C ambient; a juvenile male (weighing 500-600 kg) had skin temperatures of 18^0-27^0 C at 10^0 C (Ray and Fay 1968). Since the adult walruses in my study were considerably larger than these seals (which weighed 20-40 kg) or the juvenile walruses, I feel it is conservative to predict that solitary wild walruses should also be able to achieve high skin temperatures at basal metabolic rate even at the lowest temperatures I observed. Therefore, no additional energy should be saved by making contact with neighbors and I reject the hypothesis that walruses make contact with neighbors to regenerate their skin at basal metabolic rate.

I have demonstrated that walruses form dense groups even when it is unlikely to be thermally beneficial. I propose the following hypotheses:

1. *Making contact may be maladaptive.* One view might be that dense walrus groups formed to conserve energy during arctic winters, and that the phenomena is not adaptive during warm months of the year. This explanation is weak for several reasons:

a) Walrus groups are larger on terrestrial locations during summer than on the ice during winter (Fay and Ray 1968; Estes and Gilbert 1978; Wartzok and Ray 1980; Fay 1982).

b) During subfreezing temperatures, heat loss may be greater in air than in water (Lavigne et al. 1976; Pierotti and Pierotti 1980). Walruses would not be predicted to leave the marine environment at all during these conditions, but should instead form groups in the water.

c) This hypothesis implies that forming dense groups is a fixed trait, and that walruses are not able to learn how to modify their inter-individual distance. Through operant conditioning, California sea lions (*Zalophus californianus*) can learn to reduce their heat load by pushing a lever which activates a shower (Whittow et al. 1971). This demonstrates that at least some pinnipeds are able to learn how to modify their thermal environment.

d) The spacing pattern of numerous mammalian species has been shown to be very flexible, responding to subtle changes in ecological and physical parameters (Estes 1969; Brown and Orians 1971; Jarman 1974; Camenzind 1978; Bowen 1981; Bekoff & Wells 1982; Kruuk & Parish 1982; Mills 1982; Macdonald 1983; Zabel 1986). Since forming dense groups is a type of spacing pattern, I see no a priori reason to view the formation of dense walrus groups as being an inflexible behavior. The correlation between temperature and density in my study demonstrated that the phenotypic expression of walrus grouping behavior is flexible.

2. *Walruses may make contact for reasons other than heat*

conservation. Interspecies comparisons between pinnipeds do not support the hypothesis that contacting neighbors is a heat conservation adaptation. Walruses are the only ice breeding pinniped that make contact, but this behavior is common among pinnipeds living in warmer climates (Stirling 1975, 1983). Thus heat conservation is not an adequate explanation for contact behavior among pinnipeds.

First let us assume that the primary reason walruses have to come ashore is to warm the skin[1]. Making contact with neighbors may have secondary benefits that are independent of thermoregulation. For example, the role of predation (by primitive man or polar bears) may have been important. Dense walrus herds might be an extreme example of a selfish herd where each individual tries to minimize the probability it will be consumed and thus tries to move to the center of the herd (Hamilton 1971).

The role of parasites as an evolutionary force has recently received much attention (Bell 1980, 1982; Hamilton and Zuk 1982). Few ectotherms could tolerate the dramatic temperature change that occurs when walruses leave the cold arctic water and join a dense herd on land (or ice). Thus forming dense groups might be viewed as a behavior mechanism to "bake off" ectoparasites. Although body contact has not previously been suggested to be an anti-parasite mechanism, many species have behavioral mechanisms such as grooming to reduce parasites (Sparks 1967).

---

[1] Alternative primary reasons might be to escape marine predators or for information exchange (see Chapter V).

3. *Making contact may allow walruses to minimize their time ashore.* I have argued that once a walrus leaves the marine environment, making contact will not save additional energy because high skin temperatures can be achieved even at cool ambient temperatures at basal metabolic rate. All of the energetic arguments so far have concerned the parameters on the right side of equation I (M_{water}- M_{shore}). An additive hypothesis might be that the amount of time ashore (T_{rest}) is costly because it is time not spent feeding. Skin tissue cultures showed that maximum mitotic rates occurred at 37^{0} C (Feltz and Fay 1966). This temperature is approached only when a walrus is near it's upper critical temperature (maximum vasodiolation occurs near upper critical temperature). Thus individuals in hot walrus groups approach their upper critical temperature, and they may save energy because they can regenerate their skin faster and thus depart for the next foray sooner.

Summary

In this chapter I have argued the following: 1) Walruses cannot save energy by leaving the marine environment unless they are constrained by an inability to regenerate their skin at low skin temperatures. 2) After leaving cold water, no additional benefit can be accrued by making contact with neighbors. 3) Thus the most likely explanation for dense walrus groups is that they evolved for reasons independent of heat conservation, or that by approaching upper critical temperature walruses reduce their time on shore.

BIBLIOGRAPHY, CHAPTER III

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.

Bekoff, M. and Wells, M. C. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use and resource defense. *Z. Tierpsychol.* 60:281-305.

Bell, G. 1980. The costs of reproduction and their consequences. *Am. Nat.* 116:45-76.

Bell, G. 1982. The Masterpiece of Nature: The Evolution and Genetics of Sexuality. University of California Press, Berkeley.

Bowen, W. D. 1981. Variation in coyote social organization: the influence of prey size. *Can. J. Zool.* 59:639-652.

Brodie, P. F. 1975. Cetacean energetics, an overview of interspecific size variation. *Ecology* 56:152-161.

Brown, J. L. and Orians, G. H. 1970. Spacing pattern of mobile animals. *Ann. Rev. Evol. Syst.* 1:239-263.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. Coyotes: Biology, Behavior, and Management. Acad. Press, New York.

Estes, J. A. and Gilbert, J. R. 1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). *J. Fish. Res. Bd. Can.* 35:1130-1140.

Estes, R. D. 1969. Territorial behaviour of the wildebeest (*Connochaetes taurinus* Burchell 1923). *Z. Tierpsychol.* 26:284-370.

Fay, F. H. 1982. Ecology and Biology of the Pacific Walrus, Odobenus rosmarus divergens Illiger. U.S. Dept. Int., Fish &

Wildl. Serv., Wash. D.C. N. Amer. Fauna, no. 74. 279 pp.

Fay, F. H. and Ray, C. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). *Zoologica* 53:19-32.

Feltz, E. T. and Fay, F. H. 1966. Thermal requirements *in vitro* of epidermal cells from seals. *Cryobiology* 3:261-264.

Folk, G. E. 1974. Textbook of Environmental Physiology. Lea and Febiger, Philadelphia.

Gallivan, G. J. and Ronald, K. 1979. Temperature regulation in freely diving harp seals (*Phoca groenlandicus*). *Can. J. Zool.* 57:2256-2263.

Gentry, R. L. 1973. Thermoregulatory behavior of eared seals. *Behaviour* 46:73-93.

Gentry, R. L. 1981. Northern fur seal - *Callorhinus ursinus* (Linnaeus, 1758). Pages 143-1160 in S. H. Ridgway and R. J. Harrison, eds. Handbook of Marine Mammals. Volume I: the Walrus, Sea Lions, Fur Seals and Sea Otter. Academic Press, London.

Gentry, R. L. and Kooyman, G. L. 1986. Fur Seals: Maternal strategies on Land and at Sea. Princeton University Press, Princeton.

Gold, A. 1973. Energy expenditure in animal locomotion. *Science* 181:175-176.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Ther. Biol.* 31:295-311.

Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384-387.

Hart, J. S. and Irving, L. 1959. The energetics of harbor seals in air and in water with special consideration of seasonal changes. *Can. J. Zool.* 37:447-457.

Irving, L. and Krog, J. 1955. Temperature of skin in the Arctic as a regulator of heat. *J. Appl. Physiol.* 7:355-364.

Irving, L. and Hart, J. S. 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. *Can. J. Zool.* 35:497-511.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.

Kruuk, H. and Parish, T. 1982. Factors affecting population density, group size and territory size of the European badger, *Meles meles*. *J. Zool., Lond.* 196:31-39.

Lavigne, D. M., Barchard, W. W., Innes, S. and Øritsland, N.A. 1976. Pinniped bioenergetics. ACMRR/MM/SC/112. FAO Scient. Consult. Marine Mammals. Bergen, Norway. 31 August - 10 September, 1976.

Laws, R. M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. Falkland Islands Dependencies Survey, Scientific Reports, No. 13.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379-384.

McLaren, I. A. 1958. Some aspects of growth and reproduction of the bearded seal, *Erignathus barbatus*. *J. Fish. Res. Bd. Canada* 15:219.

Miller, E. H. and Boness, D. J. 1983. Summer behavior of Atlantic walruses *Odobenus rosmarus rosmarus* (L.). at Coats Island, N.W.T. (Canada). *Z. Saugetierkunde* 48:298-313.

Mills, M. G. L. 1982. Factors affecting group size and territory size of the brown hyaena, *Hyaena brunnea*, in the southern Kalahari. *J. Zool., Lond.* 198:39-51.

Pierotti, R., and Pierotti, D. 1980. Effects of cold climate on the evolution of pinniped breeding systems. *Evolution* 34: 494-507.

Ray, G. C. and Fay, F. H. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). *Zoologica* 53:19-32.

Sparks, J. 1967. Allogrooming in primates: a review. Pages 148-175 in D. Morris, ed. Primate Ethology. Morrison and Gibb Ltd, London and Edinburgh.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.*169:205-212.

Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489-527 in J. Eisenberg and D. Kleiman, eds. Advances in the Study of Mammalian Behavior. Am. Soc. Mammal., Spec. Publ. 7.

Wartzok, D. and Ray, G. C. 1980. The hauling-out behavior of the Pacific walrus. U.S. Marine Mammal Commission, Rep. MMC-75/15, 46 pp.

Whittow, G. C., Ohata, C. A. and Matsuura, D. T. 1971. Behavioral control of body temperature in the unrestrained California sea lion. *Comm. in Behav. Bio.* 6:87-91.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. XI Internat. Congr. Genet.* 1:356-366.

Zabel, C. J. 1986. Reproductive behavior of the red fox (*Vulpes*

vulpes): a longitudinal study of an island population. Ph.D. diss., University of Calif., Santa Cruz.

CHAPTER IV

HAUL-OUT BEHAVIOR DURING THE SOUTHWARD MIGRATION: AGGRESSION IN FEMALE AND MALE WALRUSES

Introduction

Parental investment has been defined as any investment by a parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring (Trivers 1972). The reproductive cycle of walruses (*Odobenus rosumaus divergens*) is slow relative to most pinnipeds. Pregnancy lasts 15 to 16 months: there is delayed implantation of approximately four to five months, followed by gestation of approximately 11 months (Fay 1982). The calf then stays with the mother for two years, and some calves nurse for the entire two year period (Fay 1982). Thus, the length of time from conception to the end of the mother calf bond is approximately 39 months. The time and energy requirements of nursing and caring for a walrus calf must have an affect on a female walrus's future reproductive potential. If a female walrus prematurely terminates her parental care, and the calf dies, she wastes her investment up until that time (Trivers 1972). Therefore, one would predict that female walruses should be extremely protective of the calves which they invest so much time in rearing.

The few observations that have been made of cow and calf walruses on the pack ice indicate that this is true. It has been reported that the "attachment of mother and calf is absolutely unbreakable, even after one or the other has been killed, unless the carcass is removed" (Brooks 1954: p. 53). Walrus cows are highly solicitous of their offspring, their separation rarely occurring except under the most "frightening circumstances" (Fay 1982). During 50 encounters with Eskimos hunting cows with calves, cows became separated from their calves in only six instances (Fay 1982). "Cows often pushed calves into the water before entering themselves", and young animals were often "herded" away by older walruses when they became alarmed (Burns 1965: p. 32).

Most behavioral studies have been conducted on animals that haul out in all male aggregations along the Alaskan coast (in the Bering Sea, Miller 1975, 1976) and along the Siberian coast (in the Bering and Chukchi Seas, Fay 1982). The behavior of female walruses has been largely unstudied because they usually remain associated with the inaccessible pack ice. Walrus herds of mixed sex and age haul out on the Punuk Islands (63^{0}05'N 168^{0}49'W) (near the east end of St. Lawrence Island, Alaska) as they migrate south ahead of the advancing sea ice in the autumn. Due to severe weather and difficult access, the animals that come ashore onto Punuk Island had never before been studied. We (S. J. Taggart, C. Zabel and B. Kelley) were able to observe animals on Punuk Island from 1 October through 4 December 1981. Our broad objectives were as follows: 1) Observe female/calf associations and measure the costs of bringing walrus calves ashore into dense groups of conspecifics. 2) Observe intersexual interactions immediately preceding the breeding season and determine if male and female walruses segregated or formed mixed herds when they hauled out together on land. 3) Determine the timing of the haul-out at Punuk Island

Methods

Walrus observations were made with the aid of binoculars and spotting scopes. The following data were collected:

1. Number of walruses ashore. The total number of walruses on Punuk Island was estimated most days from a vantage point approximately 50 m in elevation about one half km away from the hauling ground. The lack of topographic relief and the large numbers of animals made estimates of the herd size difficult. Three observers made independent estimates and then an average was taken. To facilitate censusing, we erected drift wood posts at 25 m intervals perpendicular to the field of view near the haul out. Using this grid, the animals that occurred within 625 m^2 could be counted and then the herd size could be extrapolated based upon the number of grid sections that the herd occupied.

2. Behavior of walruses entering the herd. Individual walruses were observed as they attempted to enter the herd on shore (using focal animal sampling, Altmann 1972). Observations began when a selected walrus landed on the beach. We recorded the time from initial landing to when the walrus either swam away, or joined the herd. We terminated each sample when the subject had made body contact with an animal in the herd and had not interacted with another walrus for 60 seconds (to avoid collecting data on sleeping animals). We estimated the sex and age class of the animal (as calf/yearling, 2-4 year old, or adult)

and noted whether it had a calf. Calves/yearlings included dependent young who were small, very dark in color, and had no visible tusks; 2-4 year olds were larger, had lighter and browner coat color, and the tips of the tusks were visible (Fay 1982). Once the walrus had made physical contact with the herd, we recorded the number of jabs it dealt out, the number of jabs it received, the number of walruses which were displaced by the subject walrus, and the number of walrus body lengths the animal moved through the herd.

3. Dyadic interactions. We sampled different sex/age class walruses that were interacting with other individuals. Tusk and body size of the two animals were ranked relative to each other. Walruses were ranked as being much smaller (-2), moderately smaller (-1), of about equal size (0), moderately larger (+1), or much larger (+2) than their opponent (see Miller 1975). The behavior of the subject walrus and the response of the interactant were recorded as: jab, threat, move, displacement, interaction with a third walrus, or no response. A sample was terminated when neither walrus had interacted with the other for 60 seconds.

4. Costs of resting in the herd. We sampled various sex/age class animals within the herd for five minutes each, and recorded the frequency of tusk jabs dealt, jabs received, threats received, and threats dealt. Animals were selected to make sure that both sexes and all age classes were represented. A tusk display was classified as a threat following Miller (1975, 1976), i.e., a walrus either holding it's tusks in a horizontal upright position, or swinging them vertically at the opponent without making physical contact. Whenever calves were observed receiving jabs, we

recorded the mother's response (i.e., whether she jabbed back, threatened the opponent, or did not respond) and the sex/age class of the walrus which did the jabbing.

5. Nursing behavior. Whenever nursing bouts were visible along the edge of the herd, we recorded the number of interruptions, the causes of interruptions, and if the mother, calf, or another walrus caused termination of the nursing bout. Nursing bouts were not recorded in the center of the herd due to poor visibility.

6. Mortality. The carcasses of recently killed walruses were sexed, aged, and tagged whenever the herd temporarily departed the island. Fresh calf carcasses were collected, and six of these were necropsied.

Results

Number of walruses ashore. Beginning in early October, there were several hundred male walruses ashore, but larger numbers of walruses (in the thousands) did not arrive until one month later (Fig. IV.1). The total number of individuals increased substantially on 6 November, and then declined four days later. This first peak in the number of walruses ashore was followed by two additional peaks. The total number of walruses peaked at approximately 10,000-18,000 on November 16 (Fig. IV.1).

All the animals ashore in October were males, and the proportion of females in the herd increased from early November until 16 November, at which time females predominated. On 8 November, the herd consisted of 70% males, 15% females, and 1-2% calves. By 20 November, the proportion of females had increased to 52% with 10% calves and 29% males.

Females with and without calves joined with the males in a continuous herd on the flat, sandy beach of Punuk Island. Regardless of the sex composition of the herd, the animals formed one group.

Behavior of walruses entering the herd. Although females joined the mixed group of walruses, females with calves appeared to be more hesitant to do so than females without calves. Significantly fewer females with calves that attempted to join the herd actually did so than females without calves (Fig. IV.2a). Females with calves often landed on the beach, surveyed the herd, and then swam away. On the other hand, females without calves and males behaved similarly when entering the herd. Moreover, among those walruses entering the herd, females with calves took more time to join the herd than did males or lone females (Fig. IV.2b).

Once newly arriving walruses made contact with the herd on land, they had to find an area among the densely packed animals in which they could rest. This involved climbing over hauled-out animals until the intruder successfully displaced a resident animal. Females with calves and males were more aggressive than females without calves while attempting to find a resting place (i.e., they dealt significantly more jabs than did females without calves--Table IV.1). However, females with calves also received significantly more jabs than either males or lone females (Table IV.1). Males displaced more walruses and moved further toward the center of the herd than did females (Table IV.1).

Dyadic interactions. We further investigated aggressive differences among the sexes by sampling encounters between individuals that were established in the herd. Females accompanied by calves dealt more jabs during encounters than did males or females without calves (Chi. sq.=12.8, p<.001, 2 d.f., Fig. IV.3a). This trend remained even when walruses of equal size were compared (Chi. sq.=15.1, p<.0005, 2 d.f., Fig. IV.3b). Females with calves were displaced by other walruses less often than males or females without calves, when interacting with all size classes of animals (Chi. sq.=7.3, p<.02, 2 d.f., Fig. IV.3a). However, there was no significant difference in displacement rates between females with calves, males, or females without calves when interacting only with walruses of equal size (Chi. sq.=1.3, p<.53, 2 d.f., Fig. IV.3b). These data suggest that females with calves were more aggressive, and that they lost space or were forced to move less often than were males or females without calves. Such aggressive female behavior probably helped protect calves from injury. Calves had difficulty climbing over the bodies of adult walruses and such movement was likely to provoke a strike directed at the calf. Therefore, females with calves avoided risking injury to their offspring by fighting for space and remaining stationary.

To further determine if there were sex differences in aggressive behavior, we sampled agonistic interactions between the following categories of pair-wise encounters: male-male, female-female, and female-male. We calculated the proportion of interactions in which at least one strike was dealt, and the proportion of encounters in which one walrus displaced the other. No significant differences existed among the three sets of paired interactions (Chi. sq.=.31, p<.86, 2 d.f., for strike; Chi. sq.=2.9, p<.24, 2 d.f., for displacement; Fig. IV.4a). No change was apparent in the results when only pairs of animals which were equal in size were used in the analysis (Chi. sq.=1.6, p<.46, 2 d.f., for strike; Chi. sq.=4.4, p<.11, 2 d.f., for displacement; Fig. IV.4b). The proportion of interactions with strikes that featured strikes by both animals was 5.9% for male-male, 8.3% for female-male, and 9.8% for female-female (Table IV.2). These differences were not significantly different (Chi. sq.=.83, p<.66, 2 d.f.), and indicate that male-male fights were no more intense than female-female or male-female fights. These data are similar to those obtained by others (Miller 1975, 1982; Salter 1980) as indicated in Table IV.2. However, these data may mask interesting differences in aggression because females with calves appear to be more aggressive than males or females without calves, and females without calves appear to be no different than males.

In all-male walrus herds, body size, and to a lesser extent tusk size, are the most important determinants of the outcome of agonistic encounters (Miller 1975). Our data were analyzed to determine if this was true in mixed herds, using relative body and tusk size as the independent variables. As expected, walruses with larger tusks and/or body size dealt strikes more frequently than did smaller walruses with smaller tusks (Chi. sq. p<.0001, Fig. IV.5a). Walruses with smaller tusks and/or body size were displaced more often than were walruses with larger tusks or body size (Chi. sq. p<.0001, Fig. IV.5b).

