BEHAVIORAL ADAPTATIONS BY HARBOUR SEAL MOTHERS AND PUPS TO AN AMPHIBIOUS LIFESTYLE

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BY

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ABSTRACT

Prolonged observation from unusually close range provided data on interactions between mother and pup Harbour seals, Phoca vitulina concolour, on Miquelon (45° 45' N, 56° 14' W) located 19 kilometers southeast of Newfoundland, Canada. Records of intrapair distance changes, nursing bouts, responses to pup vocalizations, nose-to-nose contacts, haul-outs and exits from the nursery and emergences and submergences were analyzed quantitatively to ascertain the contributions of the mother and her pup to the maintainance and eventual dissipation of the nurturant relationship. Both animals exhibit behavioural adaptations which reduce the risk of separation arising from their amphibious lifestyle and the extreme precocity of the pups. The pups remain with their mothers constantly as a result of a specific predisposition to follow which seems to develop soon after birth. The mothers also establish a specific bond to their pups and modify their behaviour such that they are most attentive to the pups when in the water and during periods of major disturbance. This attentiveness decreases prior to weaning as the mothers show fewer nursing initiations and more frequent rejections of pups' nursing solicitations.

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CHAPTER ONE: INTRODUCTION

The Harbour seal, Phoca vitulina concolor, is difficult to approach in the wild because of its extreme wariness and amphibious lifestyle. As a result, most behavioural studies of this species have been limited. In particular, there has been a paucity of research during the pupping season since mothers retreat with their young to the water at the slightest disturbance. In this thesis I used techniques which allowed me to observe a group of Phoca vitulina mothers and pups from unusually close range on the French island of Miquelon (45° 45′ N, 56° 14′ W) off the south coast of Newfoundland. From this vantage point I accomplished two things. First, I was able to describe the events from birth to weaning in detail not possible to date. Second, I obtained quantitative data on the behavioural interactions between mothers and pups which allowed some assessment of the roles played by each member of the pair in ensuring the pup's nurturance until its independence.

The relationship between Harbour seal mothers and pups is probably unlike that found in any other pinniped. In species like the Alaskan Fur seal (Bartholomew, 1959), Stellar Sea-Lion (Marlow, 1975), the Northern Elephant seal (Petrinovich, 1974; Christenson and Le Boeuf, 1977; Le Boeuf and Briggs, 1977; Reiter et al., 1978), the Grey seal (Smith, 1968; Fogden, 1971; Boness and James, 1974), the Harp seal (Terhune et al., 1979; Merdsoy et al., 1978; Ronald and Dougan, 1982) and the Weddell seal (Tedman and Bryden, 1979) the pups do not normally enter the water prior to weaning. The mothers go to sea and return to nurse their young on energy-rich milk (Jelliffe and Jelliffe, 1976). In

several of these species the pups are left in rookery nurseries after each nursing bout (Bartholomew, 1959; Fogden, 1971; LeBoeuf and Briggs, 1977; Trillmich, 1981) and when females later return to the beach they must distinguish their pups from among a large group of cohorts, any of which would suckle if permitted (Bartholomew, 1959; Tedman and Bryden, 1979). However, the mothers should be able to establish contact with their own pups relatively easily since the latter do not leave the terrestrial nursery and can be found in the same general location for nursing each time the mothers return from the sea.

The Miquelon Harbour seal pups face an entirely different situation. At Miquelon the nursery area is exposed twice per 24 hour period by the ebbing tides (Poupin, 1981). As a result both mother and pup are forced back into the water as the tide returns to flood the sands, and during disturbances. Harbour seals are able to use such nursery areas because pups are able to follow their mothers into the water immediately following birth (Klinkhart, 1967; Newby, 1973; Knudtson, 1977). Giving birth to an extremely precocial mammalian offspring results in greatly reduced development time and high pup mobility. Even the fetus is capable of swimming (Newby, 1966), and pups are not unduly stressed by cold water (Miller et al., 1976). Thus even in locations where haul-out beaches are always available, the pups accompany their mothers to sea each day (Boulva and McLaren, 1979).

