THE TERRESTRIAL BEHAVIOR OF THE HARBOUR SEAL, PHOCA VITULINA CONCOLOR, AT MIQUELON

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The Terrestrial Behavior of the Harbour Seal, *Phoca vitulina concolor*, at Miquelon.

BY

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ABSTRACT. A breeding colony of harbour seals (Phoca vitulina concolor) was studied from close range at Miquelon. Quantitative records were kept of the manner in which the herds settled onto sand flats exposed at low tide. The pattern with which various sexes and age classes assembled on the beach, their site fidelity, the role of agonistic behavior and play, the impact of human and natural disturbances and the manner in which the seals returned to sea were compared over segments of the breeding and moulting seasons. Contrary to some earlier beliefs that these seals are merely loosely gregarious, the results suggested that they are organized socially, though in a simpler fashion than those pinnipeds which copulate on land.

Acknowledgements

This thesis is dedicated to my parents, Victor and Frances Davis, who gave me the tools to shape the course of my life.

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Chapter 1.

INTRODUCTION

In this thesis, a breeding colony of harbour seals (*Phoca vitulina concolor*) was observed from distances as close as two metres. Study from such close range has never been achieved in other investigations of this species. As a result, my thesis reports novel observations of the seals' behavior. These data have also allowed some insight into the possible nature and extent of their group structure, dynamics and organization.

The terrestrial behavior of the harbour seal is not well understood because it has been impossible to approach them without causing a disturbance. Their typical reaction to being disrupted is to flush off the beach or exposed rocks they use as hauling grounds. If a disturbance continues, they do not resettle. For example, I once observed a clump of discarded fishing gear wash ashore near a group which caused all the animals to return to the water. The gear remained grounded until the next rising tide, and the seals, although apparently curious about it, did not haul out again until it had washed away.

The wariness of the seal groups to human approach is at least in part the result of a long history of commercial harvesting and bounty kills (Imler and Sarber 1947; Bigg 1969;

Boulva and McClaren 1979), fisheries protection (Scheffer and Slipp 1944; Bonner 1978), incidental kills as the result of fisheries operations (Sanger 1974), habitat destruction (Bonner 1978; Clifton 1971; Summers, Bonner and van Haaften 1978), and tourist activity around breeding areas (Rice 1964; van Haaften 1974; Vaughan 1978; Renouf et al. 1981). Some researchers have indicated that seal colonies adapt to some disturbances (Boulva 1973; Renouf, pers. comm.) but none report adaptation to the point of apparent indifference to humans.

The problems of getting close to the seals are compounded at some locations where they do not haul out in the same place over successive days (Boulva 1973; Mansfield 1967) so it is not possible to observe the same group of animals for a sufficiently long time to see any behavioral consistencies. At some breeding grounds, even with the best possible placement of observation blinds, the terrain obscures portions of the herd (Venables and Venables 1955) or the rising tide forces the cessation of watches prior to the dispersal of the seals (Wilson 1978). In the present study of harbour seals at Miquelon, I was able to install observation blinds on traditional hauling grounds before the animals returned for the pupping season. The seals became accustomed to these structures and congregated close by. From these vantage points, I was able to document their social interactions.

Since harbour seals copulate and feed in the water, activities therefore rarely observed, controversy exists in the literature regarding the nature and extent of any social organization they might have. There are many reports which suggest minimal structure. Scheffer and Slipp (1944) described Phoca vitulina richardsi as "gregarious on land but as a rule, solitary when foraging". A similiar situation was described by Bishop (1968) in the Gulf of Alaska and Button (1975) for Phoca vitulina concolor at Miquelon. Knudtson (1974) postulated that the harbour seal formed "societies of strangers" on land and that associations were never of an enduring nature. In contrast, Wilson (1978) and Wilson and Kleiman (1974) have suggested that complex social interactions occur between juvenile seals at terrestrial sites in the Gulf of Maine and in the Shetlands. They did not indicate if these relationships continued into adulthood. They believed that "a longterm network of social relationships" existed and attributed the durability of these relationships to the long period of immaturity. They based their conclusions on the fact that juveniles formed separate terrestrial groups and engaged in bouts of play before settling on tidal ledges. Wilson (1978) and Wipper (1975) have proposed that the terrestrial herd is structured socially into subgroups characterized by adult sentries. Wilson also suggested that the groups were cohesive in the water and took part in cooperative feeding activities. Sullivan (1982) described a dominance hierarchy where space on rocky ledges was the limiting resource. Ranking was linear and related to size and sex with adult males dominating all other age classes.

During my pilot studies of harbour seals at Miquelon during 1981 in which I developed some of the observation methods used in the present study (See Appendix A) I documented, in a preliminary fashion, three characteristics which are typical of socially organized pinnipeds. First, the Miquelon harbour seals always hauled out in groups, second they appeared to form these groups at the same locations each day and third, many animals spent much of their time engaged in social play. In the following breeding season, I decided to document these characteristics in more detail and to describe the behavior of the seals in general in the hope that from close range I might be able to add some new and quantitative information about the behavior of harbour seals.

Chapter 2.

METHODS

STUDY SITE

The breeding colony of *Phoca vitulina concolor* at the Grand Barachois on the French Island of Miquelon (47°00'N, 56°20'W) was observed during 1982 from 6 May to 5 July, and 31 July to 17 August.

The Grand Barachois is a shallow triangular lagoon approximately 13 km in perimeter. It is connected to the Atlantic Ocean by the Goulet de Langlade, a 200 m X 400 m long channel. With each falling tide, a series of sand flats become exposed in the centre of the Barachois. Up to 800 harbour seals traditionally haul out at four sites around the edge of the exposed sand (Figure 1). In addition, there is a small group of approximately 60 grey seals (*Halichoerus grypus*) that occupy a site on the northeast corner of the sand flats (Figure 1). Both species are forced to abandon the sites with each rising tide.

BLIND LOCATIONS

Prior to the arrival of the seals in 1982, blinds elevated 1.75 m at floor level (Figure 2), were erected on the sand flats in the vicinity of the sites where seals typically formed terrestrial groups. Groups formed at one or more of these

Figure 1. Map of Miquelon

A- Site A

B- Site B

C- Site C

D- Site D

+- Blind Locations

● Grey Seal Haulout Site

AS- Alternate Haulout Site for Harbour Seals

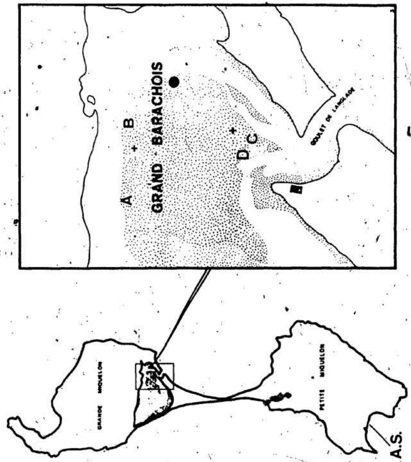

GRAND BARACHOIS
A
B
C
D
GOULET DE LANGLADE
GRANDE MIQUELON
PETITE MIQUELON
A.S.