Costs of resting in the herd. To determine if different age classes of animals incurred different costs by joining dense groups, we sampled various age and reproductive categories of walruses for five minute periods and recorded the number of jabs dealt and the number of jabs received. These data indicate that two to four year old walruses receive more jabs than any other age class (Fig. IV.6). These animals were much smaller than adults and appeared to have more aggression directed at them than any other age class. They retaliated less with reciprocal jabs than did the adults. Calves and yearlings received an average of 2.4 jabs per hour. Although they received fewer jabs than adults, young animals that were jabbed were more likely to be severely hurt because their skin is much thinner than that of adult walruses, and they weigh an order of magnitude less than adults. (Skin thickness is approximately 9 mm in one month old calves, 13 mm in 3 year olds, and 35-40 mm thick in adults, Fay 1982.) Adults are further protected from jabs by the thick shield of skin on their necks whereas calves and young walruses have no such protection. Therefore, the consequences of jabs to young animals probably is severe.

Females accompanying calves were observed opportunistically to determine whether they directed their aggression toward protecting their offspring. The mothers of calves usually showed no response when their calf was struck by another walrus (Table IV.3). Only one female out of 31 observed reacted to her calf receiving a jab by jabbing back at the aggressor, which happened to be a yearling. All age classes dealt jabs to calves and yearlings. Of 30 walruses which were observed jabbing calves, 14 were adult females, 12 were adult males, and 4 were immature animals. Of the 14 females who jabbed calves, two were accompanied by their own calves.

Nursing behavior. Dealing with aggression is only one of the costs associated with bringing a calf into a mixed walrus herd. Mothers also need to nurse their calves. Nursing may be especially important during the migration when young animals travel great distances and probably expend large amounts of energy. The nursing bouts that we were able to observe appeared to be interrupted regularly by disturbances from other walruses (Table IV.4) and were terminated by these disturbances about 25% of the time. These interruptions may be detrimental to the calves.

Mortality. The consequences of bringing calves ashore into a mixed herd of walruses are severe. This is indicated by the following observations. On 23 November, the entire group of walruses departed Punuk Island. Left behind were 119 fresh carcasses. Of these, 40% were calves. In contrast, the maximum proportion of calves among the herd during the period of our observations was approximately 10%, thus indicating a disproportionately high calf mortality. The sex ratio of the calf carcasses was 29 females:19 males ($p<.07$, approximation to binomial, $Z=1.46$). Of 64 adult carcasses, 66% were females. The total number of animals using Punuk Island during this same time period is uncertain because we do not know the rate of turnover of individuals. At Round Island, individuals remain on land for 1-3 days before departing for 7-10 days at sea (Chapter V). At Punuk Island we do not know if the same individuals were present during the entire observation period. Consequently, it is not possible to calculate an overall mortality rate, or to determine whether female mortality was disproportionately high compared to males.

We necropsied six fresh calf carcasses. All appeared to have been trampled and tusk jabbed by other walruses. All had severely hemorrhagic skeletal musculature, so much that no free blood remained in the circulatory system. Two had several broken ribs, one had a prolapsed rectum, and one had a broken scapula.

Seasonal variation in male aggression. We compared interaction rates at Punuk Island with data that Miller (1975) collected during the summer at Round Island in 1973-1974 to determine if there were seasonal differences in male behavior. We hypothesized that walruses at Punuk Island would be more aggressive since our study preceded the breeding season by only one to two months (Fay 1982), and that individuals would be more likely to escalate an interaction into overt aggression by striking the opponent with their tusks. On Punuk Island, 35.6% of the males that were involved in encounters struck their opponent (n=348; Fig. IV.3a). Miller (1975) found that 31.6% of the summering Round Island male walruses struck their opponent when they were involved in interactions (n=3170, Chi. sq.=2.2, p<.14, 1 d.f.). Of 101 male-male encounters on Punuk Island, 68.3% involved striking (Fig. IV.4b); of 1585 encounters on Round Island, 58.2% involved striking (Miller 1975; Chi. sq.=2.5, p<.12, 1 d.f.). Miller (1975) reported that only 4.9% of the interactions involved strikes by both animals; on Punuk Island this percentage was 5.9% (Table IV.2). Similarly, there were no significant differences between aggressive encounters at Punuk Island and those observed in a mixed herd by Salter (1980) at Bathurst Island, N.W.T. during summer 1977 (Table IV.2). Although the data collected on Punuk Island preceded the breeding season by only one to two months, males did not appear to be more aggressive than they were during summer months.

Discussion

In October, the number of walruses on shore at Punuk Island fluctuated between zero and approximately one thousand animals. During November there were three peaks in the census data. Similarly, marked fluctuations in the number of animals ashore have been observed during summer months at male hauling grounds (see Chapter V; Salter 1980). Telemetry data of individual walruses demonstrates that these fluctuations are the result of walruses arriving from and departing to sea in a highly synchronous manner (Chapter V). Census data from Punuk Island suggests that walruses also migrate through the Bering Straits in a highly synchronous manner.

The sex ratio of adult walrus carcasses on the northern beach of Punuk Island during 1978 was 1 male:6 females (n=181; Fay & Kelley 1980). There also was a higher proportion of fetuses per mature female on the northern beach, compared with the western and southern beaches (Fay & Kelley 1980). This led us to hypothesize that female and calf walruses had formed separate herds from male walruses when they came ashore on Punuk Island during 1978. Our observations from Round Island contradicted this prediction, where all individuals demonstrated a strong affinity to join the large main groups. There was no segregation by age at Round Island although there was a tendency for small animals to be displaced toward the peripheral edges of the group as a consequence of agonistic interactions (Miller 1976; Taggart & Zabel unpubl.). At Punuk Island, males were able to move further toward the center of the herd than were females. Thus, females tended to occur on the edges of the group much as young males did at Round Island.

Female walruses were as aggressive as males (e.g., there were no sex differences in the frequency of striking or threatening other animals within the herd; male-male and female-female interactions did not differ in the proportion of interactions involving strikes or displacement). Females with calves were more aggressive than lone females and males (e.g., when joining the herd, females with calves dealt jabs as frequently as males and more frequently than lone females; once established in the herd, females with calves dealt jabs during a higher proportion of interactions and were displaced less often). The aggressive behavior demonstrated by females with calves may function to protect their offspring. Calves received a lower frequency of jabs relative to all other age classes, and this was probably due to the protective behavior of the mother. However, the lack of female response to their calves receiving jabs on Punuk Island is difficult to explain.

Relative tusk size of male walrus opponents is a significant predictor of the number of strikes dealt during encounters (Miller 1975); therefore, walruses seem capable of judging tusk size. Yet aggressive fights occurred between all age classes and both sexes. Male walruses exhibit unusual aggressive behavior by tending to initiate agonistic interactions with smaller individuals (Miller 1975) and as a result, subordinates receive many jabs and threats.

Costs of resting in the herd. Bringing calves ashore into a dense group of walruses is clearly costly. Injuries resulted from aggressive encounters, particularly from the large adult males. Male walruses are 45% heavier than adult females and six month old calves weigh 10% that of adult males (Fay 1982). Calf mortality was disproportionately high relative to adult mortality, and appeared to result from trampling and tusk jabbing by larger walruses. Walruses clearly exemplify an extreme case of the "large parental investment that strongly decreases the parents ability to produce other offspring" (Trivers 1972). Female walruses invest approximately 39 months in each calf. On this basis, it seems reasonable to conclude that loss of a calf is a significant cost.

These are not the first observations of high walrus mortality within herds on land. In November 1978, Eskimos from the village of Savoonga, Alaska reported that many walruses were dying on St. Lawrence and Punuk Islands. Fay and Kelley (1980) surveyed this area the following spring and found that hundreds of walruses had died, and that the main cause of death was traumatization by other walruses. They counted 420 carcasses on Punuk Island and estimated that approximately 32,000 walruses had been ashore on Punuk Island the preceding winter, judging from the total area that had been utilized.

High mortality is not unique to the mixed sex herd on Punuk Island. In September 1975, 150 carcasses were left at Cape Blossum, Wrangell Island after a mixed sex herd of about 36,000 walruses departed (Tomilin & Kibal'chich 1975). Similar mortality occurred at Wrangell Island in 1958 where 50 dead animals remained following the departure of 5000 animals, and in 1964 when 250-300 walruses died after 33,000-35,000 animals came ashore (Gol'tsev 1968).

However, much less mortality has been observed on all male haul-outs. At Round Island where 10,000-14,000 males haul out, we counted only 33 carcasses over a four month period in 1978 (Taggart and Zabel, unpubl. data). On the Inchoun haul-out of northeastern Chukotka, about 10,000 males came ashore in October 1962. Here Gol'stev (1968) observed only eight carcasses.

High mortality of young animals is not unusual on pinniped haul-out areas. Pup mortality ranges from 2-16% in southern elephant seals, *Mirounga leonina* (L.) (Carrick 1962); 2.3-23% in grey seals, *Halichoerus grypus* (Coulson & Hickling 1964); 17-22% in Hawaiian monk seals, *Monachus schauinslandi* (Wirtz 1968); 7-13% in Alaska fur seals, *Callorhinus ursinus* (Anonymous 1969a, 1969b), and 13-26% in northern elephant seals, *Mirounga angustirostris* (Le Boeuf et al. 1972). In all reported species, a proportion of pup mortality is attributed to injuries by adults, including bites and trampling. However, in all cases this mortality is associated with the breeding season. The costs of pup mortality are presumed to be less than the benefits of mating with superior males who can out-compete "marginal" males (Bartholomew 1970; Cox & Le Boeuf 1977). Females will risk losing their pups in the large, preferred herds in order to benefit by leaving more viable offspring that are sired by top ranking males (Le Boeuf & Briggs 1977).

This explanation does not seem to apply to walruses. Breeding occurs on the pack ice during January and February (Fay 1982). Thus, females which brought calves ashore on Punuk Island apparently did not realize any benefits from mating. Male aggression was not elevated at Punuk Island as compared to Round Island, nor were males more aggressive than females. Furthermore, since walruses are biannual breeders, many of the females that hauled out on Punuk Island would not copulate during the upcoming breeding season.

The calf and adult mortality that we observed demonstrates that individuals which join large dense walrus groups do incur considerable costs, thus indicating that group living in walruses is not selectively neutral. Thus, there are two broad evolutionary ways to view walrus groups:

1) Walrus grouping behavior is currently maladaptive. This can be stated as two more specific hypotheses:

a) The intense grouping behavior may be fixed or inflexible. We reject this hypothesis for the following reasons: (1) Even behaviors which appear to be very stereotyped, such as pecking in chicks, have been shown to have considerable plasticity. (2) Grouping behavior is not a single trait, but is a syndrome of behaviors, each of which is likely to at least have phenotypic variability (developmental, learning) if not genetic variability.

b) The intense grouping behavior is currently being selected against. A potential problem with studying walrus behavior is that the population has undergone very large abundance and distributional changes. Historically, walruses hauled out on numerous islands and beaches along the coast of Alaska. Before the early 1900's, there were major hauling grounds at the Walrus Islands, the Diomede Islands, the Pribilof Islands, Amak Island, Hall Island, St. Matthew Island, Besboro Island, and Port Moller (Fay 1957). At the southern edge of their range, walruses were common as far south as Unimak Pass and the Shumagin Islands in Alaska, and Karaginskoi Island (on the east coast of Kamchatka) [see review by Fay (1957)]. These terrestrial herds must have been particularly vulnerable to hunting. In fact, most of the herds at the southern hauling grounds were extensively exploited commercially during the 18th and 19th centuries. Fay (1957) concluded that extinction of the herds at the southern hauling grounds was probably caused by this commercial exploitation. These changes may effect the behavior seen today. For example, the reduction in hauling grounds may have had the effect of: (a) concentrating walruses onto a few inaccessible locations like Punuk Island and/or (b) forcing walruses to migrate very long distances before resting.

2) There are counterbalancing benefits to the costs of grouping. According to Alexander (1974), group living evolves only because the benefits to the individual outweigh the detriments. By this view, calf mortality is a cost to a female walrus that must be outweighed by some advantage derived from being gregarious.

We have shown that both male and female walruses are aggressive and that some individuals that join the group incur high costs. Since tusks are used in aggressive encounters, they are fundamental to these costs. There appear to be parallels between walruses and ungulates in group living and tusk, horn, or antlers function. Among ungulate species in which only males have horns or antlers, the primary function is probably combat between males during the breeding season (Geist 1966, 1971; Lincoln 1972; Clutton-Brock et. al. 1979; Clutton-Brock 1982). However, among species in which both sexes have horns or antlers, the explanations for their functions are more complex. Among African antelope species in which females have horns, the cross sectional area (at the base) is less for females but the length of male and female horns are similar for a given body weight (Packer 1983). Packer argued that the relatively thicker horns of males reduces breakage during male-male combat while the long but thinner female horns are more specialized for stabbing predators. The presence of horns was correlated to body weight, and Packer argued that this reflects a difference in antipredator strategy between large and small females; i.e., females of small species rely on crypticity and flight while large species females will engage a predator in direct combat (Jarman 1974). The presence of horns in African antelope females was also correlated to large group size (Packer 1983) which is considered to be an antipredator behavior (Hamilton 1971). Among cervids, females have antlers only in caribou and reindeer. These species are unusual among cervids because males and females occur in the same herd during the winter. Female antlers in caribou are thought to function as antipredator weapons and in settling intraspecific disputes over food during the winter (Espmark 1964; Barrette and Vandal 1986). Among a group of individually recognizable caribou, antler size was the best predictor (relative to age and sex) of the occurrence and outcome of competition for food (Barrette and Vandal 1986). Another difference between antlered and antlerless species is that reindeer, caribou, and female antelope species with horns all have precocial calves (Clutton-Brock 1982) which follow them shortly after birth (Espmark 1971; Lent 1974).

Tusk-like appendages (tusks, antlers, horns) are rare in marine mammals (occurring only in walruses and the male narwhal, *Monodon monoceros*, Silverman & Dunbar 1980). Although male walruses may use their tusks in male-male combat during the breeding season, there is evidence that tusks serve other functions in this species: 1) Both female and male walruses use their tusks in aggressive contexts outside of the breeding season. 2) The size of female walrus tusks implies that they are not simply a vestigal appendage carried along by selective advantages of male combat. Although female walrus tusks are smaller in cross-sectional area, they are only slightly shorter than a male tusk for a given age (Fay 1982). Since mature males are considerably larger than females, tusk length per body weight of females is actually greater than that of males.

Similar to calves of reindeer, caribou, and female antelope species with horns, walrus calves are precocious. They ride on their mother's back in the water shortly after birth (Fay 1982) and are not left behind on rookeries while the mother feeds, as occurs in most other otariids (Gentry 1986). Aquatic nursing appears to be common in walruses, and is better developed and more frequent than in any other pinniped species (Miller and

Bonness 1983).

In addition to predator protection, we suggest that another function of female walrus tusks may be protection (for themselves and their young) during aggressive encounters with conspecifics while ashore in densely packed large groups.

Seasonal variation in male aggression. When we compared interaction rates at Punuk Island (one to two months prior to the breeding season) with data that Miller (1975) collected at Round Island (during the non-breeding season), there appeared to be no significant differences in the probability of an encounter involving strikes. The lack of seasonal differences suggests the following hypotheses concerning aggression in male walruses: 1) Walrus aggression may be context specific, occurring in the aquatic environment where mating apparently takes place (Fay 1982). 2) Aggression in walruses may be maintained by selective forces that occur beyond the breeding season.

A study of wood rats (*Neotoma fuscipes*) demonstrated that seasonal changes in male aggression were independent of hormonal cycles (Caldwell et al. 1984). Post-pubertally castrated and intact males were equally aggressive even though only the intact males had a seasonal peak in androgen levels associated with breeding. It was suggested that such independence was adaptive in a species that defended resources (i.e., a territory with a house) outside the breeding season.

Although changes in androgen levels of walruses have not been measured seasonally, they are known to be seasonal breeders and males undergo a seasonal cycle in size of the testes (Fay 1982). High levels of female aggression further support the hypothesis that walrus aggression may be independent of androgen levels [although high levels of androgens do occur in some females (e.g., Spotted hyenas, *Crocuta crocuta*, Lindeque et at. 1986; Glickman et al. 1987)]. Our comparison of seasonal male aggression is inconclusive because aggression levels need to be studied during the breeding season. However, these data suggest that it may be useful to explore alternative hypotheses that view walrus aggression as an adaptation that extends beyond the breeding season.

CHAPTER IV, BIBLIOGRAPHY

Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5: 325-383.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.

Anonymous. 1969a. Fur seal investigations, 1966. Spec. Sci. Rep. No. 584. U.S. Bureau of Commerical Fisheries, Marine Mammal Biological Laboratory, Washington D.C.

Anonymous, 1969b. North Pacific Fur Seal Commission Report on investigations from 1964 to 1966, Headquarters of the Commission, Washington D.C., April.

Barrette, C. and Vandal, D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97:118-146.

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evol.* 24:546-559.

Brooks, J. W. 1954. A Contribution to the Life History and Ecology of the Pacific Walrus. M.S. thesis. Spec. Rep. #1. Ak. Coop. Wildl. Res. Unit. 103 pp.

Burns, J. J. 1965. The walrus in Alaska, it's ecology and management. Alaska Dept. Fish and Game, Juneau. 48 pp.

Caldwell, G. S., Glickman, S. E., and Smith, E. R. 1984. Seasonal aggression independent of seasonal testosterone in wood rats. *Proc. Natl. Acad. Sci.* 81:5255-5257.

Carrick, P. H., Csordas, S. E. & Ingham, S. E. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). IV. Breeding and Development. C.S.I.R.O. Wildlife Research 7:161-197.

Clutton-Brock, T. H. 1982. The functions of antlers. *Behaviour* 79:108-125.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Beh.* 27:211-225.

Coulson, J. C. & Hickling, G. 1964. The breeding biology of the grey seal, *Halichoerus prypus* (Fab.), on the Farne Island, Northumberland. *J. Anim. Ecol.* 33:485-512.

Cox, C. & Le Boeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.* 111:317-335.

Espmark, Y. 1964. Studies in dominance-subordination relationship in a group of semi-domestic reindeer (*Rangifer tarandus* L.). *Anim. Beh.* 12:420-425.

Espmark, Y. 1971. Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). *Z. Tierpsychol.*29:42-81.

Fay, F. H. 1957. History and present status of the Pacific walrus population. Trans. N. Amer. Wildl. Conf., 22:431-443.

Fay, F. H. 1982. Ecology and Biology of the Pacific Walrus *Odobenus rosmarus* Divergens Illiger. U.S. Dept. of the Interior Fish & Wildlife Service. *N. Amer. Fauna*, No. 20. Washington D.C. 459 pp.

Fay, F. H. and Kelley, B. P. 1980. Mass natural mortality of walruses (*Odobenus rosmarus*) at St. Lawrence Island, Bering Sea, autumn 1978. *Arctic* 33:226-245.

Geist, V. 1966. The evolution of horn-like organs. *Behaviour* 27:175-214.

Geist, V. 1971. Mountain Sheep A Study in Behavior and Evolution. Univ. of Chicago Press, Chicago & London. 383 pp.

Gentry, R. L and Kooyman, G. L. 1986. Fur Seals: Maternal Strategies on Land and at Sea. Princeton Univ. Press. 291 pp.

Glickman, S. E., Frank, L. G., Davidson, J. M., Smith, E. R., and Siiteri, P. K. 1987. Androstenedione may organize or activate sex-reversed traits in female spotted hyenas. *Proc. Natl. Acad. Sci.* 84:3444-3447.

Gol'tsev, V. N. 1968. Dynamics of coastal walrus herds in connection with the distribution and numbers of walruses. In: Lastonogie severnoi chasti Tikhogo Okeana. (V.A. Arsen'ev & K.I. Panin, eds.) Pischevaya Promyshlennost', Moscow. pp. 205-215.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295-311.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.

Le Boeuf, B. J., Whiting, R. J., & Gantt, R. F. 1972. Perinatal Behavior of northern elephant seal females and their young. *Behaviour* 43:121-156.