Some controversy has arisen as to whether the mother or pup is accountable for ensuring that the pair does not become separated. The difficulties the pair face in this endeavor include strong currents, poor underwater visibility and moderate levels of ambient noise

exacerbated by the possibility that the pup does not recognize its own mother (Fogden, 1971).

Early studies by Venables and Venables (1955) in Shetland of a breeding group of Harbour seals produced primarily qualitative descriptions of what behaviour could be seen through binoculars from distances of 100 meters atop nearby cliffs. In a study of Harbour seal mothers and pups (Phoca vitulina vitulina) on the coast of Ireland, Wilson (1974) concluded, as the Venables' work had implied, that the mothers were primarily responsible for maintaining contact. But, like the Venables, Wilson was forced to study the Irish colony from some distance and restricted her observations primarily to aquatic interactions. At Miquelon, prior to this study, it has been suggested instead that pups are instrumental in keeping contact with their mothers (Renouf and Diemand, 1983; Renouf et al., 1983). Although Renouf and Diemand (1983) used similar measures to those which Wilson employed, the former recorded behavioural interactions on land toward the end of the pupping season whereas the latter observed the animals in the water throughout the nurturant period. These two studies suggested that there are behavioural distinctions between the eastern and western Atlantic Harbour seal groups. However, the differences seen in the mother's role in keeping track of the pup may have been a result of the fact that she faces a different set of problems when the pair are in the water.

One might expect the mothers to assume greater responsibility for intrapair propinquity in the water where the precocial pups have much higher mobility, compared to land, and face the hazards described above. On land the mothers can afford to be less overtly attentive since the

pups stay relatively still. Also, Renouf and Diemand's observations were made near the time of weaning, when, as predicted (Trivers, 1974), and as is the case with other mammals (e.g. Hinde and Atkinson, 1970), the mother might be expected to show less concern about her offspring.

Renouf et al. (1983) addressed some of these problems in their second study and found that throughout the nursing season, regardless of whether the pairs were on land or at sea, the pups were instrumental in maintaining contact with the mothers, though the latter took control when necessary. The pattern seen was unlike that observed in other mammals wherein the onus of responsibility shifts from mother to young as weaning draws near.

There has been some controversy about the weaning process in Harbour seals. Finch (1966), using information gained from observations on two captive mother/pup pairs in California, concluded that the pups establish their own independence at weaning with the mother exhibiting no behavioural changes over the lactation period. This is contrary to the normal mammalian pattern in which the mother gradually weans the offspring by initiating fewer suckling bouts and increasingly rebuffing initiations by the young (Hinde and Spencer-Booth, 1971). Wilson (1974) corroborated Finch's conclusions while Lawson (1982), Renouf and Diemand (1983) and Renouf et al. (1983) suggested that though weaning was a sudden process, it was determined by the mother's rejections of her pup. However, in the case of Renouf's studies, these conclusions were drawn primarily from data which were limited to initiation of distance changes between the mother and pups. Other indications of the processes involved in the relationship between females and their young should

include observations of nursing, immediate postpartum behaviour and other measures of interaction such as responses to vocalizations and tactile contacts, haul-outs and exits from the nursery, emergences and submergences, and play.

This thesis first presents a description of the events from birth to weaning which includes novel observations made possible by the close observation distances. Then quantitative analyses of the interactions between mothers and pups will rectify the discrepancies in the literature which have led to the controversies described above.