Figure 2. Observation Blind.

The blind superstructures were constructed of angle iron bars welded into automobile tire rims to form the legs and feet. The legs were topped with a 1 m X 1 m angle iron and wood platform. A small canvas tent was erected over a tubular aluminum frame and lashed and stapled to the wooden portion of the platform. Clear plastic windows on three sides of the tent provided a 270 panorama of the sandflats and waterline. The windows were secured along three edges with either Velcro adhesive material or brass zippers and were generally rolled up out of the line of view of the observer and the seal group during observations periods. The fourth side of the tent had a floor to ceiling slit opening which allowed entry and exit to the observer. The opening was also secured with either Velcro or brass zippers. The front of the blind at Site B faced north while the blind at Site C faced east.

locations whether I was in the blind or not, so I assume the seals were not affected by my presence or by the close proximity of the blinds themselves.

For the first three weeks of May, the lack of seals at other sites restricted watches to the blind at site B. Once groups started to assemble at site C, observations were made primarily from that site with one or two visits per week to site B. The seals abandoned sites C and D after 5 July. During the moult period in August, observations were undertaken exclusively at sites A and B, since groups did not regularly form at sites C or D.

Before the seals started forming groups at site C, a 200 m X 30 m grid in 5 m X 5 m squares was anchored in the sand (Figure 3). Grid markers were constructed from heavy-guage aluminum wire topped with knotted fluorescent surveyors' tape. The grids were used primarily to determine site fidelity of the group itself and of animals I was able to identify. I also used the grid to measure the distances that separated animals in a group and as reference points when group counts were being made from photographs.

Figure 3. The Grid at Site C.

OBSERVATION METHODS AND PHYSICAL PARAMETERS MEASURED

Recording sessions were undertaken during every daylight low tide cycle except when weather conditions were so severe that terrestrial groups did not form.

Shortly after the tide peaked, I was transported by boat to a blind where I remained until the following rising tide or until the seals were prematurely dispersed by a disturbance.

One adult male (Figure 4), one lactating female and nine pups were marked with a mixture of red marine paint diluted with solvent. The mixture was applied by lobbing a paint-filled chicken egg from the water into a settled group. The group always returned to the water after an egg was thrown, thus limiting the number of animals marked. Other methods of marking the seals with various substances met with failure. Unlike other studies (Sullivan 1982), I was able to classify most animals according to age class as adult male, adult female, female with pup, juvenile, yearling, pup and weaned pup. Adults included animals which were probably age five years and older and characteristically had thick foreheads and necks and a large size relative to juveniles, whose heads and necks were narrower and sleeker, and were probably two to four years of age. Juveniles were always of smaller stature than the adults. Yearlings were smaller than juveniles but distinguishably

Figure 4. Paint-marked Male Seal

larger than pups, which were easily recognized by their small size and fuzzy grey pelage. Weaned pups were identified by their pelage and fat condition and the lack of an adult female in attendance.

The seal groups were photographed during all phases of their terrestrial occupation with a tripod-mounted, motor-driven Canon AT-1 35 mm camera fitted with a Canon FD 200 mm f4 lens. Kodak Kodachrome 25, Ecktachrome 200, Panatomic-X, Plus-X, and Tri-X films were used during the May to July portion of the 1982 season. During August, Kodak Kodachrome 64, 2415 Technical Pan and Ilford XP-1 films were also used. The type and film speed chosen for a particular day depended on the amount of available light for maximum grain resolution.

Composite photographs of the groups were taken at 2-5 min intervals during the group formations and at 30-45 min intervals once the group had settled. Two to eight frames were generally required to cover the entire group at one time. Whole-group composites were constructed from contact sheet prints of the rolls of film. Sex (where possible), age class, and group numbers were extracted from the composites by examining them with a Nikon compound dissecting microscope at 7X magnification. Colour slides of the group were examined directly with the dissecting microscope for the same information. Visual counts of the numbers of seals in a group were taken at the same time I photographed the group to determine the accuracy of the photo counts.

BEHAVIORAL PARAMETERS MEASURED

Observations on shallow-water activity were tape recorded. These observations were later transcribed into a field notebook. After the initial group activity had subsided, observations were recorded directly on paper.

Movement

Prior to group formation, all seal movement in the shallows over the terrestrial site and in deep water off the site was monitored for direction of movement and the age class of the animals involved. The shallows included the water over the sand flats that drained off with each falling tide. This water was deep enough for seals to swim in and played an important role in group formation.

I have defined a primary group as a variable number of seals gathering at a site for the first time on a specific falling tide. A secondary group was one which hauled out after the primary group had been disturbed and displaced back to deep water. The same or some of the same animals from the primary group could comprise the successive group or groups if a number of disturbances occurred. Primary and secondary groups could form concurrently at the four sites around the sand flats.

Aggression

Conflicts between seals were identified by the occurrence of one or more of the following behavioral acts: (1) a rapid up-and-down motion of the foreflipper (flippering or flipper waving) (2) snorting (3) an abrupt motion of the head toward the approaching animal and (4) biting. The duration, when possible, and whether the response involved multiple encounters were recorded, (i.e. if the combatants stopped the fight, turned from one another and then re-engaged). Pauses in conflicts with neither animal turning away but then re-engaging were recorded as one encounter.

Occasionally, the brevity of some conflicts and limited visibilty made it impossible to determine which seals were involved and where the conflict occurred in the group. These encounters were not included in the results.

Play

1. Solitary Play: This activity was identified when single animals repeatedly slapped their hind and fore flippers on the sand or on the surface of the shallow water, rubbed themselves laterally on dorsal and ventral surfaces, rubbed antero-posteriorally on their ventral surfaces or engaged in rapid, apparently non-directed movement over the surface of

the sand. Slapping and rubbing between bouts of rapid movement were recorded as one bout. Bouts of rubbing with the seal remaining in place on the sand were assumed to be scratching or "comfort movements". Digging in the sand with a foreflipper was recorded as solitary play as was mouthing of objects such as grid markers, sea weed and drift wood.

2. Torpedoing: This behavior consisted of high speed swimming just below the surface of the water and occurred in both deep and shallow regions of the Barachois. A small bow wave was created by the torpedoing animal and this assisted in determining the direction of movement and whether it involved approach or departure from the group if a group were present.