Le Boeuf, B. J. & Briggs, K. T. 1977. The cost of living in a seal harem. *Mammalia* 41:167-195.

Lent, P. C. 1974. Mother-infant relationships in ungulates. In: Behaviour Of Ungulates And Its Relations To Management. (V. Geist & F. Walther, eds.). I.U.C.N., Morges.

Lincoln, G. A. 1972. The role of antlers in the behaviour of red deer. *J. Exp. Zool.* 182:233-250.

Lindeque, M., Skinner, J. D. & Millar, R. P. 1986. Adrenal and gonadal contribution to circulating androgens in spotted hyaenas (*Crocuta crocuta*) as revealed by LHRH, hCG and ACTH stimulation. *J. Reprod. Fert.* 78:211-217.

Miller, E. H. 1975. Walrus Ethology. I. The social role of tusks and applications of multidimensional scaling. *Can. J. Zool.* 53:590-610.

Miller, E. H. 1976. Walrus Ethology. II. Herd structure and activity budgets of summering males. *Can. J. Zool.* 54:704-715.

Miller, E. H. 1982. Herd organisation and female threat behaviour in Atlantic walruses *Odobenus rosmarus rosmarus* (L.). *Mammalia* 46:29-34.

Miller, E. H. and Boness, D. J. 1983. Summer behavior of Atlantic walruses *Odobenus rosmarus rosmarus* (L.) at Coats Island, N.W.T. (Canada). *Z. Saugetierkunde* 48:298-313.

Packer, C. 1983. Sexual dimorphism: the horns of African antelopes. *Science* 221:1191-1193.

Salter, R. E. 1980. Observations on social behaviour of Atlantic walruses (*Odobenus rosmarus* (L.)) during terrestrial haul-out. *Can. J. Zool.* 58:461-463.

Silverman, H. B. & Dunbar, M. J. 1980. Aggressive tusk use by the narwhal (*Monodon monoceros L.*). *Nature* 284:57-58.

Tomilin, A. G. & Kibal'chich, A. A. 1975. Walruses in the vicinity of Wrangell Island. *Zool. Zhur.* 54:266-272. (Translation by F.H. & B.A. Fay, June 1975).

Trivers, R. L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, 1871-1971, (B. Campbell, ed.), Chicago: Aldine, pp. 136-179.

Wirtz, W. O. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. *J. Mamm.* 49:229-238.

Figure IV.1. Punuk Island census data, 28 September to 30 November 1981. Line connects the mean of 3 independent counts. Vertical bars are high and low estimates.

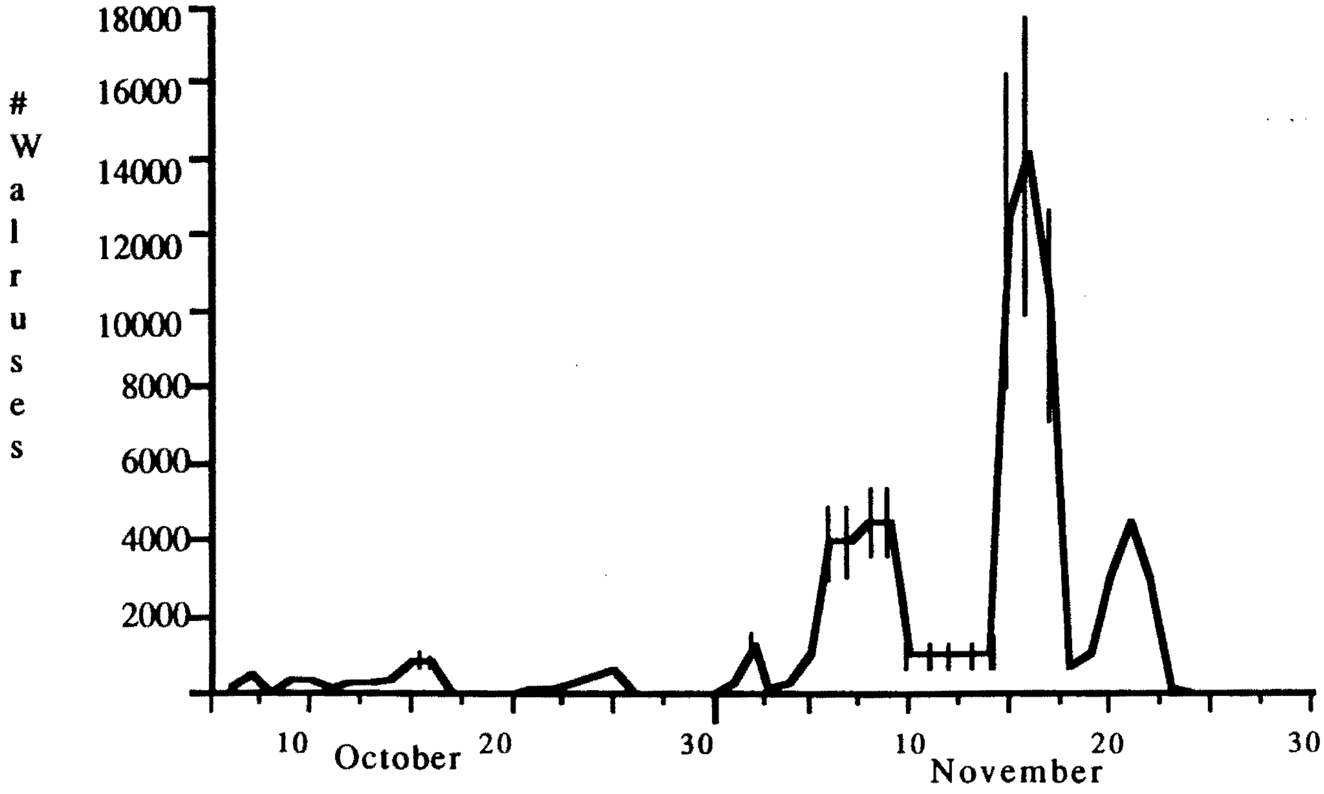


Figure IV.2. Sex differences in behavior of walruses entering the herd. 2a.) Success of walruses attempting to join the herd. 2b.) Time to enter the herd. Observations began when a focal animal landed on the beach. Time to enter was calculated from initial landing to when the walrus either swam away, or joined the herd. Each sample was terminated when the subject had made body contact with an animal in the herd and had not interacted with another walrus for 60 seconds (to avoid collecting data on sleeping animals). Values are means ± std. dev.

Figure IV.2a. Chi. sq. $p<.05$

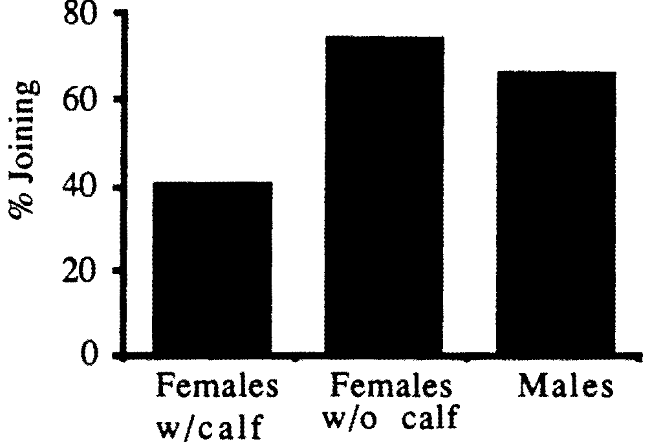


Figure IV.2b.

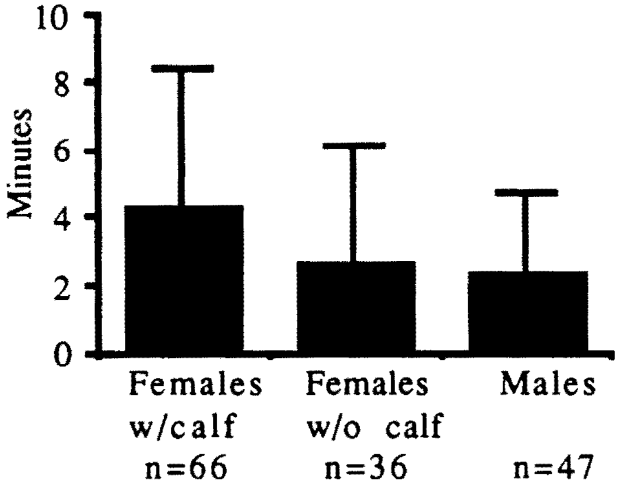


Figure IV.3. Sex differences in dyadic interactions between walruses that were established in the herd. 3a.) The percentage of walruses which struck their opponent or were displaced during encounters. 3b.) Percentage of walruses which struck or were displaced by equal sized walruses.

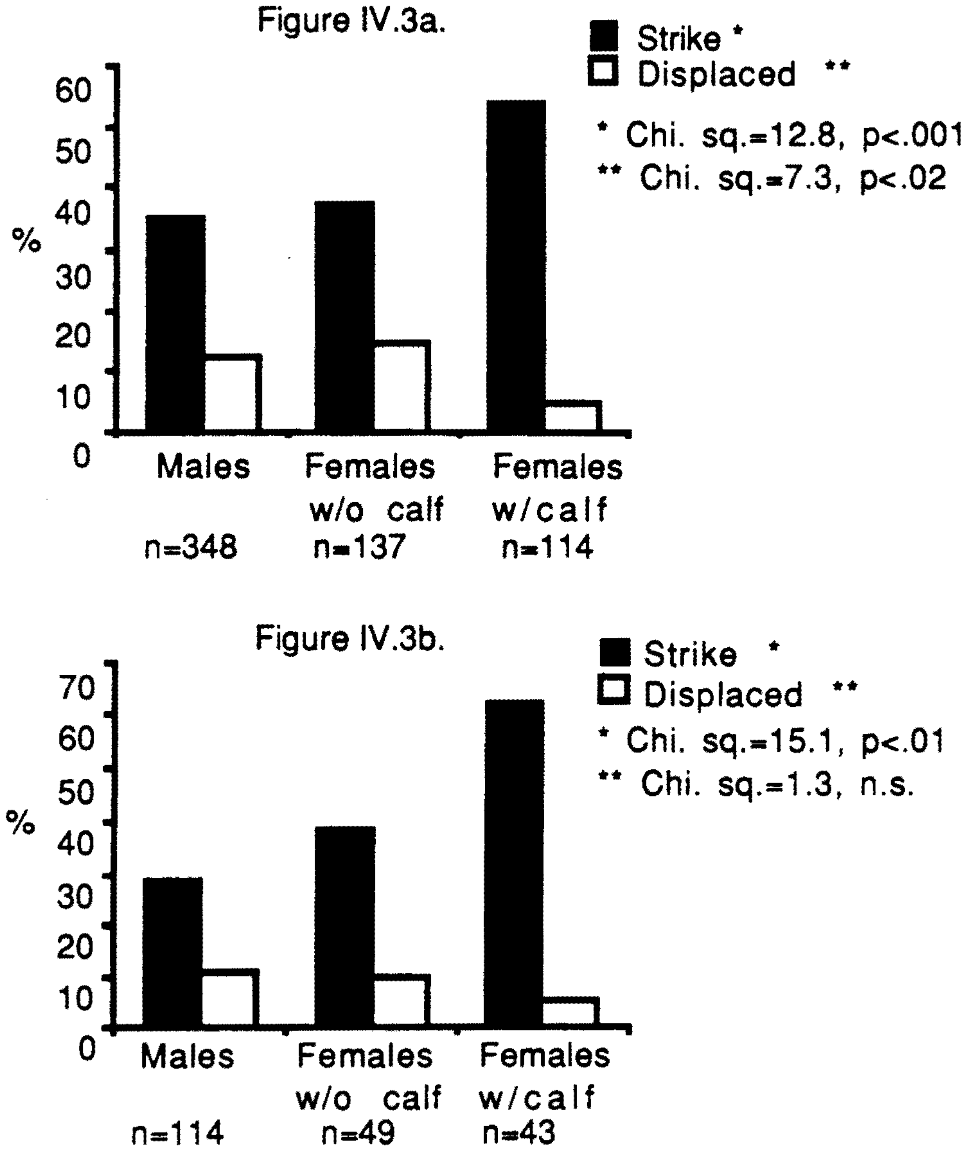


Figure IV.4. Sex differences in aggression between male-male, female-female, and female-male encounters. 4a.) Proportion of interactions in which at least one strike was dealt, and one walrus displaced the other. 4b.) Proportion of interactions between equal sized walruses involving strikes and displacement.

Figure IV.4a.

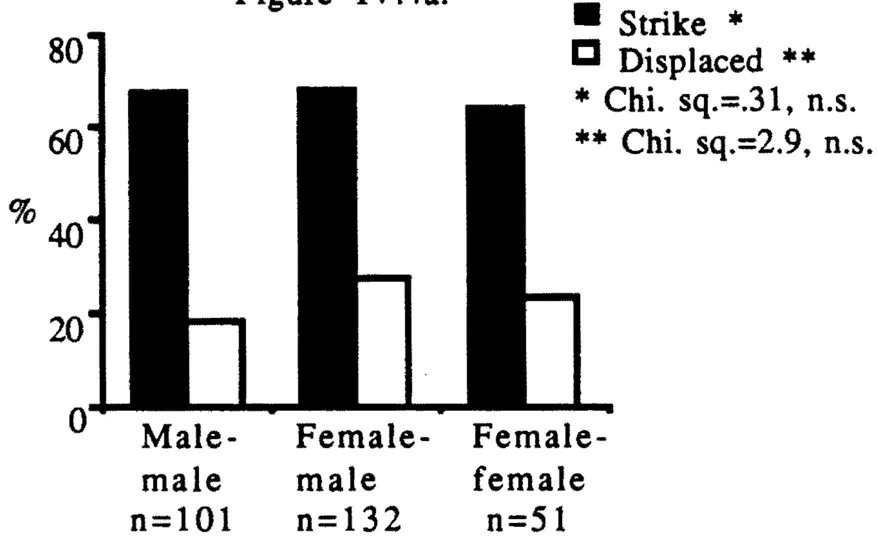


Figure IV.4b.

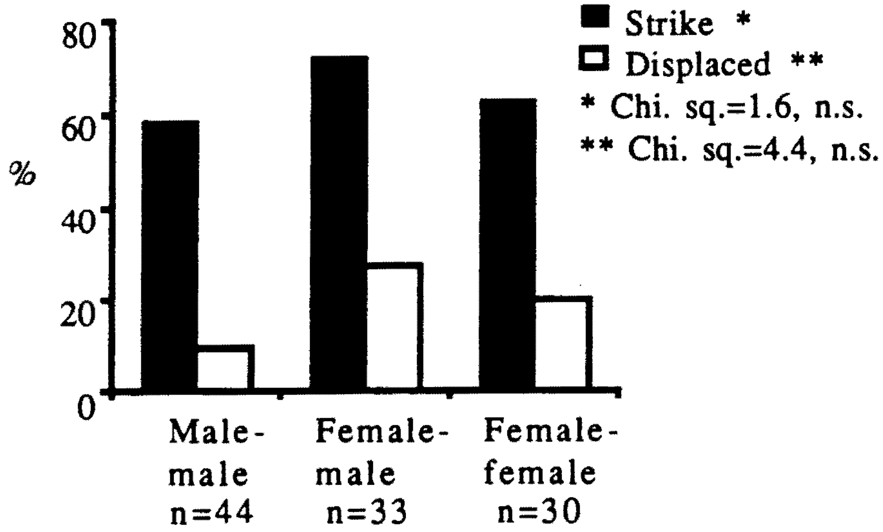


Figure. IV.5. Relationship between aggression and relative size of walruses during dyadic interactions. Tusk and body size of the two animals were ranked relative to each other (see methods). A sample was terminated when neither walrus had interacted with the other for 60 seconds.

Figure 5a. Proportion of walruses who dealt strikes.

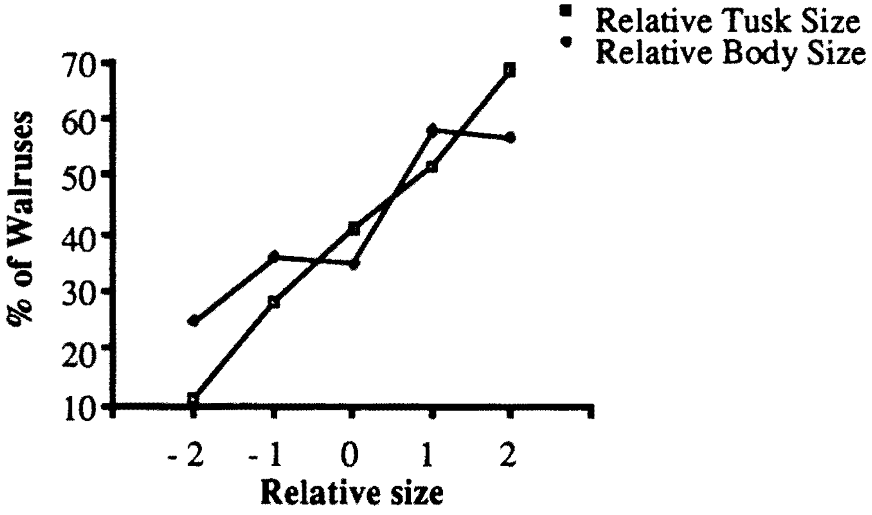


Figure 5b. Proportion of walruses who were displaced.

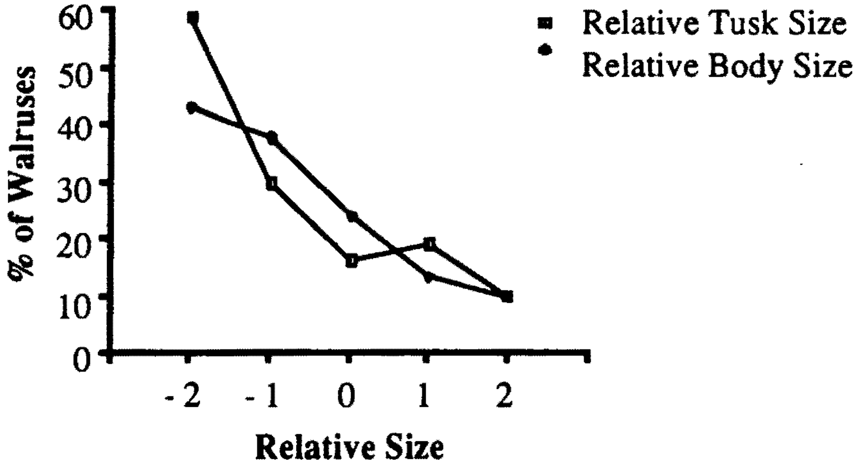


Figure IV.6. Age and sex differences in aggression within a walrus herd. Values are means ± std. dev. of the number of tusk jabs dealt and received during 5 minute focal animal samples. All values are significantly different at p<.003, ANOVA; except the mean number of jabs dealt by adult females and males.