CHAPTER TWO: METHODS

Study Site

In 1981 and 1982, from late May to early July, I studied one subgroup of a herd of more than 600 Harbour seals. The herd congregates every year in a large, sandy tidal bay, the Grand Barachois, on the island of Miquelon located approximately 19 kilometers southeast of Newfoundland, Canada at 45° 45′ N and 56° 14′ W (Figure 1). During the second and third weeks of May, the number of Harbour seals in the Grand Barachois began to increase from the 50 that were present at my arrival. These 50 had in all probability overwintered there (Poupin, 1981). The seals hauled out in large groups in the middle of the Barachois on a three square kilometer sand flat which became exposed as the tide ebbed. A nursery group of 40 to 50 mothers and their pups returned to a specific location on the southern side of the sand flats (::: in Figure 1) during the final week of May. The nursery area was not the only location in which pups were born since there was more than 200 adult females in the entire Barachois, most of which produced offspring. However, the nursery group was the largest, regular congregation of mothers and pups.

Haul-outs occurred as the sand became exposed during ebb tides and the seals settled in large discrete groups as shown in Figure 2.

Observation Procedures

I used two methods to observe the behaviour of the mothers and pups during the summer of 1982: A) the establishment of an observation blind positioned on the nursery two weeks before the seals arrived (+ in Figure 1), and B) observation of behaviour in the water from an elevated vantage point on shore (cabin in Figure 1).

The observation blind was a small, rectangular canvas tent 1.5 meters in height with a one-meter-square wooden floor and mounted on four angle-iron legs 1.5 meters long (Figure 10). Each leg had an automobile tire rim welded to its end; the four rims were buried in the sand for increased stability. Three removable transparent vinyl windows were situated on the front and two sides of the blind to allow observation regardless of the exact location of the nursery herd relative to the blind. In general the seals did not seem to be disturbed by the presence of the stationary blind or the sounds of the camera motor wind and occasional fidgeting by the observer. They rarely glanced at the blind, even during periods of disturbance, and sometimes pairs would actually crawl past, or under, the blind on the way to another location. In fact, a number of times pups crawled under the blind and remained there until retrieved by their mothers or leaving of their own accord.

The blind was placed in a position on the sand flats which corresponded to the upper center of the nursery as determined by repeated monitoring of the herd and from experience during previous years. At full ebb tide the blind was 35 meters from the water's edge

facing the narrow tidal channel running parallel to the beach (see Figure 1).

I entered the blind at high tide prior to the start of the seals' haul-out to ensure minimal disruption of the settling mothers and their pups. In all but a few cases I left the blind after the nursery had emptied as a result of external disturbance or the returning tide.

During these observation periods in the blind, which exceeded 500 hours, I was equipped with a pair of 7X35 binoculars, three 35mm cameras with telephoto lenses, a portable tape recorder and an 8mm color movie camera. The resultant photographs comprised a reference for the diary record of behaviour that I kept all season. They also corroborated the following specific records of the behavioural interactions between mother/pup pairs:

1) Intrapair distance reductions in both land and water (with records of events leading to these reductions). The initiators of as well as responses to the distance reductions, were recorded.

2) Intrapair distance increases in both land and water as above. Initiators of these increases and the response of the other seal was recorded.

3) Which member of the pair led haul-out and exit to and from the nursery. Leading could have been by mothers, or by pups or the two seals could have moved side by side ("together").

4) Which member of the pair led emergence and submergence at the surface. "Piggybacking" by the pup when the pairs were in the water was also recorded.

5) Short range contacts involving nose-to-nose or nose-to-body touching (with any resulting distance changes or pup vocalizations). The identities of the initiators, as well as the responses to the contacts, were recorded.

6) Nursing initiations and terminations with additional data regarding time of day, time in relation to haul out and duration. Rejections of nursing solicitations by either member were also recorded.

7) Numbers of incidents of approach, pursuit or acceptance of a foreign female by pups. Acceptances were taken as those situations in which a pup allowed a strange female to approach and actively responded to the latter's nose-to-nose contacts, either by initiating its own nose-to-nose contacts or by crawling closer to the incorrect female. Acceptances of foreign pups by females were also recorded.