3. Social Play: Non-aggressive contact between seals was described as social or dyadic play. Non-aggression was determined by the long duration and the non-vocal nature of the contact and its consequence. Components of play included: (1) mouthing of hind flippers by one or both of the animals sequentially or simultaneously, (2) mouthing of head and neck regions, (3) mounting, where one animal positioned itself on the back of another making dorso-ventral contact, and attempted mounting, where one animal attempted to postion itself dorso-ventrally with another but would be dislodged by the bottom animal before the mount was completed, (4)

rolling, where a pair chased each others hind flippers forming a tight circle in deep water and (5) one slapping any region of the other with a fore flipper. The location of the play activity, either on land or in the water was recorded.

Shadowing

Individuals followed females and pups around deep and shallow water prior to group formation and sand exposure. This following behavior which I have termed shadowing was characterized by the animal swimming in a head-up, alert posture orienting toward the female and pup while maintaining a distance of 2-5 m.

Flushing

Disturbances resulted in a movement of seals back to the water and was termed flushing.

Chapter 3.

RESULTS

GENERAL OVERVIEW OF THE SEASON

The seals began to form terrestrial groups over successive days at sites A and B during the second week of May and at sites C and D during the third week of May. Though 50-100 seals remain in the vicinity of the Barachois during the winter months (Poupin 1981), they do not form groups on the sand flats. For the first time in over 30 years, the Barachois was completely frozen over during the winter of 1982 (J. D'etcheverry pers. comm.) which undoubtedly reduced the overwintering numbers even further. Therefore, the numbers I recorded in May may have been unusually low. The peak number of seals in the Barachois during the breeding season reached approximately 700 animals in mid-June.

On 13 May, the tracks left in the sand by 197 seals were counted at site A after a group had returned to the water. On the same date, what was believed to be the first pup of the season was discovered dead on the sand flats. The pup was a normally formed female which appeared to have gone full term in utero including shedding of the lanugo fur. The pup's neck was broken, a condition found in four of five dead pups recovered. This might possibly occur during the birth process.

Although no still-births were witnessed, I observed nine mothers engaged in flailing of the hind quarters during parturition. Perhaps the dead pups I discovered had their necks broken during an unusually vigourous bout of these movements. Pupping occurred at all sites during the last two weeks of May and the first few days of June with the first live pup of the season sighted on 16 May. Approximately 150 pups were born during that period with peak numbers of births occurring during 26-29 May. The first weaned pups were sighted on 16 June. The last female and pup pair of the 1982 season was observed on 3 July. Weaned pups banded together in groups of up to 30 animals and attached themselves to the groups at sites A, B and C. No weaned pups were seen in the Barachois after the first week of August.

I left the field station on 5 July and returned on 31 July to observe the moult period. The moult progressed during August reaching its peak around 13-14 August. Based on previous reports, (Ling et al. 1974; Button 1975; Poupin 1981), I had expected the seal population to be at a seasonal high of around 800-900 animals but was never able to count more than 225. Tourist activity in and around the Barachois was unusually high during August due perhaps to the absence of the usual swarms of mosquitoes and blackflies. Direct and indirect harassment of the seal groups by humans might have contributed to the decreased numbers although the typically heavy tourist traffic during the pupping season did not cause the seals to leave the area in June. An alternate site on the south coast of Petite Miquelon (Figure 1) used by the seals and never visited by tourists was also empty of seals when I checked it on 10 August.

SITE UTILIZATION

At three of the four terrestrial sites that the seals used around the Barachois during the breeding period, I observed 45 primary and 73 secondary group formations. From 7 May to 21 May, all age classes and both species of seals formed groups exclusively at sites A and B. After 21 May, groups formed at sites C and D as well. These latter formations coincided with the onset of pupping. All groups which formed at site C occupied the same 100 m stretch of sand. Initially, pregnant and lactating females with pups and immature animals were the primary users of site C until 16 June when one adult male arrived with the primary formation. Prior to that time, adult males were only occasionally present, arriving after the group was established and settled on the sand. After 16 June, from one to nine adult males were observed to settle with the group at site C with the falling tide. Primarily mothers and pups used site D. After 5 July, the seals abandoned sites C and

D and formed groups at sites A and B only. Abandonment of sites C and D coincided with the last weaning of pups.

I observed at least some adult males to be site specific over days. The first adult male observed to settle on site C, identified by a unique scarring pattern on the left side of his neck just posterior to and ventral to his ear, used the same grid location (2 m) over six successive days and was consistently the first animal to settle with the falling tide. The one adult male I successfully paint-marked settled on land four times at one grid location although not over successive days. He also consistently returned to the same location on a day when three naturally caused flushes occurred.

Over 17 days of the moult period, I observed 18 primary group formations. Sites A and B were used nearly exclusively during this period. Of these 18, eight (44.4%) occurred at site A only with site B not utilized for those days. Five (27.7%) occurred at site B only with site A vacant. On three of the five days the group settled at site B however, disturbances from boats early in the tide cycle shifted the group to site A. By definition, the groups forming on these three disturbed days did so as secondary formations. Two group formations (11.1%) occurred concurrently at sites A and B. Sites A, B and C were used concurrently on three days when fog reduced visibilty to less than 500 m.

Primary group formations did not appear to be affected by limited horizontal visibility during the breeding season. At site C, there was no significant difference in the average size of the group at the time of sand exposure when visibilities of more and less than 500 m were compared ($F=4.07 \times 10^{-4}$, $df=1,28$, $p<.05$). In addition, windspeeds less than galeforce and wind direction did not significantly affect group formations at site C ($F=1.72$, $df=2,24$, $p>.05$, $F=1.08$, $df=3,24$, $p>.05$). However, when the wind was galeforce out of the northeast (N=4), i.e. running onshore to the sandflats at site C, the seals did not form a group. If, during a NE gale, groups formed anywhere around the Barachois, sites A and B and on one occasion, site D, were utilized. Groups did not form on sites A and B when northerly or northwesterly gale's occurred. Only one westerly gale occurred with site D being abandoned for the duration and the largest group numbers of the season were recorded at site C although some seals were also present on sites A and B.

Reduced visibility affected use of the sites during the moult period. Observations in very dense fog were limited to walking tours around the perimeter of the sand flats. However, it was discovered that when visibility was less than 50 m, small groups of seals (N<30) returned to site C though sites A and B were used in fog as well.

GROUP FORMATION

The method of group formation along the sand flats followed a consistent pattern throughout the breeding period from May to July. During falling tides, prior to the exposure of the sand flats, 15 or more seals of all age classes and both sexes (except site C where adult males were not present until late in the season) congregated in deep water just off the sites. Solitary adults, juveniles and adult females with pups swam into and back out of the shallows prior to group formation. At site C, I recorded detailed movement during 164 of 715 forays into the shallows. Of these 164 forays, 94.6% lasted less than two minutes. The seals swam up to 30 m into the shallow water before returning to deep water. Females with pups always tried to nurse when they swam into the shallows but returned to deep water if this proved unsuccessful, apparently because the flats were still too far submerged. The other 5.4% of the forays involved animals attempting to cross the shallows from site C to site D. Of 9 seals attempting to cross the shallows from 21 May to 3 July, only 3 animals went all the way to site D and remained. The other 6 aborted their journeys before site D was reached, returning to site C or deep water. One apparently blind mother and her pup remained midway between sites for 25 min before returning to site C. Over the breeding period, an average of 15.9 forays into the shallows per falling tide occurred prior to primary group formation (N=715, sd=12.9).