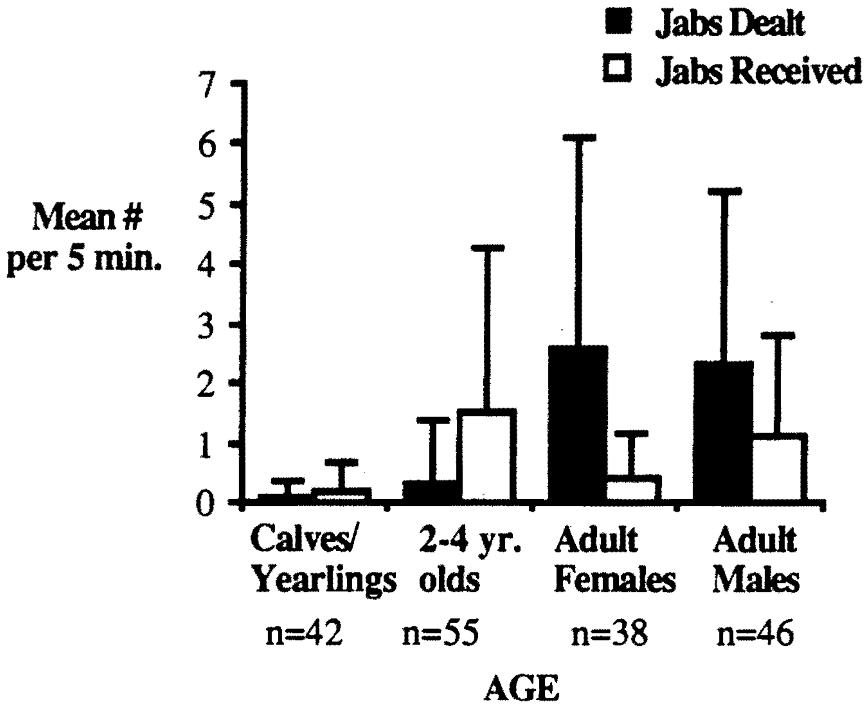


Table IV.1. Behavior of walruses joining the herd. **

	Females with calves n=20	Females without calves n=17	Males n=15	Chi. Sq. Prob.
Jabs delt	2.8±4.5*+	.6±.7*	3.2±4.5+	p<.001
Jabs received	1.9±5.7*	.1±.3*	.3±.7	p<.001
Animals displaced	.4±.5	.1±.3	1.1±1.3	p<.001
Ranks moved through herd	.3±.7	.5±.7	1.1±1.1	p<.02

** Values are the mean frequency ± std. dev. of each behavior, beginning when initial contact is made with the main herd, until subject animal does not interact with another walrus for 60 seconds. Total observation time=3 hours 24 minutes.

* Females with calves were significantly different than females without calves, p<.001, Chi. Sq. test.

+ No significant difference between males and females with calves.

Table IV.2. Percentage of encounters involving strikes; a comparison among studies.

	Strike behavior								
	Neither strike			One strikes			Both strike		
Study:	a.	b.	c.	a.	b.	c.	a.	b.	c.
Male-male	41.8	36.1	31.7	53.4	56.9	62.4	4.9	6.9	5.9
Male-female		32.6	31.1		62.8	60.6		4.6	8.3
Female-female	58*	25.7	35.3		57.1	54.9		17.1	9.8

a. Miller1975, n=585.
b. Salter 1980, n=150.
c. Taggart 1987, n=284.
* Miller 1982, n=564.

Male-male: Chi. sq.=4.4, n.s., (p<.36).
Male-female: Chi. sq.=.64, n.s., (p<.73).
Female-female: Chi. sq.=1.5, n.s. (p<.47).

Table IV.3. Female response to calf receiving a jab.

	Total calves jabbed n=31
Jab back	1 (3%)
Threaten	8 (26%)
No response	22 (71%)

Table IV.4. Who caused disturbances during nursing bouts *

	Interruptions n=18	Termination n=12
Other walruses	16 (88%)	3 (25%)
Mother	1 (6%)	2 (17%)
Calf	0	6 (50%)

* Observation time=3 hours 26 minutes of nursing.
There was an average of .9 interruptions per 10 minutes of nursing.

CHAPTER V

SYNCHRONOUS LAND-SEA MOVEMENTS OF WALRUS SUPER HERDS: A NEW HYPOTHESIS OF WALRUS SOCIAL ORGANIZATION

Walruses (*Odobenus rosmarus divergens* Illiger) are perhaps the most gregarious of all pinnipeds. Dense terrestrial herds containing more than ten thousand animals commonly occur where contact between individuals is virtually continuous (typical measurements = 0.5 walruses/m^2; see Chapter II). The existence of large walrus groups is important because extant hypotheses for the evolution of pinniped groups are not applicable for walruses.

Although few hypotheses for pinniped groups *per se* have been proposed, there has been considerable discussion on the relationship between pinniped grouping behavior and pinniped polygyny. Pinnipeds generally are thought to be asocial animals (Gentry 1981) that form aggregations or colonies during the breeding season (Wilson 1975; Crook et al. 1976; Wittenberger 1981) but are "... highly dispersed during the nonbreeding season" (Bartholomew 1970: p. 550). Based on this assumption, sexual selection and other selective forces that occur during the breeding season have been emphasized to explain the evolution of the extreme gregariousness of pinnipeds (Nutting 1891; McLaren 1967; Bartholomew 1970; Le Boeuf 1974; Stirling 1975, 1983; Cox and Le Boeuf 1977; Pierotti and Pierotti 1980).

Terrestrial parturition (and thus terrestrial copulation; post-partum estrus is assumed) and limited terrestrial mobility resulted in pinnipeds utilizing predator free islands where space was limited. This limited breeding space resulted in an initial degree of clumping (Bartholomew 1970), but some gregarious pinnipeds appear to clump closer than limited space alone would dictate; "the tendency to aggregate is carried seemingly to nonfunctional extremes" (Bartholomew 1970: p. 554). This phenomenon has been explained by the "marginal male effect" (Bartholomew 1970), which suggests that females form dense groups because single females are likely to mate with marginal males who are not successful at male-male competition, and hence are genetically inferior. Mating with dominant males is thought to outweigh the costs of grouping, such as physical trauma to the young, which are correlated with the dense groups (Le Boeuf and Briggs 1977).

These explanations do not apply to the evolution of walrus groups because: 1) walruses do not breed on islands; 2) walruses do not copulate on land (walruses apparently copulate in the water; Fay 1982); and 3) walruses do not have post-partum estrus (Fay 1982). Only one explanation has been suggested for this disparity: "Aquatic mating could be an evolutionary response to the problem of a large mammal mating on variably-sized floes in the pack ice, but the gregariousness of females and the long weaning period may be phylogenetic relicts" (Stirling 1983: p. 517).

In this paper I present data for walruses that suggest an alternate hypothesis for walrus groups. Rather than being aggregations of asocial individuals that form groups only for breeding, walruses may belong to large social groups[1] throughout the year, and these may maintain cohesion while at sea. Evidence for pinniped grouping behavior outside the breeding season and grouping at sea is particularly important, because it suggests that polygyny in walruses needs to be viewed as an epiphenomenon of grouping rather than a cause.

Materials and Methods

My field research was done from May-September, 1980-1982 at Round Island, Alaska (56°02'N160°50'W) where male walruses (approximately 12,000) come ashore during summer. I also worked at Cape Peirce, Alaska (58°35'N 161°45'W) from 16 June to 5 October, 1984 (with C. Zabel, K. Taylor, D. Fisher & T. Pogson) where male walruses come ashore. Further observations of male and female walruses at Punuk Island, Alaska (63°05'N 168°49'W) from 28 September to 10 December, 1981 during the autumn southward migration were made with C. Zabel and B. Kelley.

Census data were collected daily at Round Island during 1980 from 16 June through 20 September. I divided the island

---

[1] I use Wittenberger's (1981: pp. 621) definition of social group: "A group of conspecific individuals that persist because individuals gain mutual (cooperative) benefits by remaining together."
Note that Gentry (1981: pp 155) uses a different definition of social. Even though Northern fur seals are highly gregarious, he considers them to be "asocial" because "no lasting social bonds form within any segment of the society".

coastline into 136 fifty meter sections. Where natural landmarks were not suitable, temporary colored markers were placed on the cliffs above the beaches. The fifty meter sections made it possible to track the location of groups through time and facilitated estimating the number of animals on the long continuous beaches. Walrus numbers were estimated in each section from cliffs overlooking the beaches.

At Punuk Island censuses were conducted from 28 September through 30 November. The walruses on Punuk Island used one large continuous beach. I divided this beach into 25 m sections and erected drift wood posts as temporary markers. Estimates were made from a vantage point approximately 50 m in elevation about one half km away from the hauling ground. Three observers made independent estimates (simultaneously) and then an average was taken.

At Cape Pierce censuses were conducted approximately every other day from 16 June to 20 July and daily from 21 July through 5 October. The number of walruses on each of seven beaches was estimated and then totalled.

The land-sea movements of individual walruses were recorded at Round Island. VHF transmitters were attached to the tusks of 21 sleeping walruses in 1980 with a hydraulically powered tool (n=15) and with a latex banding tool (n=6; see Chapter VII). Daily I searched each herd with a radio receiver to determine the presence or absence of radio-tagged individuals. Thus the duration of a period at sea (presumably a feeding foray) was the number of consecutive days a radio-tagged walrus was absent, while a period on shore was the number of consecutive days that an individual was located on the island. I attached VHF transmitters to nine walruses at Round Island with the hydraulic banding tool during 1981. These animals were last monitored in late August when I departed Round Island for Punuk Island. A radio-tagged walrus was discovered at Punuk Island (on 11 November) and I subsequently monitored for the transmitters (twice daily) until the walruses departed Punuk Island.

Results

Radio-tagged walruses at Round Island were on land and at sea 26% and 74% of the time, respectively. The mean foray lasted 7.6 days (mode=7), while the mean period on shore was 2.7 days (mode=2, Fig. V.1). The number of walruses on land underwent six precipitous and regular increases and declines from June to September (Fig. V.2). The percentage of radio-tagged walruses on land underwent similar increases and declines, thus indicating that the radio-tagged walruses adequately represented the population (r^2=.74). Therefore, the portion of the population on land versus at sea could be estimated from the radio-tagged walruses. These data indicate that land-sea movements of walruses occur with remarkable synchrony.

Similar fluctuations in numbers of walruses ashore were observed at Cape Peirce and at Punuk Island (although detailed studies of radio-tagged individuals were not done at these locations). At Cape Peirce, nine peaks in the numbers of walruses on land were observed during a three month period (Fig. V.3). These data indicate land-sea movements of similar magnitude and period to those seen at Round Island. Punuk Island was utilized primarily by a small number of male walruses from 28 September-5 November. During this period, the number of males on shore fluctuated from zero to approximately 1,000 individuals. On 6 November large numbers of males and females began to arrive and three major peaks in the number of individuals on land occurred from 6 November-22 November (Fig. IV.1). The maximum peak (of approximately 16,000 individuals) occurred on 16 November. These data indicate that synchronous land-sea movements also occur in female groups and are maintained during the fall migration.

I was able to observe the spring arrival of males to Round Island in 1982, when the pack ice receded unusually late in the central and southern Bering Sea. From 10 April to 2 June, one group of approximately 150 walruses was on shore for less than one week. Large numbers of animals began arriving on 3 June and by 4 June approximately 10,000 walruses were hauled out on the island. These data further indicate that migratory walruses come ashore synchronously.

The walruses at Punuk Island formed one group, even though there was additional space available on the continuous sandy beach. In contrast, the largest beaches at Round Island were too small to accommodate all of the walruses utilizing the island. Characteristically, walruses at Round Island began hauling out on one of the three largest beaches, forming a dense group on a small part of the otherwise empty beach. Eventually, as more animals arrived, the large beach filled completely, whereupon incoming walruses utilized adjacent beaches. Beaches composed of boulders one to three m in diameter were filled in sequence, even though the animals had considerable difficulty maneuvering on beaches with large rock substrate. During low tides, walruses often abandoned the peripheral beaches to haul out on the temporarily exposed strip of intertidal substrate in front of the central beaches. Thus although walruses did not form a single group on Round Island they appeared to attempt to do so.

Three of nine radio-tagged walruses from Round Island were located at Punuk Island on 11, 12 and 15 November. These animals traveled northward approximately 850 km to reach Punuk Island (Fig. V.4). The females that were on Punuk Island probably had traveled southward from the Chukchi Sea a similar distance. The probability that three of nine transmitters would be recovered at Punuk Island is very low unless a considerable proportion of Round Island males were involved in the movement between Round Island and Punuk Island. Although the sample size is small, I can estimate the number of males that migrated from Round Island to Punuk Island using sample statistics (Schefler 1979). I will make the following assumptions: 1) the tagged animals were a representative sample of the walruses using Round Island; 2) all radio-tagged walruses that migrated to Punuk Island would be recovered (missed radio-tags would bias the estimate low); and 3) the probability that each radio-tagged walrus would migrate to Punuk Island (isolated events) approached a poisson distribution. I can infer the size of the migration (at the 90% confidence-limit) by:

$$M = (m \pm 1.65 \sqrt{m}) \ \text{X} \ (P_{RI}/m_{tot})$$
$$= (3 \pm 2.86) \ \text{X} \ (12{,}000/9)$$
$$= 4{,}000 \pm 3{,}812$$

Where M = # walruses that migrated; m = # radio-tagged walruses that migrated; m_{tot} = total # of radio-tagged walruses; P_{RI} = population at Round Island (estimated to be 12,000).

Thus the best estimate (at the 90% confidence interval) is that 4,000 walruses migrated from Round Island to Punuk Island. The occurrence of these radio-tagged walruses at the onset of the peak haul out further emphasizes that this event was unlikely to have been the occurrence of a small number of individuals.

Discussion

Observations by other investigators. Large temporal fluctuations in the number of walruses ashore have been observed by other investigators, thus suggesting that the phenomenon is a general behavioral characteristic of the species. These reports are summarized below:

1) The number of walruses on shore at two locations on St. Matthew Island underwent "cyclic and regular" (Irons 1983: p. 4) fluctuations during the summer months. The maximum number of walruses that hauled out at both sites was approximately 150 walruses. However the average length of time between peaks differed for the two sites (10 and 4 days, Irons 1983).

2) Observations by other investigators suggest that synchronous behavior is not unique to walruses of the Bering and Chukchi Seas.

a) A small mixed herd of Atlantic walruses (*Odobenus rosmarus rosmarus* (L.)) were censused at Bathurst Island, N.W.T. for one month during the summer of 1977 (Salter 1979). "Strong fluctuations in numbers" occurred with six major peaks. The peak numbers were 41, 129, 54, 54, 84 and 57 walruses, and the minimum was 0, 0, 24, 22, 5, 16, and 0 walruses between peaks respectively.

b) Eight peaks in abundance (during 44 days) were observed in the Pronchishchev Bay, Laptev Sea (north coast of Siberia) where primarily female walruses haul out during summer months (Visnevskaia and Byhkov 1985)[2]. The minimum and maximum counts were (minimum:maximum): 0:209, 15:328, 60:283, 60:581, 60:209, 30:432, 0:358 and 89:402 for the eight peaks, respectively.

3) On 19 September 1975, 1,200 walruses were counted on Arakamchechen Island. Two days later, 42,000 walruses were present (Estes and Gol'tsev 1984). On 19 September, 630 walruses were counted at Nunyangan Island; two days later 20,000 were observed (Estes and Gol'tsev 1984). Both islands were characterized by large beaches, on which virtually all of the walruses present were in single groups. This observation again demonstrates that walruses form large dense groups, even when additional space is available.

4) Although little is known of walrus behavior on the pack ice, they rest in groups [although group sizes are considerably less than they are on land (Fay and Ray 1968; Wartzok and Ray 1980; Fay 1982)] and may have synchronous ice-sea movements. Long

---

[2] The taxonomic status of the Laptev walrus is uncertain. See Fay (1982: pps. 5-6) for a review.

term observations on the formation and dispersal of walrus herds on the pack ice have not been made. Some interesting patterns have been documented, however, from aerial surveys. Randomly selected transects were flown perpendicular to the ice edge on four survey days (Estes and Gilbert 1978). Mean group sizes among days were 10.0, 26.7, 8.9, and 48.7 walruses. Most of the walrus sightings were between 162^0 and 165^0 W. longitude. On September 8, an order of magnitude increase in the number of groups was seen relative to the remaining survey days. The groups were also larger on that day; twelve groups greater than 50 and 62 groups greater than 25 walruses were observed. On other survey days, only one group greater than 50 (225 walruses) and six groups greater than 25 were observed. The high variance among survey transects indicates that walruses are spatially grouped on the pack ice. The high variance among survey days indicates that the number of animals resting on the ice changes dramatically from day to day, which is consistent with the hypothesis that walruses have synchronous ice-sea movements.

Extant views of pinniped gregariousness. From the preceding data and observations, several obvious but important conclusions are evident:

1) Walruses form large dense groups. Grouping behavior of walruses is not a subtle phenomena; thus it is difficult to invoke weak or neutral selective forces as an explanation. Walruses evolved from a terrestrial carnivore ancestor which was undoubtedly characterized by comparatively small groups. Modern walruses form groups that are much larger than those of

terrestrial carnivores; their group sizes are as large as many ungulate herds. Thus it seems reasonable to infer that the extreme grouping behavior of walruses is an evolutionary response to selective forces associated with their marine existence. The large size of walrus groups alone makes me skeptical of the phylogenetic relict hypothesis (Stirling 1975, 1983).

2) Grouping in walruses is not the direct result of limited space. Walruses form groups on the pack ice where space is not limited (Burns et al. 1980). When utilizing islands, walruses clump into dense groups even when there is available space on large beaches.

3) Large, dense groups of walruses occur on shore during the nonbreeding season. Therefore, the tendency to form groups is not related strictly to the breeding season.

4) Grouping behavior is characteristic of both sexes. Although female gregariousness has been emphasized as an important component of pinniped polygyny, male gregariousness (although not unique to walruses) has not been discussed. It is difficult to imagine how the marginal male effect (Bartholomew 1970) or other factors during the breeding season would promote male gregariousness. Based on the occurrence of male gregariousness, I reject the view that the marginal male effect alone provides an adequate explanation of walrus grouping behavior.

I am thus led to reject the view that grouping behavior of walruses is strictly the result of sexual selection and/or selective forces during the breeding season. Instead I infer that walrus grouping behavior is likely to be the result of natural selection forces that occur throughout the year.

An alternative hypothesis for walrus groups. Rapid changes in the number of walruses observed on shore are a general characteristic of walrus groups. Detailed data from radio-tagged walruses (at Round Island) demonstrate that large changes in the number of animals ashore was due to repeated synchronous land-sea movements of the majority of the population. How do walruses arrive on shore synchronously? There are two alternative hypotheses for walrus social organization that explain synchronous land-sea movements.

Hypothesis I. Walruses are dispersed while feeding at sea. According to this hypothesis, they leave the feeding grounds and swim back at the same time by keying in on environmental parameter(s), endogenous rhythm, or both (Fig. V.6). If future research supports this hypothesis, it might be useful to consider walrus herds as analogous to avian roosts. The arrival and departure cycle of walruses, however, would be unique because all other roosting species are on a diurnal cycle (Hamilton et al. 1967; Hamilton and Watt 1970). Numerous authors have discussed the factors likely to be important in the evolution of avian roosts: information exchange, predator swamping, etc. (Hamilton et al. 1967; Hamilton and Watt 1970; Zahavi 1971; Ward and Zahavi 1973; Yom-Tov et al. 1977; Yom-Tov 1979; Loman and Tamm 1980; Nuechterlein 1981; Waltz 1982; Weatherhead 1983; Morrison and Caccamise 1985). Although timing mechanisms for the synchronous arrival of walruses on islands seems plausible, the aerial survey data suggests that synchronous arrival may also occur on the pack ice. It is difficult to imagine a timing and orienting mechanism that would facilitate synchronous arrival when the pack ice is constantly moving.

Hypothesis II. In my view a more likely hypothesis is that synchronous land-sea movements occur because walruses remain in large groups while at sea (Fig. V.7). Thus the dramatic fluctuations in census data may represent the arrival and departure of large herds rather than the synchronous arrival of dispersed individuals. This hypothesis suggests that terrestrial groups of walruses might be largely a carryover of aquatic groups. This is fundamentally different from the view for other pinnipeds that has grouping behavior to be the result of selective forces on land. Walrus groups might be analogous to large wildebeest or caribou herds. There are several intriguing parallels between walruses and ungulates that form large herds:

1) Walruses form large groups and have large body size. Among African bovid species, the occurrence of large body size is correlated to large group size (Packer 1983).

2) Both male and female walruses have tusks. When comparing equal aged animals, female walruses have tusks which are smaller in diameter than male tusks but of similar length (Fay 1982). Females have longer tusks than males for equal sized animals. Female bovid species that have horns as long as male horns also live in large groups and have large body size (Packer 1983).

3) The especially large walrus groups at Arakamchechen and Punuk Islands were observed before and during the walruses' fall migration. Wildebeests form large super-herds just prior to and

during the migration (Jarman 1974).