8) Play within or between pairs with records of the identities of initiators and terminators of the behaviour. Play included climbing (one member of the pair climbing onto the other), chasing (one member chasing the other), play biting (one member lightly biting and/or slapping the other with its fore flippers)and sparring (one member thrusting its nose towards the others face and neck without growls or an open mouth).

To obtain these detailed behavioural accounts it was necessary to limit the number of pairs observed to five to ten at any one time. A focal subgroup was chosen using the irregular sampling technique (Altmann, 1974) such that the pairs chosen were distinctive and continuously observable during the initial haul-out, and usually for the entire low tide period. To ensure a larger number of observations, additional pairs were selected after the initial pairs either settled to sleep or returned to the water. The data collected thus represented the observer's maximum possible number of continuous behavioural sequences.

During all observation I maintained a regular account of time, weather, tide state, total number of seals on the nursery and descriptions, timing and consequences of disruptive disturbances.

Individual pairs were usually difficult to recognize over subsequent observation days due to their fairly uniform pelage markings, the large number of pairs present and the obscurring effect of the populous nursery group which prevented me from viewing some of the more distant seals. The generally consistent number of pairs seen on the nursery, and my ability to recognize a small number of individuals for

much of the season, suggests that this nursery might have been composed of many of the same animals until its dissolution in early July.

Data Analysis

In addition to traditional comparative statistical treatment of the data, the following more esoteric analyses were employed.

(A) Distance Changes

Initial data analysis used a Hinde (Hinde and Atkinson, 1970) coefficient to determine which member of the pair was responsible for maintaining contiguity, if this responsibility shifted during the initial period immediately postpartum and over the course of the season, and if there were any significant differences between pair interactions on land or in the water. A coefficient was calculated for each mother/pup pair per day. In total 371 pairs were recorded on land, nine pairs of which were mothers who had just given birth, and 252 pairs in the water. The formula for Hinde's coefficient is:

$$H = \begin{bmatrix}\text{percentage distance} \\ \text{DECREASES} \\ \text{initiated by mother}\end{bmatrix} - \begin{bmatrix}\text{percentage distance} \\ \text{INCREASES} \\ \text{initiated by mother}\end{bmatrix}$$

where the mother's respective distance changes are calculated as a proportion of the total distance changes for both members and the coefficient has percentage values ranging from -100 to +100. In this

application, a negative value indicates that the pup is actively trying to remain near its mother; a positive Hinde coefficient would mean the converse, that the mother followed the pup's movements (Hinde and Atkinson, 1970).

The existence of trends in behaviour recorded over the nursing season was detected using a conservative, nonparametric statistical test known as "Page's L" (Page, 1963; Sokal and Rohlf, 1969). A critical acceptance level of not less than 95 percent ($p < .05$) was adopted as significant in all but two cases. Page's L is robust but is subject to decreased reliability primarily when a large number of ties exist in the ranked data; the effects, if any, of a small number of ties can be countered by choosing a $p < .01$ level of acceptance as was done with piggybacking daily frequencies and the data for nursing.

In other statistical manipulations a critical acceptance level of not less than 95 percent ($p < .05$) was adopted as significant. Comparisons between certain response types were made with consideration that dependancy between the categories possibly existed. Since the sample sizes were large, resulting in the Chi test statistic's distribution approximating that of the T-test's, statisticians recomended that the latter test be used under these conditions (Drs. Graham Skanes and Michael Sherrick, personal communications). T-tests were completed using the MINITAB statistical package (Ryan et al., 1980).

(B) Nursing

The Hinde coefficient was modified to determine which member of the

Harbour seal pair was acting to prolong suckling throughout the nursing season. This modified coefficient was calculated using daily percentages of initiations and terminations from 512 observed nursing bouts. The formula for the coefficient is:

$$Hn = \left[\begin{array}{c}\text{percentage nursing} \\ \text{INITIATIONS} \\ \text{by the mother}\end{array}\right] - \left[\begin{array}{c}\text{percentage nursing} \\ \text{TERMINATIONS} \\ \text{by the mother}\end{array}\right]$$

Values range from −100 to +100. A negative value indicates that the pup is actively trying to continue suckling; a positive value would indicate that the mother was primarily accountable for nursing continuation. As with the unmodified coefficient, a check for the presence of a trend over the nursing season was carried out using a Page's L test.