When the water reached a specific depth, group formation usually proceeded unless a human disturbance occurred in the preceeding 30 min. I have termed this water level "critical depth for adults" and defined it as that depth of water in which an an adult seal could reach the substrate with its abdominal region while keeping its head above water without being destabilized by wave or current action. Critical depth, as measured from photographs or measured with reference to the legs of the blind was approximately 40 cm for adult males, non-lactating females and when lone adults and lactating females were present. Critical depth was 25 cm if females with pups were the only animals present at a site. Critical depth did not apply to juveniles or yearlings which never hauled out until after a number of adults had established themselves in the shallows or on the sand. It was not possible for a seal to settle before the critical depth was reached.

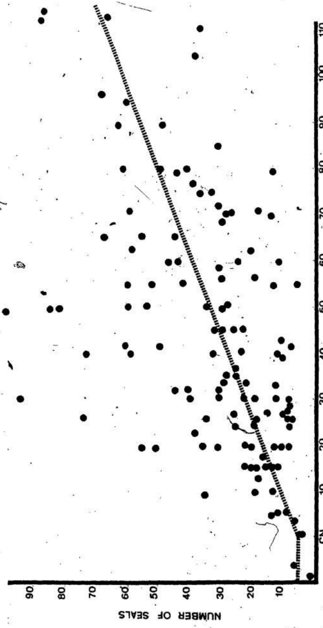
Once the adults could reach the substrate with their abdomens, they would assume a "U"-shaped posture. This stance involved the seal rolling on its side or remaining on its belly and elevating its head and hind flippers well out of the water, physically forming a "U" shape.

A "critical number" of adults was necessary to stabilize a forming group. I have defined critical number as that number of adults of either sex whose presence was necessary for a terrestrial group to linearly increase in size. Animals who formed the critical number at site C arranged themselves, on average, 17.26 m apart (s.d.=15.30, N=114). Throughout the breeding season, the critical number was four adults for all sites. Once the four animals were settled on the sand, the group size was never observed to drop below four seals and then increase in size unless a disturbance caused a flush (Figure 5). Prior to the critical number settling on the site, 1 to 3 seals were transiently present. If the critical number were not present at any time after the critical depth occurred, seals that attempted to settle in the shallows or on the sand did not remain in place for longer than five minutes and a group did not form. Juveniles and yearlings were never observed as members of the critical number although they were observed to settle around the adults after the critical number had settled.

At sites A and B, adult males and/or lactating females formed the critical number. During May and the first sixteen days of June, lactating females formed the critcal number at site C. After 16 June and until site C was abandoned on 5 July, primarily adult males formed the critical number.

Figure 5. Increase In Group Size After Critical Number

CN denotes 4 animals settled on the sand.


NUMBER OF SEALS
90
80
70
60
50
40
30
20
10
MINUTES
CN
10
20
30
40
50
60
70
80
90
100
110

Juveniles and yearlings were never observed to succeed in initiating a terrestrial group. Their forays into the shallows prior to critical depth being reached were usually in association with a female and pup. Juveniles occasionally settled on their own in small groups after a disturbance but their placement on the sand was never any deeper than 2 m inland and they typically flushed and dispersed within 1-5 minutes after settling on land. On one occasion, I observed seven juveniles form a group and disperse four times in succession.

SPACING

Spacing measurements for the breeding period were obtained from composite photographs of the groups, supplemented by field observations.

Prior to the birth of pups at sites A and B, the distance separating pregnant females from other seals ranged from 10 to 12 m (N=83 seals). Adult males, non-lactating females, yearlings and juveniles maintained distances of 0.5-1.5 m (N=200). This resulted in groups forming with a central concentration of adult males, females with pups, yearlings and juveniles surrounded by pregnant females and/or females with pups born during that tide cycle (Figure 6). Approximately half of the females who delivered pups away from the main

Figure 6. Pupping Season Group Arrangement.

PF- Pregnant Female

congregation of seals returned to the water with their new pups and joined the end of the group that was settled on the sand closest to their previous location. The others remained where they had pupped until they were dispersed on the next rising tide. After pupping and until weaning, lactating females maintained distances of 4-5 m (N=50) from one another. Juveniles and solitary adults settled 1-2 m (N=200) from these females without conflict. The gaps created by females and their pups either joining the ends of the group after the sand became exposed or from lactating females forming the critical number were filled by juveniles, yearlings or solitary adults arriving after the mother and pup.

During the moult period, groups consistently formed more than 250 m away from the blinds necessitating the use of binoculars for observations. The distance separating the blind from the group also made it impossible to obtain photographs that could be used to determine the distances that separated the seals. However, based on an adult seal length of 1.75 m, it appeared that both sexes and all age classes except weaned pups which did not join the groups maintained a distance of 0.5 m or less throughout the moult period without any sign of conflict.

GROUP FORMATION RATE AND GROUP SIZES

The rate of group formation, measured as the number of seals settling on the sand per minute from the time of the critical number being achieved until the time of sand exposure on the grid was compared over ten-day blocks. The mean daily formation rate was significantly slower during the ten-day time block which included the period of peak pupping ($F=4.64$, $df=3,14$, $p<.05$) when compared to any other ten-day block post-pupping. However, maximum group numbers were not significantly different over the entire breeding season ($F=2.74$, $df=3,14$, $p>.05$). The daily torpedoing index was not significantly correlated with the mean daily group formation rate ($F=.031$, $df=1,14$, $p>.05$).

The group at site C averaged 64.6 animals (N=30, s.d.=27.14) at the time of sand exposure. On three occasions, complete, naturally caused flushes occurred approximately 30 min prior to the first sand becoming exposed but after the critical depth and number had been reached. The mean formation rate after the flushes was 65% faster then the mean preflush rate for those days (mean primary rate of 1.48 seals min^{-1} N=43 vs. mean secondary rate of 2.25 seals min^{-1} N=6).

Increases in group size followed a consistent pattern of expansion on both sides of the seals which formed the critical number. The group increased in size linearly during all portions of the breeding season.

DISPERSAL

1. Natural: There were only three tide cycles (6.67%) wherein the seals were undisturbed for the entire time the sand was exposed. Flushing due to natural or human disturbances affected the other 42 formations.