4) The walrus mating system has been described as a "mobile lek" (Fay et al. 1984). Male walruses display in the water adjacent to ice floes where females are resting. They maintain an interindividual distance of only 5-10 m while engaging in ritualized behaviors that include continuous diving and surfacing, acoustic signaling (including whistles and "bell-like" and "knock" sounds), and inflating the pharyngeal air sacs (Fay et al. 1984: p. 94). The shifting territorial behavior described for migrating wildebeests (Jarman 1974) is similar to the preceding observations of walruses in several respects. Like walruses, male wildebeests station themselves near female herds, engage in conspicuous vigorous displays, and tolerate close proximity to other males (they maintain very small territories).

There are a number of reasons why the second hypothesis might be correct, yet not obvious by simple observation.

1) Walruses are not easily observed when they are at sea because: a) they are on the surface only a small portion of the time; b) the observer only sees the crest portion of the waves; c) ship time is expensive; d) at Round Island, the animals apparently travel long distances to feed; and e) stormy weather is common in the Bering and Chukchi Seas which causes reduced visibility.

2) Walrus herds at sea could be of low density and still function as a herd, i.e., have coordinated movements. Water transmits sound efficiently (Payne and Webb 1971) hence walruses could maintain acoustic contact from considerable

distances[3]. Although an observer may see an individual animal and operationally classify it as solitary, functionally that individual may be part of a large group.

Some information is available indicating that walruses are grouped at sea. Aerial surveys in Bristol Bay suggested a highly aggregated distribution of Round Island walruses at sea (Fay and Lowry 1981). Mean group size of walruses observed at sea along the pack ice during aerial surveys was 2.8 (Estes & Gilbert 1978). These groups were clustered. On numerous occasions at Round Island, large numbers of small groups (three to ten individuals) were observed arriving from a single direction (pers. obs.). On several occasions when the seas were calm and immigration was high, I observed from the summit of Round Island (elevation=440 m) chains of small groups extending to the horizon that were arriving from the southeast. These observations of continuously arriving groups at Round Island does not discount the possibility that the walruses coalesced from dispersed distribution at sea before returning to Round Island. (This is a more complex hypothesis than either hypothesis I have proposed.)

Why form aquatic groups? My proposed hypotheses address what kind of social organization walruses might have. The next obvious question is what function do groups serve in the aquatic environment? There are several possibilities:

1) *Social foraging.* Social foraging is thought to be an important factor promoting group living in many species of

---

[3] See Ray and Watkins (1975) for acoustic analyses of underwater sounds of walruses. Schevill et al. (1966) and Fay (1960) discuss the morphology and function of the pharyngeal pouch for underwater vocalizations.

animals (Schaller 1972; Kleiman and Eisenberg 1973; Alexander 1974; Eisenberg 1981) including some cetaceans (Wells 1986). Walruses have been observed foraging in groups:

a) Five hundred walruses were observed in the pack ice within a three km radius "diving and surfacing in remarkable synchrony and apparently feeding" (Fay et al. 1984: p. 93).

b) Approximately 50 adult females walruses were observed feeding for a five hour period, again synchronously diving (Fay 1982).

c) Eleven walrus groups were observed at St. Matthew Island synchronously diving and feeding near shore. Mean group size was 10.4 (s=9.5; range=1-40; Irons 1983).

d) Tomlin and Kibal'chich (1975) reported that walruses fed in groups of two to three animals which dove synchronously.

These data demonstrate that walruses sometimes forage in social groups.

2) *Predation.* The role of predation has been emphasized in the evolution of many large terrestrial mammals which live in groups (Hamilton 1971; Alexander 1974; Jarman 1974; Eisenberg 1981; Packer 1983). Predation may be a factor promoting aquatic grouping in walruses as well. Several lines of evidence support this possibility:

a) Killer whales, *Orcinus orca*, are abundant in the Bering and Chukchi seas (Tomlin 1957, cited in Fay 1982: p. 216).

b) Killer whales kill walruses: (1) Zenkovich (1938, cited in Fay 1982: p. 216) reported that 60-70 swimming walruses formed a compact group apparently in response to an attack by 15 killer whales. The killer whales split the group in half and consumed one of the halves. He observed a similar attack on a second group of walruses. (2) The remains of walruses were found in the stomachs of two killer whales (Zenkovich 1938, cited in Fay 1982: p. 216). (3) Four walruses were washed ashore that had apparently been killed by killer whales (Fay 1982). (4) Of 40 necropsied walruses that died on St. Lawrence and Punuk Islands in 1978, two or three died from trauma inflicted by killer whales (the evidence was unclear for one of the carcasses; Fay and Kelly 1980). (5) Part of a walrus tusk was found embedded in a killer whale that was stranded on St. Lawrence Island (Pedersen 1962, cited in Fay 1982: p. 217).

c) Walruses apparently have complex responses to predation as shown by the following observations: (1) A polar bear charged six walruses which fled into the water (Stirling 1984). This group apparently alerted four other small groups. "They appeared to be anticipating the arrival of the bear by extending their heads and necks out of the water and looking in the direction of the bear before it arrived." (Stirling 1984: p.352.) Subsequently, the walruses coalesced into a tight group, surfaced suddenly in a small pool next to the bear and charged the bear. (2) When being hunted by humans, walruses have been reported to assist one another and form group attacks. Individuals and groups of walruses will sometimes attack hunters and/or their boats (using their tusks as weapons; Brooks 1954; Burns 1965). Members of a walrus group were observed pushing injured individuals to the water's surface (Tomlin and Kibal'chich 1975). In another instance, a walrus came out onto the ice and dragged a recently killed walrus into the water by hooking it's tusks over the carcass (B. Nelson, pers. comm.).

Long distance fusion of male and female portions of the population. The northward movement of male walruses (from Round Island to Punuk Island) coincided precisely with the female southward movement (Chukchi Sea to Punuk Island). This has important implications for walrus aquatic social organization.

I. The passive fusion hypothesis. Before my studies at Punuk Island, it was generally assumed that the males from Round Island joined the females during winter after the pack ice reached Bristol Bay. The movement of radio-tagged walruses from Round Island to Punuk Island suggests that this is not true for some of the Round Island males.

II. The active fusion hypothesis. This leads me to suggest that male and female segments of the walrus population (which are separated annually by approximately 1700 km; Fay 1982) may have sophisticated mechanisms that enable them to actively fuse. This hypothesis is supported by the following evidence:

1) The movement of walruses (primarily females) from the Chukchi to the Bering Sea probably occurs because winter ice in the Chukchi is too solidly frozen to be suitable walrus habitat. Small groups of walruses do get trapped in the stable, heavy ice and apparently perish (Fay 1982). Punuk Island may be utilized during the southward migration because there is seldom ice in the Bering Strait area during the time of the migration.

2) The movement of males from Round Island to Punuk Island is more difficult to explain. Bristol Bay does have suitable ice during the winter months: large numbers of walruses are

consistently seen there (Fay 1982)[4]. Thus the movement of males from Round Island to Punuk Island cannot be attributed to a seasonal deterioration of habitat. Since the movement was one to two months prior to breeding, an alternate explanation is that the northward movement was in preparation of breeding. Male walruses from Round Island might migrate to Punuk Island because it is a place where they can predictably form associations with females as they funnel through Bering Strait.

The active fusion hypothesis is dependent on the concept that walruses travel in herds. Why should the Round Island males migrate 850 km and haul out briefly on shore with females at Punuk Island if the females were subsequently going to disperse as individuals into the vast Bering Sea? If groups of females on the ice (during the breeding season) are caused by the synchronous arrival hypothesis (i.e., dispersed aquatic individuals synchronously forming dense groups on the ice), it seems logical that the males would locate the females using the same synchronizing mechanism after the females arrived in Bristol Bay, thus saving themselves a 850 km migration.

Grouping behavior of walruses and walrus polygyny. The walrus' mating system appears to be highly polygynous (Fay et al. 1984). Female walruses have been observed in dense groups, and clusters of groups. Males have been observed displaying in the water adjacent to female groups. An apparently high degree of polygyny in the walrus is important because walruses lack several

---

[4] Fay (1982) considers the winter concentration of walrus groups in Bristol Bay to represent one of two major concentrations.

important inputs contained in Bartholomew's (1970) model for the evolution of pinniped polygyny:

1) Walruses do not breed on islands; rather they breed on rapidly moving and unstable pack ice where space is unlimited. A stable, predictable and defendable parturition habitat is central to Bartholomew's (1970) model.

2) Walruses do not have post parturition estrus and copulation (Fay 1982). Therefore the formation of female groups cannot be explained by the need to give birth.

3) Walruses apparently copulate in the water (Fay 1982; Fay et al. 1984). Terrestrial copulation and associated male-male competition are key selective forces in the model for the evolution of pinniped polygyny (Bartholmew 1970).

In this chapter I have provided evidence that walrus groups: 1) persist throughout the year, and 2) may be an aquatic adaptation. In general it seems reasonable to hypothesize that walruses are social animals living in groups, i.e. marine analogs to wildebeest. Grouping behavior in social non-pinniped mammals is thought to be the result of natural selection (Hamilton 1971) and polygyny is considered an epiphenomenon of female grouping behavior (Emlen and Oring 1977). "Understanding the evolution of polygamy in social mammals requires explanations of why females form social groups and how males compete for mates once those groups are formed" (Wittenberger 1980: p. 216).

Thus the existence of polygyny in walruses is probably best explained by the female defense polygyny model (Emlen and Oring 1977). As is generally argued for social mammals (Wittenberger 1980), I suggest that living in groups is an input into the evolution of walrus polygyny. This is considerably different from Bartholomew's (1970) model which suggests that environmental factors interact with terrestrial copulation through sexual selection feedback loops to result in extreme gregariousness, and thus extreme polygyny. Rather than being simply a reproductive adaptation, walrus grouping behavior may have to be viewed in a broader context of selective factors operating throughout the year.

Conclusions

Numerous morphological and physiological characteristics of pinnipeds are accepted as aquatic adaptations (Bartholomew 1970; Stirling 1975, 1983; Repenning 1976; Repenning et al. 1979). In this paper I hypothesize that the extreme gregarious behavior of the walrus may also be an aquatic adaptation.

CHAPTER V, BIBLIOGRAPHY

Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 5:325-383.

Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.

Brooks, J. W. 1954. A contribution to the life history and ecology of the Pacific walrus. Ak. Cooperative Wildlife Research Unit, Univ. of Ak., Fairbanks. Spec. Rep. 1. 103 pp.

Burns, J. J. 1965. The walrus in Alaska, it's ecology and management. Ak. Dept. Fish & Game, Juneau. 48 pp.

Burns, J. J., Shapiro, L. H. and Fay, F. H. 1980. The relationships of marine mammal distributions, densities, and activities to sea ice conditions. Final report, R.U. 248/249, 172 p. O.C.S.E.A.P, NOAA Environ. Res. Lab., Boulder,Colo.

Cox, C. and Le Boeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.* 111:317-335.

Crook, J. H., Ellis, J. E. and Gross-Custard, J. D. 1976. Mammalian social systems: structure and function. *Anim. Behav.* 24:261-274.

Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.

Eisenberg, J. F. 1981. The Mammalian Radiations. Univ. of Chicago Press, Chicago.

Estes, J. A. and Gilbert, J. R. 1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). *J. Fish. Res. Bd. Can.* 35:1130-1140.

Estes, J. A., and Gol'tsev, V. N. 1984. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: results of the first Soviet-American joint aerial survey, autumn 1975. Pages 67-76 in F. H. Fay, & G. A. Fedoseev, eds. Soviet-American Cooperative Research on Marine Mammals. Volume I Pinnipeds. U. S. Dept. of Commerce, NOAA, Wash. D.C.

Fay, F. H. 1960. Structure and function of the pharyngeal pouches of the walrus (*Odobenus rosmarus* L.). *Mammalia* 24:360-371.

Fay, F. H. 1982 Ecology and Biology of the Pacific Walrus. *Odobenus rosmarus divergens* Iliger.. U.S. Dept. Int., Fish & Wildl. Serv., Wash. D.C. N. Amer. Fauna, no. 74. 279 pp.

Fay, F. H. and Ray, C. G. 1968. Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linneaus). I. Evidence from thermoregulatory behavior. *Zoologica* 53:1-18.

Fay, F. H. and Kelley, B. P. 1980. Mass natural mortality of walruses, (*Odobenus rosmarus*) at St. Lawrence Island, Bering Sea, autumn 1978. *Arctic* 33:226-245.

Fay, F. H. and Lowry, L. F. 1981. Seasonal use and feeding habits of walruses in the proposed Bristol Bay clam fishery area. N. Pac. Fish. Mgt. Council rept. 60 pp.

Fay, F. H., Ray, C. G. and Kibal'chich, A. A. 1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. Pages 81-88 in F. H. Fay, & G. A. Fedoseev eds. Soviet-American Cooperative Research on Marine Mammals. Volume I Pinnipeds. U. S. Dept. of Commerce, NOAA, Wash. D. C.

Gentry, R. L. 1981. Northern fur seal - *Callorhinus ursinus* (Linnaeus, 1758) Pages 143-160 in S. H. Ridgway and R. J. Harrison, eds. Handbook of Marine Mammals. Volume I: the Walrus. Sea Lions. Fur Seals and Sea Otter. Academic Press, London.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 32:295-311.

Hamilton, W. J. III, Gilbert, W. M., Heppner, F. H. and Planck, R. J. 1967. Starling roost dispersal and a hypothetical mechanism regulating rhythmical animal movement to and from dispersal centers. *Ecology* 48:825-833.

Hamilton, W. J. III and Watt, K. E. F. 1970. Refuging. *Ann. Rev. Evol. Syst.* 1:263-286.

Irons, D. B. 1983. Hauling out and foraging behavior of walruses at St. Matthew Island, Alaska. Unpubl. ms., U. S. Fish & Wildl. Serv., Anch., Ak. 28 pp.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.

Kleiman, D. G. and Eisenberg, J. F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* 21:637-659.

Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *Amer. Zool.* 14:163-176.

Le Boeuf, B. J., and Briggs, K. T. 1977. The cost of living in a seal harem. *Mammalia* 41: 167-195.

Loman, J. and Tamm, S. 1980. Do roosts serve as "information centers" for crows and ravens? *Am. Nat.* 115:285-289.

McLaren, I. A. 1967. Seals and group selection. *Ecology* 48:104-

110.

Morrison, D. W. and Caccamise, D. F. 1985. Ephemeral roosts and stable patches? A radiotelemetry study of communally roosting starlings. *Auk* 102:793-804.

Nuechterlein, G. L. 1981. 'Information parasitism' in mixed colonies of western grebes and forster's terns. *Anim. Behav.* 29:985-989.

Nutting, C. C. 1891. Some of the causes and results of polygamy among the Pinnipedia. *Am. Nat.* 25:103-112.

Packer, C. 1983. Sexual dimorphism: the horns of African antelopes. *Science* 221:1191-1193.

Payne, R., and Webb, D. 1971. Orientation by means of long range acoustic signaling in baleen whales. *Ann. N.Y. Acad. Sci.* 188:110-141.

Pedersen, A. 1962. Das Walross. A. Ziemsen, Wittenberg-Lutherstadt. 60 pp.

Pierotti, R., and Pierotti, D. 1980. Effects of cold climate on the evolution of pinniped breeding systems. *Evolution* 34: 494-507.

Ray, G. C. and Watkins, W. A. 1975. Social function of underwater sounds in the walrus *Odobenus rosmarus*. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v Reun. Cons. Int. Explor. Mer.* 169:524-526.

Repenning, C. A. 1976. Adaptive evolution of sea lions and walruses. *Syst. Zool.* 25:375-390.

Repenning, C. A., Ray, C. E. and Grigorescue, D. 1979. Pinniped Biogeography. Pages 357-369 in J. Gray and A. J. Boucot, eds. Historical Biogeoraophy, Plate Tectonics, and the

Changing Environment. Oregon State Univ. Press, Newport.

Salter, R. E. 1979. Site utilization, activity budgets, and disturbance responses of Atlantic walruses during terrestrial haul-out. *Can. J. Zool.* 57:1169-1180.

Schaller, G. B. 1972. The Serengeti Lion: A Study of Predator-Prey Relations, Univ. of Chicago Press, Chicago.

Schefler, W. C. 1979. Statistics for the Biological Sciences. Addison-Wesley Publishing Co.

Schevill, W. E., Watkins, W. A. and Ray, G. C. 1966. Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. *Zoologica (N. Y.)* 51:103-111.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer* 169:205-212.

Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489-527 in J. Eisenberg and D. Kleiman, eds. Advances in the Study of Mammalian Behavior. Am. Soc. Mammal., Spec. Publ. 7.

Stirling, I. 1984. A group threat display given by walruses to a polar bear. *J. Mamm.* 65:352-353.

Tomlin, A. G. and Kibal'chich, A. A. 1975. Walruses of the Wrangel Island region. *Zool. Zh.* (Moscow) 54:266-272.

Tomlin, A. G. 1957. Cetacea. Zveri SSSr i prilezhaschikh stran. Tom 9. Akademii Nauk SSSR, Moscow. 756 pp.

Visnevskaia, T. IU. & Byhkov, V. A. 1985. A mixed herd of the Laptev walrus in M. Pronchishchev Bay and prospects for its protection. Pages 3-14 in V. E. Flint (ed.). Ecological

Aspects of Protection of the Beasts of the World. Ministry of agriculture, Moscow. (Transl. by F. H. Fay, 1986).

Waltz, E. C. 1982. Resource characteristics and the evolution of information centers. *Am. Nat.* 119:73-90.

Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as "information-centres" for food finding. *Ibis* 115: 517-534.

Wartzok, D. and Ray, C. G. 1980. The hauling-out behavior of the Pacific walrus. U. S. Marine Mammal Commission, Rep. MMC-75/15, 46 pp.

Weatherhead, P. J. 1983. Two principal strategies in avian communal roosts. *Am. Nat.* 121:237-243.

Wells, R. S. 1986. Structural aspects of Dolphin Societies. Ph.D. diss., Univ. of California, Santa Cruz.

Wilson, E. O. 1975. Sociobiology. Belknap, Cambridge.

Wittenberger, J. F. 1980. Group size and polygamy in social mammals. *Am. Nat.* 115:197-222.

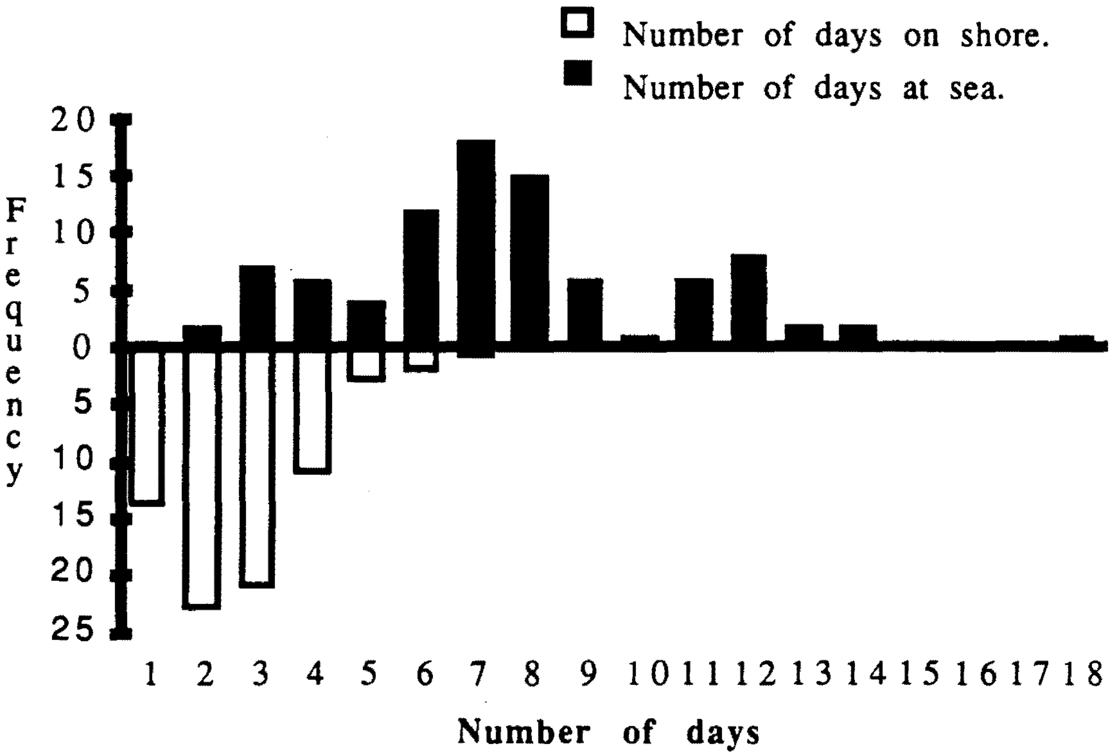
Wittenberger, J. F. 1981. Animal Social Behavior. Duxbury, Boston.