CHAPTER THREE: RESULTS

Observations of the Events From Birth to Weaning

(A) Birthing

Most of the pups were born over a short interval during the last week of May and the first week of June although there is some annual variation in the onset of the pupping period at Miquelon (Poupin, 1981). Only three single incidents of parturition have been witnessed prior to this study and from much greater distances (Klinkhart, 1967; Newby, 1973; Knudtson, 1974). I was able to record nine births, and the labours of five other females, which occurred as little as ten meters from my blind.

All of the births that I recorded occurred on exposed sand between 0627 and 1625h but the presence of several afterbirths on the nursery area at first light suggested that females also whelped during low tide conditions at night. The females about to pup were easily distinguished from those which were not pregnant by their conspicuously larger, rounded body shape, increased alertness and higher levels of apparently aimless movement. A number of seagulls were also usually present near the former to consume the afterbirth. Though Ringed seals prepare an area for the births (Mansfield, 1963; Frost and Lowry, 1981), and Northern Fur seals (Bartholomew, 1959) and Northern Elephant seals (Christensen and LeBoeuf, 1977) exclude other seals from the immediate vicinity, the Harbour seal mothers did neither.

The precise onset of contractions was difficult to determine but as labour progressed, they became pronounced enough to be visible. In most cases the females adopted a characteristic posture during contractions in which they lay on their bellies with the vaginal slit and base of the hind flippers slightly raised (Figure 3).

The birth process was rapid. The births seen in 1982 had a mean latency from the onset of obvious contractions to birth of 3.5 minutes with a minimum of 38 seconds and a maximum of 21 minutes. In seven births, the pup emerged head first still within the amniotic sac. In the remaining two instances, the pup's hind flippers emerged first while the other entailed the pup's left side appearing first, followed by the rest of its body with the head and the hind flippers together (transverse). The rear-flipper-first presentation was of approximately the same duration as the normal deliveries although it appeared that the pup had to pull its own head out from the vaginal slit. All nine pups were born alive and seemingly healthy, despite two of the mothers vigorously thrashing their hindquarters from side to side just after the pups' heads had emerged. The placenta was always passed separately and usually within 10 minutes of birth. Unlike Newby (1973), at no time did I see the mothers attempt to groom the pups despite their being covered with sand, fluid and remnants of the amniotic sac.

If disturbed, the labouring females seemed to be able to delay the delivery of their pups. In three of the longest births and five separate incidents of labour, females retracted the pup's head back into the birth canal. These occurrences took place during a disturbance and are the first concrete evidence to support suggestions that females can

voluntarily delay the birth of their young.

The newborn pups appeared to be weak but capable of awkward locomotion. The mothers remained close by at all times, and for the first few hours after birth the pairs engaged in very frequent nose-to-nose contact with open nostrils and protracted vibrissae (Figure 4). These contacts were a consistent feature of mother/pup interactions throughout the nurturant period, as they are for Northern Elephant seals (Bartholomew, 1952) and Bearded seals (Burns, 1981), but were most frequent during the immediate postpartum period. The pups made few audible vocalizations shortly after their births compared to later during the season when they vocalize almost continuously if not nursing or sleeping.

Within minutes of birth, pups approached nearby objects, such as an afterbirth, and occasionally followed strange females that passed nearby. However, by the time the tide began to return, and the seals were forced to enter the water, the newborn pups stayed with their own mothers. The mothers too were extremely attentive to the pups (I observed two females which dragged their pups with them for more than a week; this behaviour has also been noted by Trudeau (1976) with Phoca vitulina richardii). Healthy pups followed their mothers constantly on land and through the often-crowded waters near the nursery, commonly riding on their mothers' backs in the water, the latter often tilting their heads back to make nose-to-nose contact (Figure 5). This "piggybacking", which occurred throughout the nursing period, was initially described by Venables and Venables (1955).