The pattern of dispersal during the three undisturbed formations was consistent. As the tide started to rise, the seals closest to the water moved up the sand toward the main body of the group until their way was blocked by the bulk of the group. Lactating females responded aggressively to crowding and either drove the offending animal back toward the water or swam off with their pups. Approximately half the animals in the group from along its entire length and depth moved further inland to escape the rising water. The other half maintained their positions, individually assuming "U"-shaped postures as the water rose. All age classes were involved in the movement inland. Females with pups which maintained their positions within the group as the tide was rising were the first to swim off to deep water. This might be attributed to the pup starting to float at an earlier time than the rest of the group. The seals in the shallows remained in place as long as they could keep themselves stably grounded and then eased off to deep water once this was no longer possible. During the disintegration of the group, there was no play activity.

2. Dispersal Resulting From Disturbances: Flushing was the result of either human activity (34.2%, N=25) or natural/ unknown causes (65.8%, N=48) (Figure 7). Human activity included motor vehicles moving around the perimeter of the Barachois (36.0%, N=9), tourists and sight-seers walking along the beaches or on the sand flats (16.0%, N=4), boats landing on the sand flats or motoring in and out of the Goulet de Langlade (20.0%, N=5) and any low-flying aircraft (28.0%, N=7). The British Airways Concorde flew over Miquelon twice a day and 55 sonic booms were noted from those flights. The seals raised their heads and shifted in place toward the sound of the noise on 23.6% of the flights (N=13) but they were never flushed off the sand flats.

Besides the activities of the seals themselves, natural causes of flushing recorded at Miquelon included a sudden increase in the rate of falling rain, in some cases, the sudden appearance of the sun from behind a cloud and occasionally

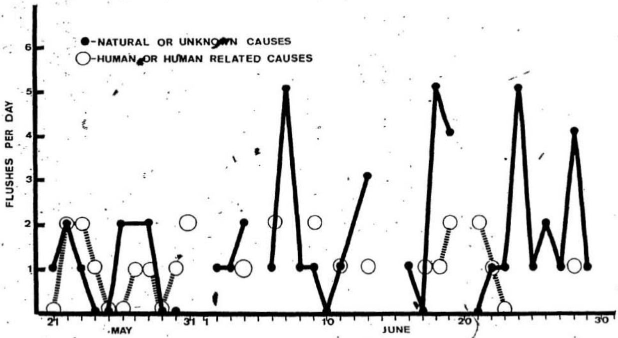


FIGURE 7 DISTURBANCES OVER DAYS.

flocking of birds above the seal group. Over a number of successive days in late May, approximately 35 grey seals arranged themselves in the midst of the harbour seal groups (Figure 8). Grey seal play activity appeared to be responsible for five of the harbour seal flushes that occurred.

During the breeding period, 42 of 45 observed primary group formations were disturbed by human-related activity or activity of natural/unknown origins resulting in 73 flushes while an observer was in place. Twenty-five (34.2%) were the direct result of human activity and 48 (65.8%) were the result of natural or unknown factors. Secondary group formations occurred after 38 (90.5%) of the 42 disturbances but often resulted in more flushing thus the higher number of flushes per primary formation relative to disturbances. Boats and a helicopter landing on or near the terrestrial sites were responsible for the four instances of secondary groups not forming after a disturbance. There were no significant differences in the number of flushes that occurred during the pupping, nursing, weaning and post-weaning periods ($F=4.61$, $df=3,24$, $p>.05$).

Each of the 18 primary group formations observed during the moult period had at least two and as many as 11 complete flushes from unknown factors prior to the group settling on the sand. However, the seals attempted to settle on the site

Figure 8. Grey Seals in Harbour Seal Group

GS- Grey Seal

before critical depth occurred and appeared to have difficulty maintaining their positions on the substrate.

There were 22 disturbances where the entire group startled and moved toward the water but did not actually flush (Figure 9). At low tide, groups were spread 20-25 m inland from the edge of the water. Movement to the edge of the water after being startled repacked the seals to a depth of 5 m or less depending on the size of the group for any particular day. Six (27.3%) were the result of human activity and 16 (72.7%) were the result of natural or unidentifiable causes. Human activity generally caused a complete flush rather than a rearranging along the waterline.

When the seals rearranged as the result of a disturbance, there were limited amounts of conflict as mothers attempted to relocate pups and chase crowding conspecifics out of bite range. The increased density also unsettled the other age classes but did not result in fights. However, complete flushes occurred within 30 min after 24 of 25 of the disturbances. The seals were never observed to return to the positions they had occupied before the disturbance.

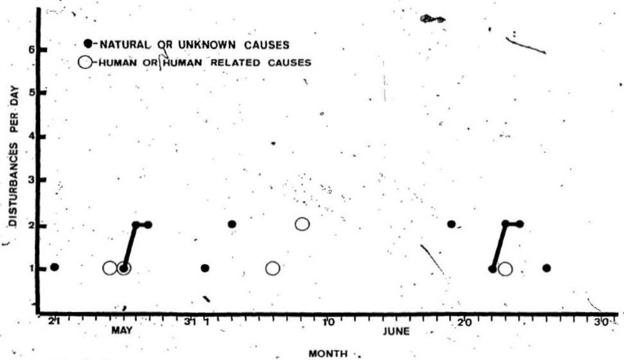


FIGURE 9 NON-FLUSHING DISTURBANCES OVER DAYS

AGGRESSION

Aggressive encounters were most often noticed after they had started. My attention was usually drawn to a conflict by vocalizations emanating from one or both of the combatants or by the high visibility of flipper waving and head jabbing. It was usually possible to determine the age class of the animals involved, though the duration of a bout was often not measurable.

Prior to the weaning period, lactating females were involved in 62.8% (N=103) of aggressive encounters recorded. Of these 103 fights, 57.3% involved pairs of lactating females (N=59), 35.0% involved lactating females and juveniles (N=36) and 7.7% involved lactating females and adult males (N=8).

Pairs of non-lactating adults were involved in 23.6% (N=39) of all fights. Of these 39, 36 (92.3%) occurred during and after weaning. Eleven of the 39 (28.2%) involved pairs of adult males. During and after the weaning period, adult male-male conflict reached a level of severity where lacerations resulted. Conflicts between other age classes were never as damaging. The duration of adult male conflicts was longer than any other age-class combination, lasting between30-120 sec (N=11). All of the observed conflicts started and ended in deep or shallow water. Fights did not occur between males on land nor did I observe males arriving or leaving terrestrial groups to engage another male. Conflicts ended when one male swam away from the other and settled in the shallows or on the sand or was lost to sight. Chasing was never observed as a component of fighting.

The remaining conflicts involved pairs of lone adults and immature animals (6.7%, N=11) or pairs of immature animals (7.3%, N=12).

The number of aggressive encounters was not significantly different over successive segments of the breeding season ($F=1.31$, $df=3,24$ $p>.05$) although, as indicated above, the participants changed from primarily adult female to adult male at the time of weaning.