Yom-Tov, Y. 1979. The disadvantage of low positions in colonial roosts: an experiment to test the effect of droppings on plumage quality. *Ibis* 121:331-333.

Yom-Tov, Y., Imber, A. and Otterman, J. 1977. The microclimate of winter roosts of the starling, *Sturnus vulgaris.* *Ibis* 119:366-368.

Zahavi, A. 1971. The function of pre-roost gatherings and communal roosts. *Ibis* 113:106-109.

Figure V.1. Resting and feeding cycles of walruses on Round Island, Alaska, 17 June to 14 September, 1980.



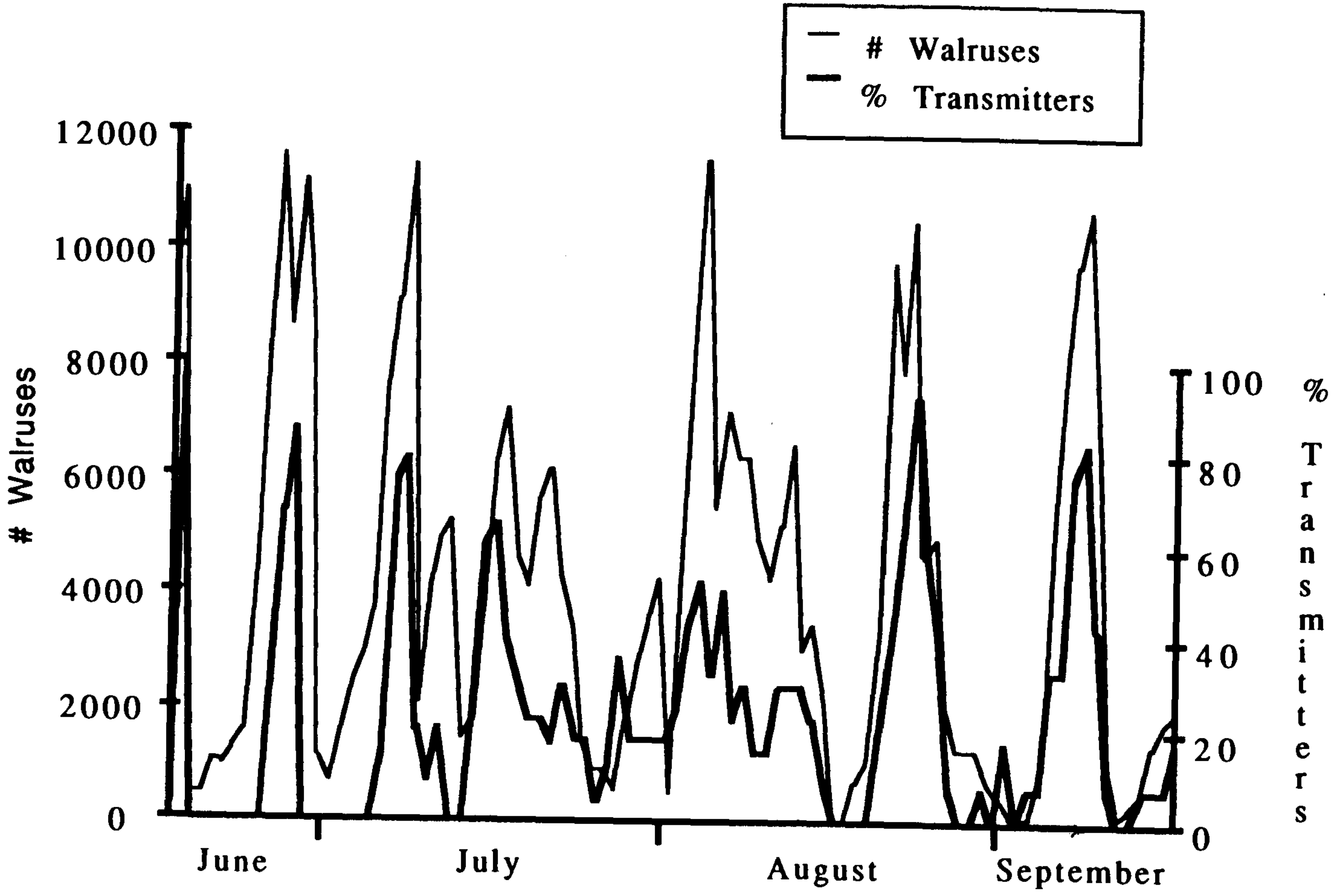


Figure V.2. Round Island census data, 17 June to 14 September 1980.

Figure V.3. Cape Peirce census data, 16 June to 5 October 1984. Symbols below the x-axis indicate missing data. Values are extrapolated for these days.

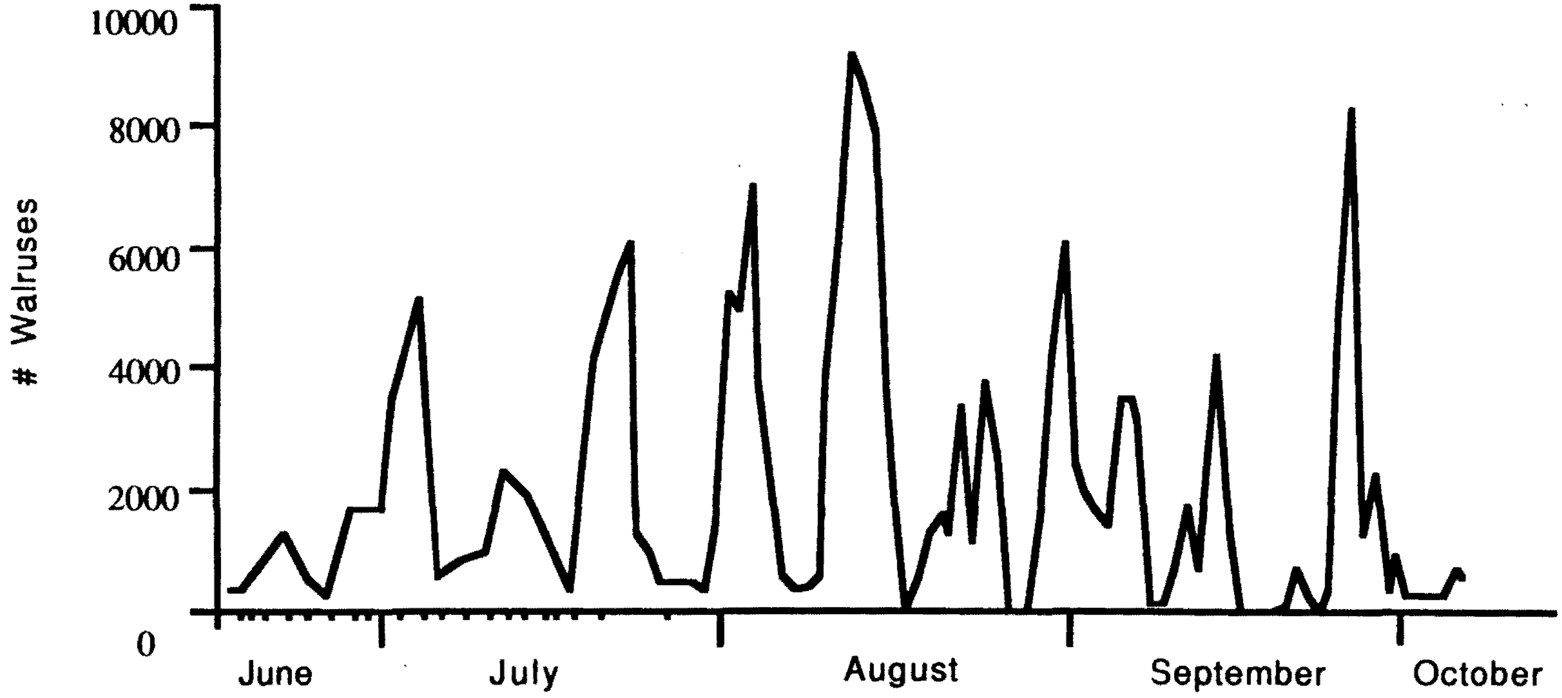


Figure V.4. Map of Round Island and Punuk Island, Alaska.

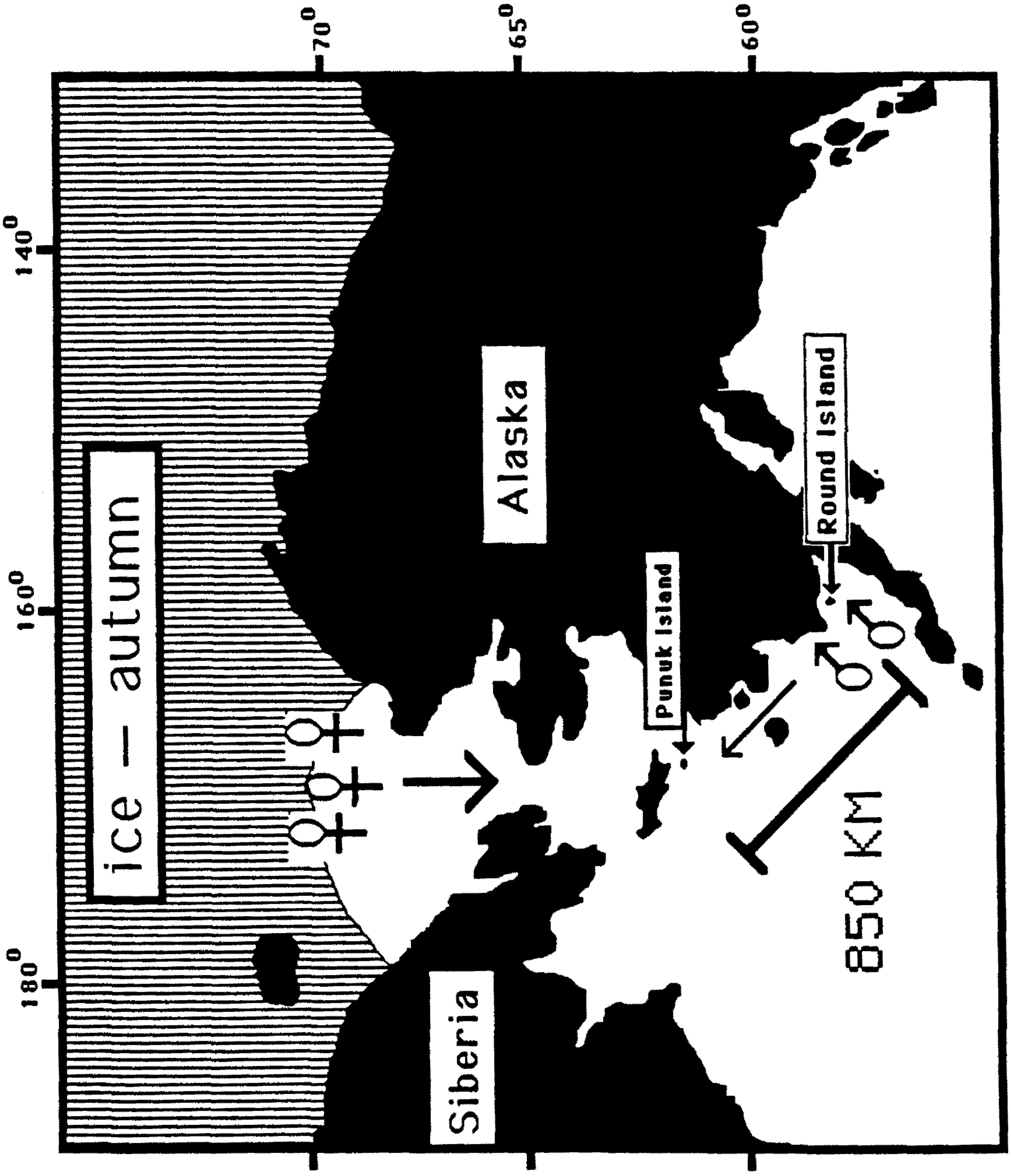


Figure V.5. Hypothesis I. Walruses are dispersed at sea and they arrive synchronously ashore.

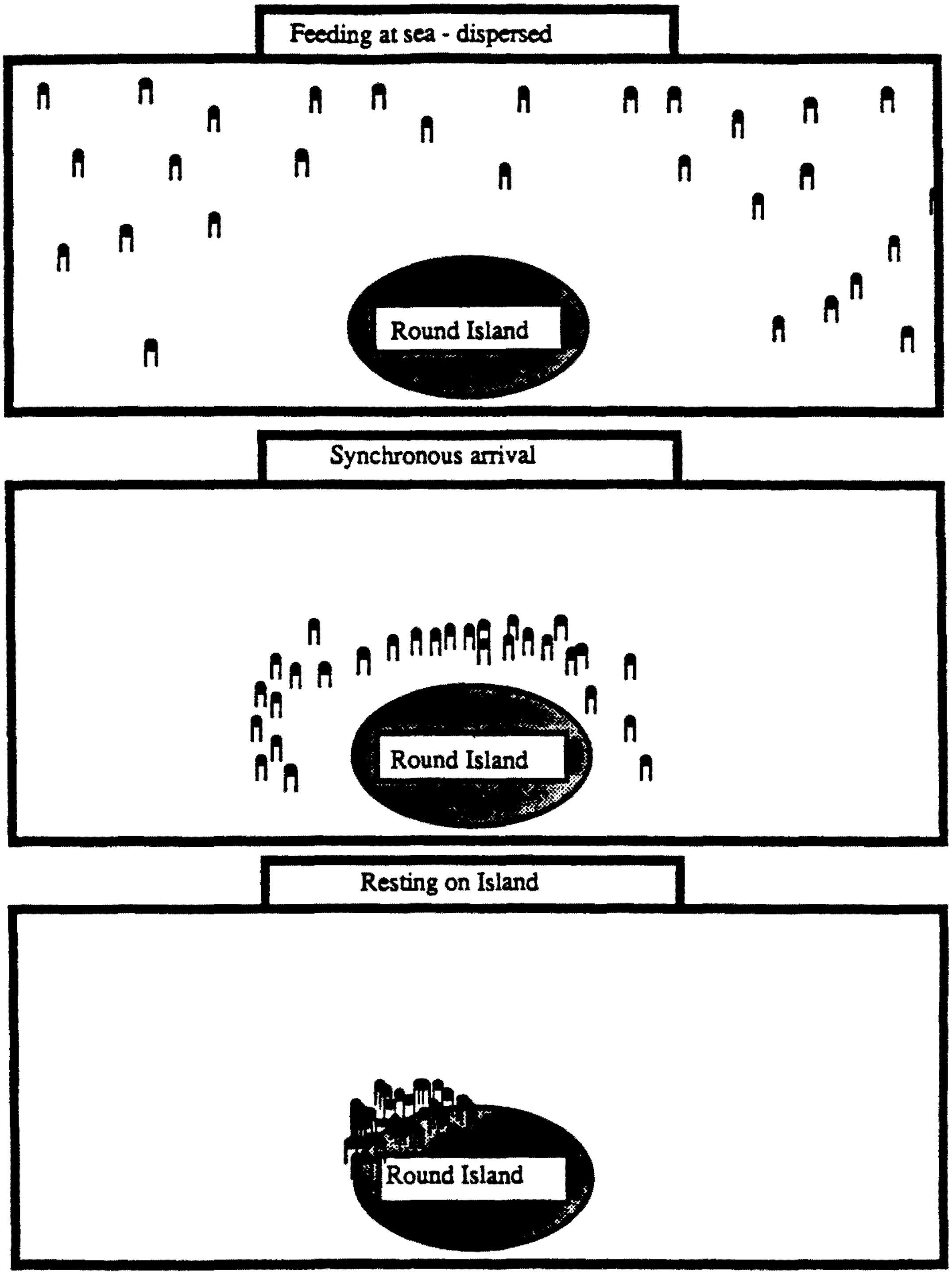
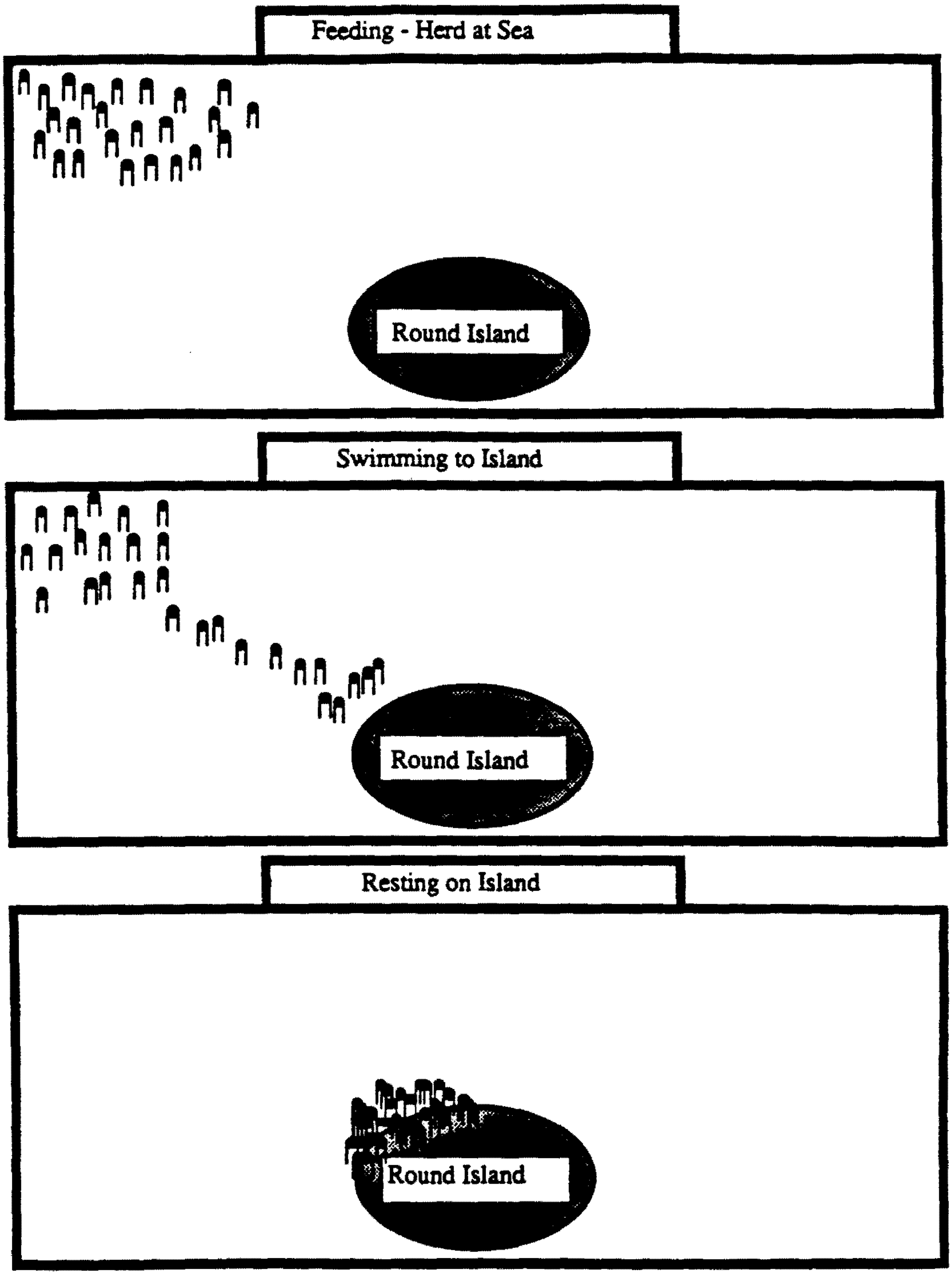


Figure V.6. Hypothesis II. Walruses arrive ashore synchronously because they remain in large herds while at sea.