(B) Weeks One and Two

With the arrival of the pups the nature of the interaction among females changed as did the structure of the nursery group. Mothers with pups became extremely aggressive toward other pairs, necessitating a doubling or tripling of the usual distances between seals and an increase in the area occupied by the group.

Normally, mothers aggressively rejected nursing attempts by strange pups. Early in the season, these attempts were made most often by the few abandoned pups. Rarely, however, there were exceptions to the mothers' specific attraction to their own pups. In 1982 a triad was seen in which two females accompanied a single pup (Figure 6). Both females nursed the pup and exhibited no overt aggression towards each other. The triad was present in the nursery during the entire pupping season.

If there was a disturbance such as tourists, boat traffic, or low flying aircraft, the mothers led the pups into the safety of the water. Usually the pups were asleep beside their mothers and had to be awakened with nudges or slaps. However they would follow her without hesitation since they had become more proficient in the adult mode of locomotion on land. The seals appeared to be sensitive to the need for adequate escape routes and were responsive to changes in the topography of the nursery site as the tide ebbed. In 1982, each time the tide approached full ebb, the nursery became separated from the deeper tidal channel by a shallow pool bordered by a newly-exposed sand bar (Figure 7). Unlike the situation during early haul-out when the tide was just beginning to

fall, this ebb tide configuration greatly increased the time required by the mothers and their pups to reach the safety of the water. Perhaps responding to these changes, most of the mothers left the nursery prior to ebb tide and took their pups to a sand bar further along the outer tidal channel (A in Figure 7) which possessed a steep slope leading directly into the deep water. The mothers would not take their pups to this "alternate nursery" as the tide first began to ebb as it was not exposed until the water level in the Barachois had dropped considerably. Further support for this substrate sensitivity arose from the fact that, in 1981, the nursery sloped more directly into the tidal channel, allowing rapid escape at all times during the tide cycle; the maternal pairs were rarely seen to leave for an alternate site during the course of a falling tide.

(C) Weeks Three and Four

By the third and fourth weeks of age the pups had become increasingly independent. They followed their mothers at a greater distance in the water and began to initiate play. The incidence of piggybacking decreased. The pups were capable of following their mothers at greater speeds and spent more time underwater. On land the pups began to initiate virtually all of the play. They more often led the pairs' movements to and from the sand flats than during the first two weeks postpartum. It was also interesting to note that the pups spent less time searching for their mothers' nipples at the start of each nursing bout and were able to nurse in increasingly adverse

situations. For example, it was not unusual to see three- and four-week old pups nursing while water still covered the nursery to a depth of 25 centimeters; this required the pups to suckle from the submerged nipples while bracing themselves against the sand. The pups nursed only during the haul-out period with an average bout duration of 3.2 minutes. The duration of nursing bouts ranged from five seconds to 21.1 minutes with great variation. The pups seemed most urgently hungry during the initial haul-out as the sand flats first became exposed. Seventy percent of all recorded nursing bouts occurred within five minutes of the mothers bringing their pups ashore.

(D) Weaning

The final stage of mother/pup interaction occurred during the fourth and fifth weeks after birth in which the mothers appeared to wean their pups. The mothers initiated fewer nursing bouts and increasingly rejected the pups' nursing attempts. Rejections were normally easy to observe as the mothers either rolled slowly away from the soliciting pups, until they were facing away from them, or they swung their bellies laterally away. The persistent pups were then forced to crawl around to the mothers' bellies, after which the mothers usually moved away again. Mothers exhibited increased aggression toward all pups including their own if the latter were exceptionally pertinacious in trying to nurse when the mothers were reluctant to do so.