PLAY, TORPEDOING AND SHADOWING

All play recorded involved juveniles, yearlings or mother-pup pairs.

Juveniles nearly always torpedoed in and out of the shallows during group formation. The 10 days from 23 May to 2 June had significantly more instances of torpedoing (measured as an index of torpedoing, number of torpedoes during the primary formation/numbers of seals present at the time of sand exposure than during any similiar time span for the breeding period ($F=4.65$, $df=3,24$, $p<.05$) (Figure 10). Comparisons between

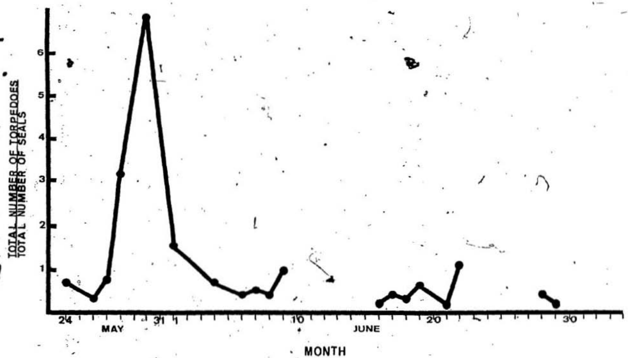


FIGURE 10 TORPEDOING INDEX OVER DAYS.

time-blocks after 2 June until the end of the breeding period revealed no significant differences ($F=1.31$, $df=3,24$, $p > .05$). During the pupping and nursing portions of the breeding season, solitary torpedoing accounted for 79.3% (N=384) of the total. The other 20.7% were bouts of multiple torpedoing where one animal would start moving either toward or away from the group and would be joined by others in the vicinity of the animals initiating the torpedo.

Social play between juvenile pairs occurred from mid-May until 9 June in both deep water and in the shallows at the periphery of a forming group (Figure 11). Bouts of play ceased once the sand became exposed and were never observed during a rising tide. Mounting was observed 95 times in 112 play bouts but protruding genitalia were never seen and the mounting animal animal was always dislodged in 15 seconds or less. Torpedoing was included in only three of the play bouts (2.7%). Bouts of social play dropped off significantly at the time of peak pupping and remained low until they disappeared altogether on 9 June ($F=5.99$, $df=3,12$, $p < .05$) At the time of the decrease in social play, there was a corresponding increase in shadowing (Figure 12). Juveniles of both sexes approached as close as one metre to mother-pup pairs which were either moving or settled in the shallows. Mothers responded aggressively toward the young animals on 14.6%

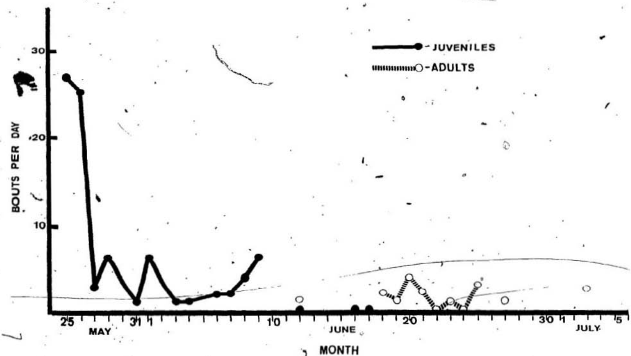


FIGURE 11. SOCIAL CONTACT OVER DAYS.

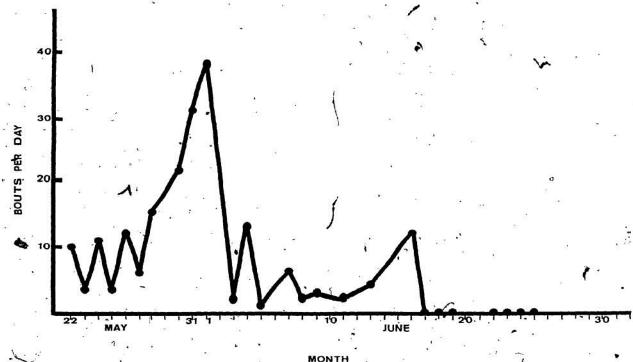


FIGURE 12. SHADOWING OVER DAYS.

Figure 13. Mother-pup Play Activity.
Pup is piggy-backing female while she looks backward.

(N=28) of the approaches. Shadowing did not occur after the sand was exposed.

Not including torpedoing, other solitary play by juveniles and yearlings averaged 16.5 recorded sessions per day per group and did not vary significantly throughout the breeding season ($F=2.14$, $df=3,24$, $p>.05$).

Mid-way through the nursing period, play between mothers and pups became evident. Mother-pup play included either animal slapping the head or neck region of the other, short bouts of thrashing in shallow water prior to hauling out and the pup climbing onto its mother's neck or shoulder region (Figure 13).

Chapter 4.

DISCUSSION

Being able to observe the Miquelon seals from unusually close range allowed me to gather information which was amenable to quantitative analysis. With the exception of investigations by Wilson (1978) and Sullivan (1982) who included some quantitative treatment, all previous accounts of harbour seal behavior have been limited to qualitative descriptions. My study has revealed the following information:

1. The sites used by the Miquelon seals were consistent over at least two seasons. Two sites, C and D, were used during the breeding period only, though site C was occupied on three days during the moult when visibility was limited. Sites A and B were used during both the breeding and moult periods. At site C, where I placed co-ordinates on the sand, the seals always used the same 100 m stretch of beach each time they hauled out. In addition, two animals I was able to consistently identify occupied the same location (2 m) each time they hauled out. Individual sites were abandoned during onshore gales. After disturbances at site C or D, the seals generally shifted northward toward sites A and B.

2. Groups began to establish themselves at these sites after forays into the shallows over the flats as the tide fell. The group increased in size only after a critical number of four adults occurred on the site. The critical number did not occur until a critical depth of water was reached over the sand flats. This depth of water was approximately 40 cm when adults without pups formed the critical number. When lactating females formed the critical number, critical depth was approximately 25 cm. When lone adults and lactating females were present on the same site, they both contributed to the critical number and critical depth was 40 cm.

3. Early in the season, the seals arranged themselves on the sand such that pregnant females were separated from the main group by approximately 12.5 m (N=83). Lone adults, juveniles and yearlings lay within 1 m (N=200) of each other. Mothers with pups maintained a 4.66 m (N=50) separation between themselves and other lactating females although juveniles, yearlings and adult males could settle within 2 m (N=200) of them. During the moult, all seals were within 0.5 m of one another, regardless of age class.

4. The groups formed more slowly during the pupping period although the overall size of the groups was the same throughout the breeding season. In all seasons, a secondary group

formation was approximately twice as fast as a primary formation.

5. When the seals returned to the sea on a rising tide without having endured any disturbances, the first seals to leave were the smallest and therefore the most affected by the rising water. With the exception of lactating females which responded aggressively to crowding, none of the aggression or play associated with group establishment were in evidence.