CHAPTER VI
AQUATIC GROUPING IN OTHER PINNIPEDS

Two hypotheses for walrus (*Odobenus rosmarus divergens*) social organization were proposed in Chapter V: either walruses are dispersed at sea and arrive on shore synchronously, or they are a herd at sea. Both of these hypotheses imply a social organization more complex than aggregated animals utilizing limited space on islands. Are these hypotheses applicable to other pinnipeds? Due to the paucity of data on nonreproductive behavior of other pinniped species, I can only enumerate the following possibilities:

1) Walrus social groups may be unique among pinnipeds. This would explain why walruses are gregarious in the pack ice, a habitat where all other pinnipeds have a dispersed distribution or are found in low density groups.

Stirling (1975) suggested that female gregariousness in walruses is a "phylogenetic relict". This idea is based on paleontological evidence that ancestral walruses evolved in the temperate latitudes, where they were sexually dimorphic and probably bred on islands (Repenning 1976). It is difficult to imagine how aggregations resulting from limited breeding space on islands would subsequently transfer into a clumped distribution in one million km^2 (Burns et al. 1980) of constantly moving pack ice, unless sophisticated adaptations which might explain synchronous land-sea movements (like communication capabilities or other synchronizing mechanisms) had already evolved before walruses left islands.

2) The hypotheses presented in Chapter V may be reasonable for other pinniped species. Although not as large or dense as walrus groups, other species of pinnipeds form terrestrial groups (of males and females) outside the breeding season. Examples include Steller sea lions, *Eumetopias jubatus* (Kenyon and Rice 1961; Fiscus and Baines 1966; Mate 1973; Harestad and Fisher 1975; Loughlin and Rugh 1984; pers. obs.), California sea lions, *Zalophus californianus* (Fiscus and Baines 1966; Mate 1973; Odell 1975; Aurioles et al. 1983; pers. obs.), Southern sea lions, *Otaria flavescens* (Vaz-Ferreira 1975), South American fur seals, *Arctocephalus australis* (Vaz-Ferreira 1975), and Galapagos fur seals, *Arctocephalus galapagoensis* (Trillmich and Mohren 1981). Peterson and Bartholomew (1967) observed that California sea lions formed denser groups during the nonbreeding season than during the breeding season. Diurnal fluctuations in the number of animals ashore were reported for adult male California sea lions outside the breeding season (Mate 1975). Synchronous land-sea movements, both during and outside the breeding season, were observed in Galapagos fur seals (and were correlated to the lunar cycle; Trillmich and Mohren 1981).

The ability to form groups in the unstable pack ice is not unique to walruses. Steller sea lions on the pack ice were described resting in clusters of thigmotactic groups of approximately 3-15 individuals per group (D. Caulkins, pers. comm.). The majority of the animals were males. These observations suggest that, like walruses, Steller sea lions may have mechanisms for locating one another in the shifting pack ice.

Groups of other pinnipeds have also been observed at sea. Mate (1973) described a "migratory wave" of Steller sea lions and California sea lions along the Oregon coast. I have seen Steller sea lions traveling in groups of several hundred individuals at sea (in Bristol Bay, Alaska). Groups of southern sea lions have been observed 120 miles offshore playing, feeding (Hamilton 1939), traveling (in groups of two to ten individuals) and sleeping in "compact" groups of three to seven individuals (Vaz-Ferreira 1975). A herd of 500 animals was observed traveling offshore (Hamilton 1939).

Northern fur seals are pelagic during the entire nonbreeding season. Gentry (1981) noted of fur seals that "the existence of some form of social organization at sea cannot be ruled out at present". It seems unlikely that pelagic seal hunters would have been able to harvest 61,838 northern fur seals in 1894 (U.S. Dept. of Comm. 1977) if they had been dispersed over the north Pacific Ocean. At sea, fur seals have been observed as singles and in small groups of up to 25 individuals, although a group of 75 to 100 individuals has been reported (Panin and Panina 1971: p.73). These singles and small groups were described as being aggregated into low density patches or areas (Panin and Panina 1971: p. 71). Furthermore, these patches were a nonrandom assemblage of fur seals that segregated with respect to sex, age and maturity according to Lander and Kajimura (1982), who also noted (p. 322) that: "Oddly, mixing is greater between Medny Island and the Pribilofs than between Medny and nearby Bering Island." If intermixing on rookeries were simply the result of navigational error by individual fur seals, one would predict intermixing to be greater between nearby islands rather than between distant islands. An alternate interpretation is that fur seals from Medny Island and the Pribilofs may have more overlap in their pelagic distribution or migratory routes (than animals from Medny and Bering Island), and they may follow the incorrect herd home.

Social foraging may be a selective force influencing grouping behavior of some pinnipeds. Clumped distribution of fur seals at sea has been attributed to locally abundant food. An alternate hypothesis is that aquatic concentrations of pinnipeds are low density herds which facilitate the location and capture of schooling prey. Once prey is located, Shusterman (1981) suggested that group feeding by Steller sea lions may help control the movement of schooling fishes and squids and facilitate their exploitation. This hypothesis is supported by data from Fiscus and Baines (1966: p. 199-200).

> They "...observed feeding behavior and collected Steller sea lions in the vicinity of Unimak Pass, Alaska. ...the sea lions left their hauling grounds in early morning, in compact groups of several hundred to several thousand animals. They then swam 5 to 15 miles out into feeding areas in or adjacent to Unimak Pass. There they dispersed into smaller groups of less than 50 animals. The feeding groups usually contained both sexes and mixed sizes of animals. In the late afternoon they again formed into large groups and returned to the hauling grounds. The massing described above occurred where sea lions were feeding on schooling fishes or squids. Where large schools of prey were absent, sea lions fed singly or in small groups of two to five animals. Similar behavior was observed for Steller sea lions in other parts of Alaska and for California sea lions off San Miguel Island, California."

Gentry (1970: p.66) reported that female Steller sea lions departed for feeding forays in groups on a diurnal cycle.

> "For example, between 1830 and 2100 hours on July 7, I observed 24 separate groups of females, totaling 106 animals, depart from area 7. The mean group size was four (range one to 12), and the groups spent an average of four-and-a-half minutes in the surf before departing. Out of 18 groups, 11 went south. When departing, females swam at the surface and sometimes joined passing groups of California sea lions. These mixed groups remained together as far toward the horizon as they could be seen. In the morning, females rarely returned in groups larger than three. Thus, departing groups may have broken up at sea. Females were never seen returning with *Zalophus.*"

Female Steller sea lions form groups and become particularly active and vocal prior to departing to sea suggesting that these behaviors may "synchronize group feeding" (R. Gisner, cited in Shusterman 1981: p.130). Maybe these group behaviors are analogous to social facilitation that occurs in African hunting dogs (*Lycaon pictus*) prior to departure for hunting (Malcolm 1979).

Grouping behavior in at least some pinnipeds appears to involve complex adaptations. My observations on walruses suggest that at least some pinnipeds may be highly social animals beyond the mating interval. This implies that natural selection throughout the year may be responsible for the grouping behavior. Rather than being simply a reproductive adaptation, pinniped grouping behavior may have to be viewed in a broader context of selective factors operating during the annual cycle as a whole.

CHAPTER VI, BIBLIOGRAPHY

Aurioles, D., Sinsel, F., Fox, C., Alvarado, E. and Maravilla, O. 1983. Winter migration of subadult male California sea lions (*Zalophus californianus*) in the southern part of Baja California. *J. Mamm.* 64:513-518.

Burns, J. J., Shapiro, L. H., and Fay, F. H. 1980. Ice as marine mammal habitat in the Bering Sea. Pages 781-797 in D. W. Hood and J. A. Calder eds. The Eastern Bering Sea Shelf: Oceanography and Resources. Vol. 2. Univ. Wash. Press, Seattle.

Fiscus, C. H., and Baines, G. A. 1966. Food and feeding behavior of Steller and California sea lions. *J. Mamm.* 47:195-200.

Gentry, R. L. 1970. Social behavior of the Steller sea lion. Ph.D. diss., Univ. California, Santa Cruz.

Gentry, R. L. 1981. Northern fur seal - *Callorhinus ursinus* (Linnaeus, 1758) Pages 143-160 in S. H. Ridgway and R. J. Harrison, eds. Handbook of Marine Mammals. Volume I: the Walrus, Sea Lions, Fur Seals and Sea Otter. Academic Press, London.

Hamilton, J. E. 1939. A second report on the southern sea lion, *Otaria byronia* (De. Blainville). *Discovery Rep.* 19:121-164.

Harestad, A. S. and Fisher, H. D. 1975. Social behavior in a non-pupping colony of Steller sea lions (*Eumetopias jubata*). *Can. J. Zool.* 53:1596-1613.

Kenyon, K. W. and Rice, D. W. 1961. Abundance and distribution of the Steller sea lion. *J. Mamm.* 42:223-234.

Lander, R. H. and Kajimura, H. 1982. Status of northern fur seals. Pages 319-345 in Mammals in the Seas, Vol. 4, Small Cetaceans, Seals, Cirenians, and Otters. Food Agric. Organ.

U.N., Rome. FAO Fish. Ser. 5.

Loughlin, T. R. and Rugh, D. J. 1984. Northern sea lion distribution and abundance 1956-1980. *J. Wildl. Mgt.* 48:729-740.

Malcolm, J. R. 1979. Social organisation and communal rearing in African wild dogs. Ph.D. diss., Harvard Univ. 215 pp.

Mate, B. R. 1973. Population kinetics and related ecology of the northern sea lion, *Eumetopias jubatus*, and the California sea lion, *Zalohpus californianus*, along the Oregon coast. Ph.d. diss., Univ. of Oregon, Eugene. 94 pp.

Mate, B. R. 1975. Annual migrations of the sea lions *Eumetopias jubatus*, and *Zalohpus californianus* along the Oregon Coast. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v Reun. Cons. Int. Explor. Mer.* 169:455-561.

Odell, D. K. 1975. Abundance of California sea lions on San Nicolas Island, California. *J. Wildl. Mgt.* 39:729-736.

Panin, K. I. and G. K. Panina. 1971. Fur seal ecology and migration to the sea of Japan during winter and spring. Pages 66-76 in V. A. Arsen'ev and K. I. Panin, eds. Pinnipeds of the North Pacific, Israel Prog. for Scient. Translations, Jerusalem.

Peterson, R. S. and Bartholomew, G. A. 1967. The natural history and behavior of the California sea lion. *Am. Soc. Mammal.*, Spec. Publ. 1.

Repenning, C. A. 1976. Adaptive evolution of sea lions and walruses. *Syst. Zool.* 25:375-390.

Schusterman, R. J. 1981. Steller sea lion *Eumetopias jubatus* (Schreber, 1776). Pages 119-141 in S. H. Ridgway and R. J. Harrison, eds. Handbook of Marine Mammals. Volume I: the Walrus, Sea Lions, Fur Seals and Sea Otter. Academic Press, London.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v Reun. Cons. Int. Explor. Mer.*169:205-212.

Trillmich, F. and Mohen,W. 1981. Effects of the lunar cycle on the Galapagos Fur Seal, *Arctocephalus galapagoensis. Oecologia* 48:85-92.

U. S. National Oceanic and Atmospheric Admin. 1977. The story of the Pribilof fur seals. U. S. Dept. of Commerce, Wash. D. C. 34 pp.

Vaz-Ferreira, R. 1975 Behaviour of the Southern sea lion, *Otaria flavescens* shaw. In K. Ronald and A. W. Mansfield, eds. Biology of the Seal. *Rapp. P.-v Reun. Cons. Int. Explor. Mer.* 169:219-227.

CHAPTER VII

TECHNIQUES FOR ATTACHING RADIO-TAGS TO THE TUSKS OF PACIFIC WALRUSES

Radio telemetry is an important tool for answering questions about movement and activity of individuals of a variety of species. Telemetry is a particularly useful technique for animal studies such as walruses (*Odobenus rosmarus*) that reside in remote habitats and are difficult to observe directly.

There is considerable data on seasonal distribution of the walrus population, but seasonal or inter-year movements of individuals are unknown (Fay 1982). Information is unavailable on exchange between portions of the population, site fidelity of individuals, and routes and timing of migration.

Radio transmitters have obvious utility for delineating movements of individual walruses, but attachment of radios (or even visual tags) to marine mammals is especially problematic because of the drag exerted by water. Attempts to mark walruses began with visual tags. The first tags were numbered metal discs that were attached to a harpoon-like metal shaft. Mansfield (1958) and Krylov (1965, cited in Fay 1982) attached 115 and 500 of these tags, respectively. Twenty three metal flipper tags were applied [11 by Brooks (1954); 12 by F. H. Fay, J. W. Brooks and K. W. Kenyon (Fay 1982: p. 243)], but none of these tags were ever resighted or recovered. The first effort to attach radio transmitters to walruses was in 1970 by G. C. Ray of Johns Hopkins University. Ray began by immobilizing one walrus;

however, the animal died from an adverse drug reaction. Eventually Ray and D. Wartzok tried to attach transmitters with a device that fired spines into the skin of resting walruses. None of these transmitters remained attached more than a few hours (D. Wartzok and G. C. Ray, pers. comm.).

I wanted to measure the duration of forays at sea and time that walruses spent on shore at Round Island, Alaska (56°02'N160°50'W). In 1977 I began tagging walruses with visual marks that included: 1) livestock marker, 2) traffic line paint, and 3) spaghetti tags. I concluded that visual tags had limited utility for measuring duration of forays or periods on shore because: 1) walruses on Round Island often rested on beaches that were inaccessible to observers; 2) neighboring walruses often covered up visual tags so they could not be seen; and 3) approximately 10,000 walruses were utilizing Round Island, so many person-hours were required to search the large herds for tags.

I began developing a telemetry system for walruses in 1978 because radio transmitters could overcome these problems. The walrus telemetry work that I initially became involved in also used drugs to immobilize animals (DeMaster et al. 1980). However, like Ray, we experienced high mortality rates of drugged walruses, or partially immobilized animals escaped into the water because the drugs took effect so slowly. Moreover, appropriate drugs were unavailable.

When working on immobilized walruses, I found that I could often approach adjacent animals (who were not immobilized) without disturbing them. I judged that it might be possible to attach transmitters to sleeping walruses. Consequently, in 1979 I began developing techniques by which I could attach transmitters to the tusks of sleeping walruses.

In this paper I describe the attachment techniques that C. Zabel and I developed and subsequently used for studying the land-sea movements of walruses. I also present data on the duration that radio-tags remained attached to walruses.

Materials and Methods

Attachment of radio-tags to immobilized walruses in 1978.

Radio-tags were attached to tusks of immobilized walruses using radiator hose clamps (*Norton*™) that were fastened around both the transmitter and tusk.

Attachment of radio-tags to sleeping walruses in 1979.

Our first prototype method for attaching radio-tags to tusks of sleeping walruses utilized the same hose clamps. The radio-tag was attached to a hose clamp that was put on an air-driven impact wrench, mounted on the end of a pole. The clamp was slipped over the tusk of a sleeping walrus and then the impact wrench was activated. The impact wrench was driven by compressed air (from a SCUBA tank).

This method was not developed to a functional point because: 1) the noise of the impact wrench frightened the animals, causing the hose clamps to break free of the impact wrench prematurely; and 2) I found that the clamps would not withstand sufficient torque[1] for durable attachment. (The longest time that a transmitter stayed on a tusk was six weeks, so I will only mention this technique briefly.)

Attachment of radio-tags to tusks of sleeping walruses, 1980-81.

I began developing a method that used a commercially available high pressure hose clamp (*Band-it*™, Denver, Colorado). These bands are tightened by pulling the end of a band through a precrimped buckle with a special tool (*Band-it* tool).

The hydraulic banding tool.

The *Band-it* tool was not applicable for my purposes because it was slow, requiring 30 seconds or more to tighten a band; and the length of the tool was short, making it necessary to work very close to the tusks of sleeping walruses. I overcame these problems by designing a tool that duplicated the action of the commercial tool but has the following advantages: 1) it is powered by a hydraulic cylinder and is thus very fast; and 2) the tool is long enough that radio-tags can safely be attached to sleeping walruses (overall length=1.94 m; Fig. VII.1). The hydraulic tool has two new features (that the previous methods

---

[1] Subsequently I located an ("auger") type hose clamp that was much stronger (*Hi-Torque*™). Although I did not test these clamps in the field, I did test them in the lab and found them to be much stronger than the clamps I had previously used. Thus, I feel that there is still potential for development of an attachment method utilizing these clamps.

did not have): 1) the tightening action is silent, thus the walruses are not alerted, and 2) the bands can be applied very tightly.

The hydraulic tool consists of the following components:

Hydraulic cylinder. The tool is activated by a custom, machine-made hydraulic cylinder. The tubular portion is constructed of stainless steel tubing (alloy=316; OD=50.4 mm, ID=44.9 mm, length=256 mm). The piston inside the cylinder is made of teflon and bronze, and is attached to the tail of the band with a pull rod (just behind the head of the tagging tool). (The pull rod is made of stainless steel rod, alloy=316, D=12.7 mm.) The stroke of the cylinder is approximately 190 mm. The front and back of the cylinder is composed of a magnesium alloy (to save weight) and teflon, and are held in place with six double-butted[2] tie rods (stainless steel, alloy=316).

Superstructure. For balance, the hydraulic cylinder is placed at the rear of the tagging tool; thus, the superstructure has to withstand the compression force of the hydraulic cylinder. The superstructure is built out of three titanium tubes (high strength to weight ratio; OD=25.4 mm, wall thickness=.9 mm, length=1,435 mm). These three tubes are cross-strutted with two magnesium alloy braces (in addition to the bracing provided by the front and back of the tagging tool).

Head of the tool. The end of the tool is built from magnesium alloy (to save weight). The slot where the tail of the

---

[2] Double-butted means that the tie rods are thinner in the center than at the ends, where additional strength is needed. Thus double-butted rods are lighter without reducing strength (D=7.9 mm at the ends; D=5.9 mm at the center).

band feeds through the end of the tool is reinforced with an insert constructed of hardened tool steel. After the cylinder is activated (pulling the band tightly around the tusk), the tail of the band is sheared off by twisting the tool with the handle at the rear. The band shears off easily when under tension exerted by the hydraulic cylinder.

Power supply. The power supply consists of an aluminum SCUBA pony dive tank, filled half with water and then pressurized to 115 kg/cm^2. (This pressure results in approximately 1365 kg of pull exerted on the tail of the band). By inverting the tank, water instead of air is pushed out of it when the valve is opened. The advantages of water (hydraulic power) over air (pneumatic power) are: 1) it is much quieter, and 2) the piston slams into the back of the hydraulic cylinder with less force when the tail of the band is sheared off[3]. The hydraulic cylinder is connected to the high pressure port of the pony tank with a high pressure hose. A valve at the base of the cylinder activates the action of the hydraulic cylinder when it is opened.

Transmitter bracket. Each transmitter is placed in a bracket that wraps around the tusk. The transmitter brackets are constructed of three layers of fiberglass cloth that are laminated with underwater epoxy resin (*Aquatapoxy* TM paint). The

---

[3] When water is used, the piston travels to the back of the cylinder proportional to the rate at which water enters the intake valve. When powered by air, the piston accelerates with the combined effects of air coming though the intake valve and the expansion of air (already in the cylinder) released from pressure when the tail of the band breaks off.

fiberglass brackets are laid up on a male semi-circular mold (D=200 mm). The attachment band goes between the compartment for the transmitter and the bracket, so that the transmitter is not crushed when the band is tightened (Fig. VII.2). Standard paint pigment is applied to the resin to aid in visual relocation of tagged individuals.

Attachment band. The band (*Band-it*) is preformed (15 mm wide; 316 stainless steel alloy) and carefully wet sanded with medium grit wet/dry sand paper and *Fantastic*TM cleaner to remove all oil and scarify the surface.

Transmitter. I use small, low output transmitters, approximately 16 mm in diameter and 90 mm long, that emit pulses on discrete frequencies between 148-149 MHz. Earlier transmitters had a whip antenna (approximately 230 mm long, D=2 mm) constructed of coated stainless steel cable. Some of these transmitters were observed with worn antennae after they had been attached to walruses. Thus, I subsequently used antennae constructed from stainless steel springs (D=6 mm) that are embedded in urethane (length, approximately 115 mm). For additional abrasion protection, these antennae are embedded in the fiberglass bracket parallel to the transmitter housing (Fig. VII.2).