The pups tried to initiate nursing more frequently than earlier in the season, but were generally unsuccessful. There was also a dramatic

increase in the amount of pup vocalization heard on the nursery.

In other Harbour seal breeding groups the pups have been reported to have doubled their birth weights by weaning (Mansfield, 1963; Bigg, 1969; Boulva, 1975) so it seems probable that the Miquelon pups had done so as well. The pups were lethargic and reluctant to return to the water during slight disturbances. Often five to ten pups were left sleeping on the nursery each day while their mothers left for periods that often extended to the time that the tide began to return.

Weaned pups began to appear on the nursery during the fourth and fifth weeks after birth. Newly separated pups initially spent much of their time during haul-out periods wandering about the nursery and surrounding waters. The only play bouts witnessed involved inanimate objects such as seaweed fronds or debris on the nursery. Vocalizations were frequent but did not seem to be directed toward any particular individuals. A number of these weaned pups tried to approach lone females or maternal pairs but were vigorously rejected. However, the following exceptions to this did occur. One weaned pup was able to "steal" milk from females still nursing their own pups. This pup, a male, adopted a strategy whereby he would quietly approach a nursing pair from the rear and displace the suckling pup (Figure 8). During the week that this pup was present he was able to nurse for an average of 42 seconds from at least 15 females before they discovered the imposter and drove him off. The females usually only did this after nosing both their own pups and the stranger. In a second unusual case a single female was seen to nurse two pups for several hours (Figure 9). She treated both pups as her own during this time and did not apparently

differentiate between them even after numerous nose-to-nose contacts with both.

Eventually, after several days of independence, the weaned pups became virtually silent during haul-out and in the water. They rarely interacted with adults except in an aggressive manner such as when an adult approached too closely. Due to their smaller size, these pups lost out on such encounters and were thus forced to the periphery of the dwindling nursery group. The nursery itself became less populated and exhibited decreased dispersion as the mothers of weaned pups either left or became more tolerant of the presence of other adults close by. By early July the nursery had rapidly disintegrated and the females and lone pups began to haul out with the main adult herds elsewhere in the Barachois.

Quantitative Analyses

(A) Distance Changes

Mean daily frequencies of each category of distance change were calculated using observations of approach and withdrawal over the entire nurturant period. The total proportions, expressed as percentages, of each type of distance change were derived by comparing the total frequencies in each medium (Table I). Both on land and in the water the mothers moved away from their pups significantly more often than the pups from their mothers {$t=8.269$, $d.f.=37$, $p=0.0000$ (land) and $t=8.655$, $d.f.=36$, $p=0.0000$ (water)}. On land the pups initiated significantly

more distance decreases ($t=6.878$, d.f.=47, $p=0.0000$) than their mothers. In the water mothers were as likely as pups to approach one another ($t=1.194$, d.f.=55, $p=0.2375$). On land and in the water mothers were more likely to increase the intrapair spacing than decrease it {$t=8.172$, d.f.=38, $p=0.0000$ (land) and $t=6.757$, d.f.=43, $p=0.0000$ (water)}. In contrast, the pups were more disposed to distance reductions than increases in both media {$t=7.102$, d.f.=44, $p=0.0000$ (land) and $t=3.558$, d.f.=47, $p=0.0004$ (water)}.

Mean Hinde coefficients were calculated on land and in water for each day and are summarized in Tables II and III. The overall mean Hinde coefficients for the season were derived by summing the Hinde index values for every pair over the entire season and dividing by the total number of pairs recorded for each medium (land or water). In all but two days (June 6 and 11) the Hinde values were negative.

Page's L was used to determine if in the two media the mean Hinde coefficients over days became increasingly negative over the season until the pups were weaned. This would suggest that the pups displayed an increasingly strong propensity to follow their mothers. The terrestrial Hinde coefficients (the daily coefficients in Tables II and III) significantly conformed to a increasingly-negative trend ($L=12,803$, $r=1$, $k=35$, $p < .05$). This trend was not due to mothers initiating more distance increases (Figure 13) but rather the pups initiating a greater proportion of distance reductions as weaning approached (Figure 12). The daily average Hinde values for water did not significantly match any predicted order ($L=6103$, $r=1$, $k=29$, $p < .05$).