6. When the seals were disturbed by human or unknown causes such that the group moved toward the water, if the intrusions were not severe enough to cause a flush, animals would reposition themselves at the water line. Repositioning appeared to unsettle the group and subsequently resulted in dispersals. The seals never reverted back to their former positions on the sand.

7. Lactating females were involved in most of the conflicts that occurred until the time of weaning. After that time, incidents of adult male-male conflict increased and lasted for the longest duration.

8. All play occurred among juveniles and/or yearlings or between mothers and their pups. The frequency of social play between juveniles and yearlings was highest early in the pupping season. After peak pupping, this behavior decreased

and shadowing increased. The incidence of solitary play not including torpedoing was constant throughout the season. Torpedoing decreased at the same time as the increase in shadowing.

These data allow some discussion of the social behavior of harbour seals. However, it must be remembered at the outset that harbour seals use both the marine and terrestrial environment which has likely led to the evolution of behavior which is unique to each location. One can only speculate on how behavior in one environment might influence behavior in the other. For example, assessing the contribution of terrestrial behavior to successful mating in the water would be difficult. With this consideration, I would like to discuss the following questions in light of the data I have collected.

1. Is there an identifiable structure to the group according to age class and/or sex and time of the season?

2. Why are harbour seals gregarious on land and attached, annually, to the same locations on the sand flats. Does gregariousness extend to the water?

3. Are there behavioral mechanisms which determine the establishment and maintenance of the groups?

Any speculation about sociality in harbour seals must consider copulatory behavior since this, ultimately, is the culmination of most social interactions. However, there is a controversy over the time of the mating period for Phoca vitulina (Venables and Venables 1959; Harrison 1963; Button 1975). The difficulty in determining when harbour seals copulate stems from the fact that they mate in the water. Venables and Venables (1959) and the unpublished data of Renouf have suggested that two mating seasons may occur in certain populations of harbour seals, one spring period for females in oestrus for the first time and a second period for multiparous females later in the summer. Positive proof of the time of the mating period would require histological sampling that, at least for the Miquelon seals, is not possible due to government regulations regarding the taking of seals. The time of the mating period can therefore only be inferred from behavioral observations. I have strong circumstantial evidence to suggest that Miquelon harbour seals mate in late June and early July shortly after the pups are weaned and that this is the only time at which mating occurs. This is in contrast to Button's (1975) study which indicated that the mating period for the Miquelon seals occurred in August and Renouf's work which suggested vernal coition.

The group formations which Button recorded in August were approximately 600 m away from his observation points. The formations I observed at that time from closer range were always accompanied by torpedoing but none of the type of behavior which has been characterized as copulatory. Torpedoing in shallow water, which Button observed over long distances, causes considerable splashing and may have led him conclude that the splashing was copulation.

Before pupping, I recorded from distances of 15-50 m, the same types of rolling, mounting, and flipper slapping that Venables and Venables (1959) and Renouf suggested were copulation. However, from my closer observation point, I was able to discern that the animals involved in the activity were all juveniles and yearlings which therefore excludes the possibilty of copulation. Harbour seals have been tentatively described as promiscuous (Bigg 1969, 1981) so if there were females in oestrus before the arrival of pups, adult males should have been actively courting females. I was unable to observe any adult male activity which would indicate such endeavors. There were no aggressive incidents between adult males typical of the post-weaning period when the same types of copulatory behaviors are observed. Based on this information, it is possible that the early spring activity was juvenile and yearling play rather than copulation. Perhaps the distances over which Venables and Venables (1959) and Renouf made their observations were too great to adequately distinguish the age classes and behavior involved and thus led to some confusion.

Increases in male-male aggression, genital inflammation in adult females and adult paired contact all suggest that the Miquelon seals, like the seals on Sable Island, Nova Scotia (Boulva 1971; Evans and Bastian 1969; Boulva and McClaren 1979), coastal Nova Scotia and New Brunswick (Fisher 1954), California (Sullivan 1982), British Columbia (Bigg and Fisher 1974) and those of the Gulf of Alaska (Bishop 1968) mate shortly after weaning their pups. Post-weaning copulation in late June to early July combined with a two-month delayed implantation (Fisher 1954) and a nine-month gestation period would result in a late May to early June pupping period. Aggression between adult males increased at the time of weaning and often resulted in lacerations. This was the only time of the season when this type of activity was observed. Consistent with male-male aggression, Johnson (1969) reported that males in captivity generally initiated chasing, neck and flipper biting and embracing during mating bouts.

The genital regions of females were swollen and appeared inflamed shortly after weaning (Figure 14). The condition of the nipples and the generally poor physical appearance and

Figure 14. Female With Inflamed Genital Region.

extreme weight loss indicated that these females had nursed a pup. Genital inflammation was not present during nursing so it was unlikely to have been the result of the birthing process.

Prolonged bouts of behavior like rolling, flipper-slapping and immobile paired contact which Venables and Venables (1957; 1959), Button (1975) and Renouf have described as copulatory were recorded shortly after weaning. What was not clear to the above authors because of the distances over which they made their observations was the age classes of the animals involved. Only adult pairs were observed taking part in the post-weaning contact I saw at Miquelon. Although juveniles were observed behaving in a similar manner earlier in the season, they were not involved in these activities after weaning.

The types of behavior which indicated mating in late June and early July had disappeared by the time of the moult. Aggression between adult males, copulatory types of behavior and signs of genital inflammation in females had disappeared by 31 July.

GROUP STRUCTURE AND GREGARIOUSNESS

The reasons suggested for terrestrial group formation in harbour seals have been general and speculative because of the difficulties of gathering systematic data. The groups have been characterized as unstructured "societies of strangers" (Knudtson 1974), as a vehicle for information exchange on the location of prey species and as a carry-over from group foraging in the water (Wilson 1978).

At Miquelon, group formation and the spatial arrangement of the seals on the sand was consistent over the breeding season. Four or more adults initiated groups by settling on a site at distances of 3-35 m from one another after the critical depth was reached. Rapid increases in group size occurred once these adults had settled (Figure 5). Juveniles and yearlings waited until these adults were on the sand before they joined the group. The rate of primary group formation was also consistent over the breeding period except during peak pupping. Since the size of the group remained constant throughout the breeding period, it might be possible that new, slow-swimming pups delayed the arrival of lactating females. In addition, the torpedoing index was highest during the period of peak pupping and may have slowed formations. Secondary formations were nearly twice as fast as primaries. This may reflect the presence of increased numbers of animals in the water near the site rather than the seals increasing the speed at which they removed themselves from the water.