Operation of hydraulic tagging tool in the field.

First the band (with bracket and transmitter) is attached to the head of the tagging tool. Next, I apply a liberal layer of underwater epoxy (*Aquatapoxy*™ Jell) to the inside of the bracket and band, that, when tightened fills the cracks and convolutions that naturally occur on most walrus tusks, resulting in a flush secure attachment. The transmitter bracket is then carefully slipped over the tusk of a soundly sleeping walrus, so that the transmitter is positioned on the proximal posterior surface of the tusk (this has to be done without hitting the walruses' tusk or the walrus will wake up before the transmitter is fully positioned). Then the valve is opened, and the band tightens in less than half of a second. By this time the walrus is usually fully awake and the tail of the band is sheared off as the walrus is lifting his head. I found that walruses slept much more soundly in hot weather, so I did most of my work on warm days.

Latex banding tool.

Simultaneously, I developed a second technique for attaching transmitters. This tagging tool is composed of a two m long aluminum pole with a semi-circular head mounted perpendicular to the pole (Fig. VII.3). The transmitter is tied (with nylon string saturated with epoxy resign) onto a loop of latex tubing (OD of loop=approximately 40 mm; OD of tubing=15-20 mm; wall thickness=3 mm). The loop is then stretched over the head of the latex banding tool, using screw drivers as levers. After the loop is on the head of the tool, the latex tube and transmitter are wrapped with fiberglass tape that has also been saturated in underwater epoxy resin (*Aquatapoxy* jell). Then the tagging tool is slipped over the tusk of the target walrus, keeping the handle of the tool perpendicular to the walruses' tusk. To release the tag, the end of the handle is quickly moved to an angle approximately 60^0 with the tusk, which levers the tubing off of the head of the tagging tool and onto the walruses' tusk. Using this method it is difficult to position the transmitter on the posterior proximal portion of the tusk.

Results and Discussion

Radio-tags were attached to walruses over a two year period. Data on the duration of retention are summarized in Tables VII.1 and VII.2. Of 24 radio-tags that were attached with the hydraulic banding tool, 20 were still attached when I left Round Island at the end of each field season (11 of 15 in 1980 and 9 of 9 in 1981), one failed electronically (the signal became very weak), one fell off after 63 days, and two were never relocated after 2 and 25 days, respectively (Table VII.1). Of the six transmitters that were attached with the latex banding tool, one remained attached longer than one field season, one was not relocated after the day it was attached, and four were recovered from the beach 1, 16, 21 and 61 days, respectively after attachment. Of the three radio-tags that disappeared (two hydraulic (ID# =7 and 13), one latex (ID#=4)) I cannot distinguish between attachment failure, the walrus not returning to Round Island, and electronic failure. For the purpose of calculating the number of days transmitters remained attached, I conservatively assumed that the transmitter fell off the day after it was last located. Since the radio-tags had a short life expectancy (four months in 1980 and eight months in 1981), it was not possible to electronically relocate the transmitters during subsequent years. However, since the transmitters were mounted in colored brackets, it was possible to visually relocate some of the transmitters (Table VII.2). (It was not always possible to trace exactly which transmitter it was from the color of the bracket.)

Lack of recovery could be due to any of the following factors: the walrus did not return to Round Island during subsequent years; the radio-tag fell off; or the radio-tag was not observed in the large, dense herds. Thus, the estimates of attachment time are minimal. However, some of the transmitters remained attached for greater than 1000 days.

The latex banding method was tested on a much smaller sample; however, it seems clear that the hydraulic technique was a more durable attachment method. Nonetheless, the latex banding tool was easier to use than the hydraulic banding tool. Future improvements on the latex banding tool might increase attachment duration of radio-tags using this technique. It should be emphasized that far less time was spent developing the latex banding tool than was spent on the hydraulic banding tool. The latex banding tool might be useful for future short term studies. For example, aerial surveys of Pacific walruses have been imprecise due to the high variance between survey days and between randomly selected survey transects (Estes and Gilbert 1978; Estes and Gol'tsev 1984). The precision of these surveys could probably be greatly increased if a large sample of transmitters were deployed so that the proportion of walruses on ice vs. in the water could be calculated. Satellite telemetry also has many applications for delineating the routes and timing of walrus migration (Fay 1982).

CHAPTER VII, BIBLIOGRAPHY

Brooks, J. W. 1954. A contribution to the life history and ecology of the Pacific walrus. Ak. Coop. Wildl. Res. Unit, Univ. of Ak., Fairbanks. Spec. Rep. 1. 103 pp.

DeMaster, D. P., Faro, J. B., Estes, J. A. Taggart, J. and Zabel C., 1981. Drug immobilization of walrus (*Odobenus rosmarus*). *Can. J. Fish. Aquat. Sci.* 38:365-367.

Estes, J. A. and J. R. Gilbert. 1978. Evaluation of an aerial survey of Pacific walruses *(Odobenus rosmarus divergens*). *J. Fish. Res. Bd. Can.* 35:1130-1140.

Estes, J. A., and V. N. Gol'tsev. 1984. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: results of the first Soviet-American joint aerial survey, autumn 1975. Pages 67-76 in F. H. Fay, & G. A. Fedoseev, eds. Soviet-American Cooperative Research on Marine Mammals, Volume I Pinnipeds. U. S. Dept. of Commerce, NOAA, Wash. D. C.

Fay, F. H., Ecology and Biology of the Pacific Walrus, *Odobenus rosmarus divergens* Illeger. 1982. U.S. Dept. Int., Fish & Wildl. Serv., Wash. D.C. N. Amer. Fauna, no. 74. 279 pp.

Mansfield, A. W. 1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus) in the eastern Canadian arctic. *Fish. Res. Bd. Can.*, Manuser Rep. Ser. (Biol.) 653. 146 pp.

Figure VII.1. Diagram of the hydraulic tagging tool.

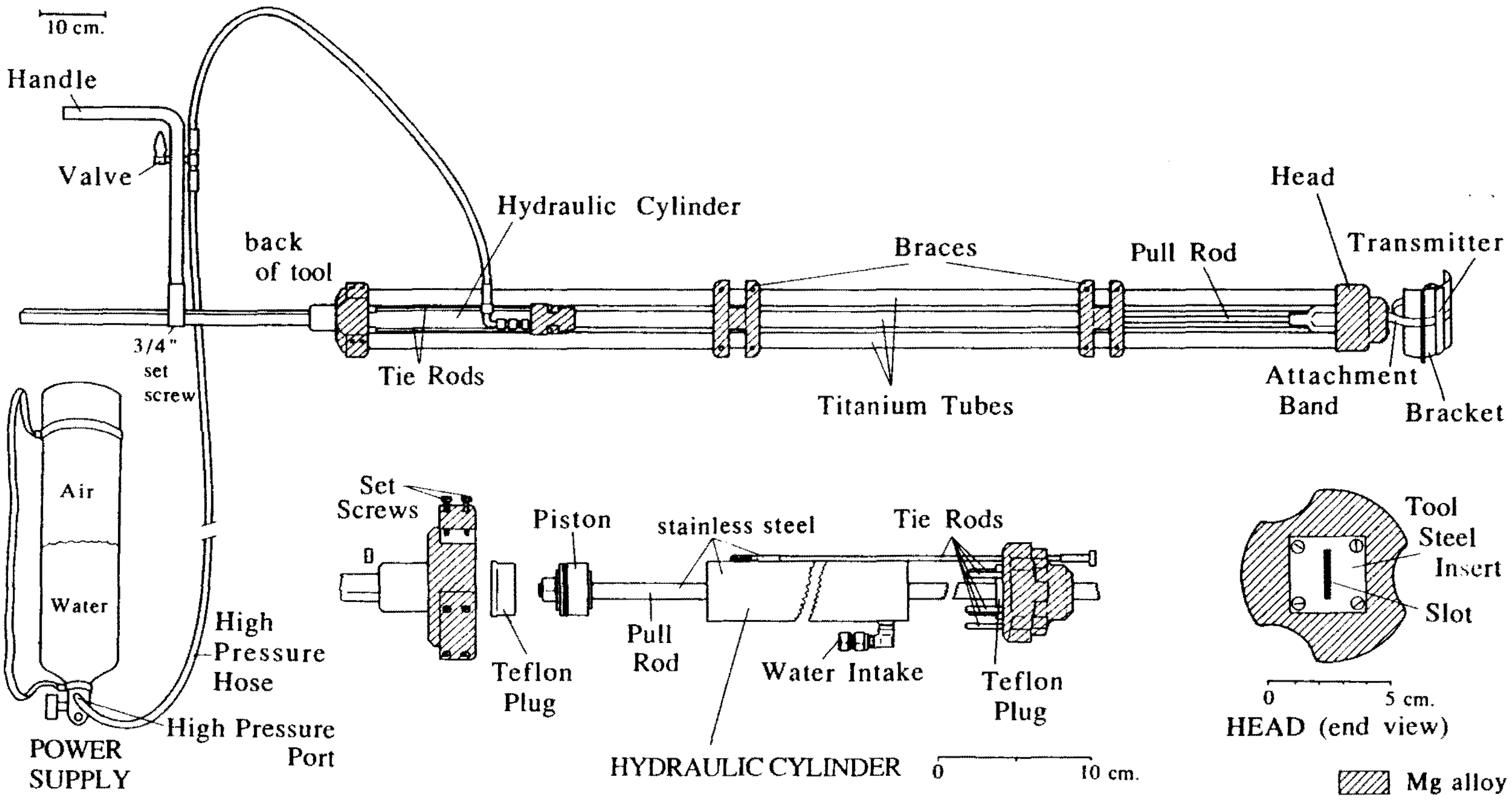


Fig. VII.2 Transmitter mounted in tusk bracket that is used with the hydraulic tagging tool.

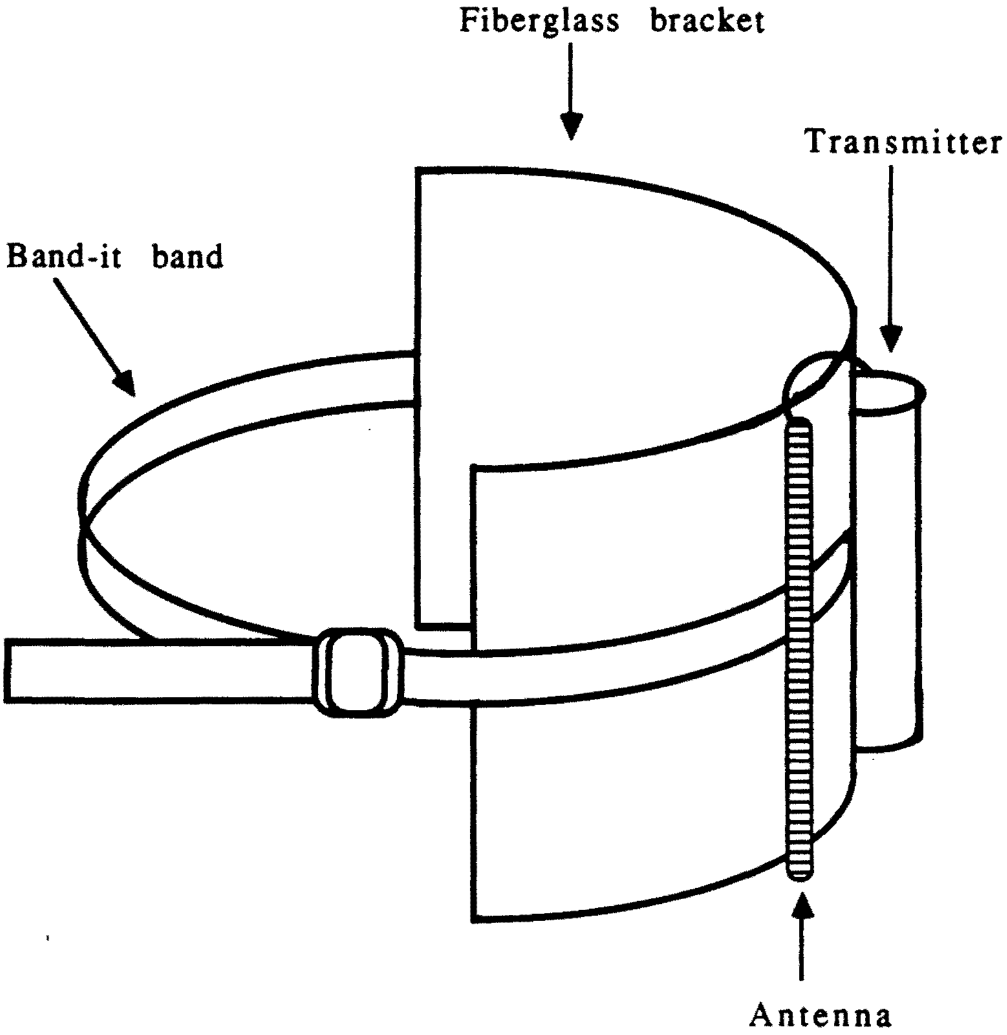


Figure VII.3. Latex banding tool for putting transmitters on walrus tusks.

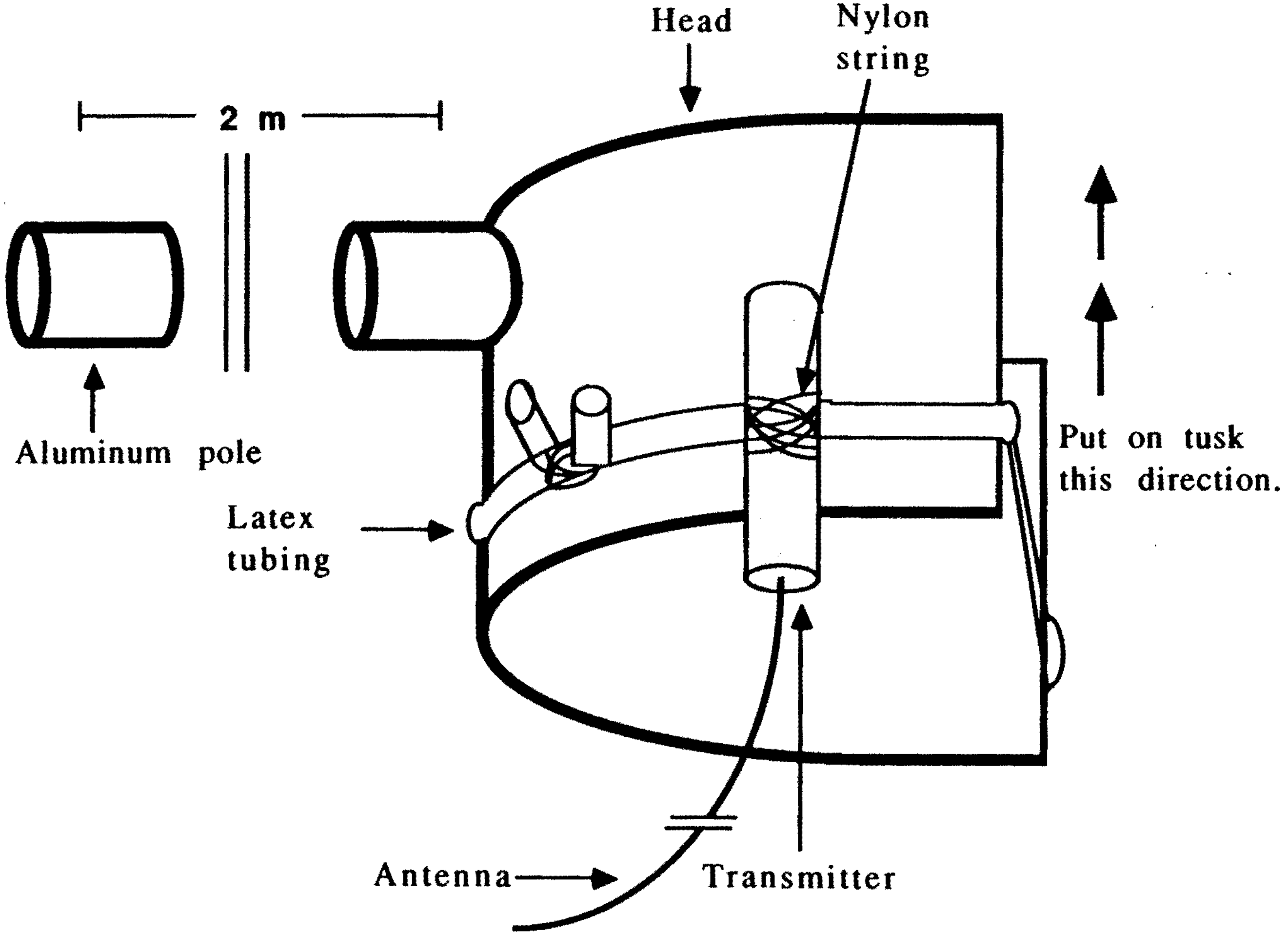


Table VII.1. Number of days that radio-tags remained attached to walrus tusks.

ID #	Frequency	Type of attachment	Date attached	Date tx fell off	Days tx attached	Tx recovered?		
1	164.040	latex bander	6/09/80	08/09/80	61	recovered		
2	164.083	latex bander	6/09/80	06/10/80	1	recovered		
3	164.460	latex bander	6/26/80		>86			
4	164.480	latex bander	6/26/80			not recovered		
5	164.439	latex bander	7/16/80	08/01/80	16	recovered		
6	164.083	latex bander	7/17/80	08/07/80	21	recovered		
7	164.056	hydraulic	6/16/80	06/18/80	2	not recovered		
8	164.100	hydraulic	6/18/80		>94			
9	164.023	hydraulic	6/27/80		>85			
10	164.188	hydraulic	6/28/80		>84			
11	164.400	hydraulic	6/28/80	08/30/80	63	recovered		
12	164.420	hydraulic	6/28/80		>84			
13	164.558	hydraulic	7/08/80	08/02/80	25	not recovered		
14	164.582	hydraulic	7/09/80		>73			
15	164.656	hydraulic	7/09/80		>73			
16	164.684	hydraulic	7/09/80			elec. malfunction		
17	164.542	hydraulic	7/13/80		>354		+	See Table VII.2
18	164.145	hydraulic	7/17/80		>65			
19	164.204	hydraulic	7/17/80		>65			
20	164.502	hydraulic	7/17/80		>65			
21	164.520	hydraulic	7/17/80		>65			
22	164.539	hydraulic	7/23/81		>115*		*	Located at Punuk I.
23	164.863	hydraulic	8/02/81		>26			
24	164.788	hydraulic	8/02/81		>26			
25	164.763	hydraulic	8/02/81		>26			
29	164.838	hydraulic	8/04/81		>24			
26	164.888	hydraulic	8/12/81		>92*		*	Located at Punuk I.
27	164.913	hydraulic	8/12/81		>16			
28	164.813	hydraulic	8/12/81		>16			
30	164.932	hydraulic	8/14/81		>89*		*	Located at Punuk I.

Table VII.2. Visual resightings of non-functional radio-tags. After batteries in the radio-tags had expired, it was possible to visually locate some of the tags and obtain additional information on attachment duration.

Observer	Date of resight	Location of resight	Possible transmitter(s) it might be (ID#)	# Days Attached		
J. Taggart	7/02/81	Round I.	17	354	+	
B. Brown	Fall/82 (Sept.-Nov.)	Bird I.(C. Newenham)	17, 29	393-841	#	
Annon.	Spring/84 (Feb.-May)	Nunivak I.	8-10,12,14,15,17-30	901-1413	#	@
J. Taggart	8/15/83	Round I.	8-10,12,14,15,17-30	731-1153		
J. Taggart	7/12/84	Round I.	13, 25-28	1065-1465		
C. Zabel	9/24/84	Cape Peirce	13, 25-28	1139-1539		
J. Taggart	9/23/84	Cape Peirce	15, 25, 27, 28, 30	1136-1537		
T. Pogson	9/04/84	Cape Peirce	25, 28, 30	1117-1129		
	# Exact date unknown					
	@ Shot in the harvest					