When lactating females hauled out either as members of the critical number or as new arrivals to a settled group, they established greater distances from each other than from any other age-class or sex. Juveniles, yearlings and solitary adults of both sexes filled the spaces between mother-pup pairs. Adult males settled at intervals greater than two metres from one another only when they were members of the critical number. Other adult males along with other age classes and sexes filled the spaces between the critical number without conflict.

The structure of the group could have been important to all seals for a number of reasons. Since adult males started to form the critical number at site C around the time of weaning, close proximity to females might have been important if male positioning within the group at that time facilitated monitoring the presence or absence of oestrous females. The larger distances between adult males which formed the critical number may have served to increase the chances of having a potentially oestrous female nearby. If only a few males are responsible for most of the mating, then settling close to another adult male would have reduced the space available for later arriving animals particularly females. Adult males which settled closer than five metres to the original male may not have been involved with mating.

Agonistic encounters between classes of animals appeared to play a role in the pattern and distribution of seals on the sand. Agonistic encounters were most numerous between lactating females. Perhaps as a result of their conflicts or in an affort to avoid them, lactating females established relatively long distances from one another on the sand. The lower number of exchanges between mothers and non-lactating seals might have been responsible for shorter separation distances between them. When this pattern was disrupted through a disturbance which resulted in a denser settling of animals nearer the shoreline, this reformation seemed unstable and the group eventually disintegrated and returned to the water without ever returning to its former density.

The highly aggressive responses of lactating females during the breeding season were similiar to those of other pinniped species (Hewer 1957; Peterson and Bartholomew 1967; Sandegren 1970; Miller 1971; Cox and LeBoeuf 1977; Christianson and LeBoeuf 1978; Boness et al. 1982). This has been regarded as protection for the young (Boness et al. 1982) and might have been a factor in the behavior I observed. If increasing separation distances minimized the chances of conflict, other benefits, particularly increased time for nursing, might have been incurred. This may have been important to the Miquelon seals since they were so regularly disturbed.

In some terrestrially copulating species of pinnipeds, female aggression may indirectly incite male competition and provide a mechanism to enhance the possibility of a female mating with a dominant male (Cox and LeBoeuf 1977; Boness et al. 1982). However, there was never any overt indication of incitation of male harbour seal in the Barachois though it may have occurred in the water and therefore out of view. Female aggression was consistently intense until weaning after which male-male aggression increased. Since females became relatively unaggressive at the probable time of oestrus, females inciting male-male competition seems unlikely.

The type of group formation I observed is quite different from the descriptions by Wilson (1978) and Wipper (1975) for seals in the Gulf of Maine and the North Sea respectively. They suggested that on land, the herd was structured socially into subgroups characterized by adult sentries. They supported their hypothesis with observations of adults which apparently encouraged naive juveniles into the water during a disturbance. Wilson suggested that the subgroups were cohesive in the water and took part in cooperative feeding activities. The only evidence that points to the possibility of subgroups at Miquelon may come from the four animals which formed the critical number and spaced themselves further apart. They may have been initiating four large groups on one site. Each group might have chosen the site because of its close proximity to deep water. Aside from these observations, the type of formations and dispersals I observed on Miquelon do not lend support to the type of structure described by Wilson. Increases in group size proceeded linearly. Subgroups that foraged together presumably should also have arrived at a site together. This would have created a stepwise, non-linear increase in numbers. Only smooth expansion through the addition of animals to each end of the group occurred in the Miquelon seals.

Group dispersals at Miquelon do not suggest the existence of subgroups. Flushing which occurred as the result of a disturbance always appeared chaotic. Mothers encouraged pups to return to the water by pushing or rolling them but this was the only type of assistance observed. Undisturbed group dispersal with a rising tide gave no indication that the group or fragments of the group were forming in the water and moving off to sea.

When harbour seals form terrestrial groups, they typically stay on land for as long as possible. Terhune (1983) has shown that increasing group size decreases the amount of time

SITE TENACITY

The seals at Miquelon have traditionally occupied four specific locations on the sand flats. Each of these sites was adjacent to the few places where the water was always deep enough to swim in and offered an escape route even at the lowest point of the tide. This factor could suggest that it is escape from disturbances rather than any social organization that leads to site fidelity and grouping occurs as a consequence of the limited number of sites from which escape is practical. However, this explanation seems unlikely for various reasons. First, Ling et al. (1974) reported that the Miquelon seals used the same locations before human disturbances became prevalent. In other populations, hunting pressure severe enough to cause a decline in population numbers (Bonner 1978), heavy construction (Clifton 1971) and pup tagging operations (Boulva 1971) appear to have few long-term effects on site use. Finally, there are other locations around the coast of Miquelon that are virtually inaccessible to humans and not flooded during each tide cycle. However, instead of relocating, the seals persisted in using the same locations in the Barachois year after year. Studies at Miquelon which specifically addressed the question of human impact on the seal colony have shown that although human presence was disruptive to the seals, it did not appear to be damaging. This may have been the due to the fast access to water afforded by the haul-out sites. Renouf et al. (1981) monitored seal traffic through the Goulet de Langlade before and after human disturbances and reported that overall, the seals did not seem to be seriously affected by the presence of humans, even though they were regularly forced into the water. Separations of pups from their mothers during disturbances were not a problem since attachments between mothers and the pups are reportedly strong enough to withstand human disruptions (Renouf et al. 1983). This firm attachment between mothers and pups is not surprising since natural disturbances, which produce similar group responses as human disturbances, occur nearly twice as often as human disruptions (Figure 7 and 9). All of this information seems to imply that something other than the physical properties of the sites were important to the seals.

The choice of a site from among the four traditional locations was to some extent related to the wind conditions and during the moult, to the horizontal visibility. When the wind was galeforce and blowing onshore at a particular site, that location was abandoned for the duration of the storm. Perhaps the effects of onshore wind and water increased ambient noise to the point where pup calls or the sound of approaching danger could not be heard. During the moult when visibility

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"irregular selection of a focal subgroup". Movements of the seals and their behaviors were recorded on acetate sheets superimposed over a grid drawn on paper to represent the coordinates laid in the sand. Every half hour, the location of each seal in the sample was transferred to a new acetate sheet and recording continued. The animals in the sample were observed for the duration of the low tide cycle unless a disturbance caused a flush. Since the animals were not identifiable upon resettling, a new sample was selected from the group.

The alphanumeric sequences were used to determine: 1. movement characteristics of individuals during all phases of the terrestrial occupation, 2. aggressive encounters and their outcome, and 3. flushing and subsequent resettling.

I analysed the terrestrial movement characteristics of the seals by comparing the mean number of moves per day per seal for moves of 1-5 m, 6-10 m and moves greater than 10 m and found that there were significantly more short distance moves (<2 metres) than moves greater than 2 metres ($F=3.74$, $df=6,126$, $p<.05$). Most movement within a settled group appeared to involve "on-site" adjustment after waking from sleep or from crowding due to adjacent conspecifics.