The overall mean for land was significantly more negative than that

TABLE I: Overall percentage and mean daily frequencies of mothers' and pups' distance changes.

		LAND	WATER
		N = 35 days	N = 28 days
Mother Increases Intrapair Distance	perc.	84.3 %	78.9 %
	freq	37.4	10.1
Pup Increases Intrapair Distance	perc.	15.7 %	21.2 %
	freq	6.54	2.24
Mother Decreases Intrapair Distance	perc.	24.6 %	48.6 %
	freq	6.66	3.62
Pup Decreases Intrapair Distance	perc.	75.4 %	51.4 %
	freq	21.6	4.45

Overall season percentages denoted by "perc."

Mean daily frequencies of distance change denoted by "freq"

TABLE II:
LAND: Mean Daily Hinde Coefficients

	Date	Mean Hinde Coefficient	# Pairs	
	23	-51	2	
	24	-4	2	*****
	25	-50	2	
M	26	-63	8	
A	27	-40	4	*****
Y	28	-59	4	
	29	-54	4	
	30	-83	4	
	31	-42	10	*****
	1	-70	23	
	3	-44	9	*****
	4	-76	13	
	6	-72	6	*****
	7	-42	9	*****
	8	-71	8	
	9	-72	9	
	10	-49	13	*****
	--	---	-	
	12	-67	3	
J	13	-69	4	
U	14	-40	10	
N	16	-74	25	
E	17	-74	17	
	18	-67	20	
	19	-73	22	*****
	20	-54	18	*****
	21	-81	22	
	22	-52	8	
	23	-63	16	
	24	-79	13	
	26	-87	8	
	27	-66	7	
	28	-87	5	
	29	-58	21	
J				
U	1	-91	9	
L	2	-44	5	*****
Y				

Mean H = -61.9 N= 362
Standard Deviation=17.8

TABLE III:
WATER: Mean Daily Hinde Coefficients

Date	Mean Hinde Coefficient	# Pairs
23	-75	2
--	---	-
--	---	-
26	-47	5
--	---	-
--	---	-
29	-39	12
30	-27	8
31	-18	14
1	-44	9
3	-25	14
4	-37	13
6	-33	6
7	+4	12
8	-33	6
9	-43	7
10	-17	9
11	+3	11
12	-2	8
13	-20	5
14	-10	7
16	-11	16
17	-12	13
18	-30	11
19	-40	6
20	-21	12
--	---	-
22	-33	11
23	-36	12
24	-63	5
--	---	-
--	---	-
--	---	-
29	-63	5
1	-33	3
2	-17	3

Mean H = -29.4 N= 252
Standard Deviation=19.2

Periods of major nursery disruption are indicated by "*****"

in water ($t=6.981$, $d.f.=62$, $p=0.0000$). This suggests that the pups spent more time following the mothers on land than in water. The Hinde indices for land and water were further examined after first subdividing them into six blocks, the first five blocks with seven days each and the sixth having two days (the last two days of the nursery's existence). Hinde coefficient means for each of these blocks were then compared for land and water to determine if the trend in the land coefficients effected the difference in overall means between the two media. A comparison of the weekly Hinde coefficients in both media revealed that the coefficients were significantly different in all but the first week (see Table IV). This similarity in the first week's land and water coefficients, obscured by the initial comparison of the overall season means, suggests that for the first week of life the mothers were significantly more involved in keeping the pairs together when on the nursery than they were later on. This involvement decreased over the season (with a concurrent increase in the pups' responsibility) for terrestrial encounters, but didn't increase in water.

(B) Interactions Immediately Postpartum

Using the data gathered from the nine observed births, Hinde movement coefficients were calculated for the period immediately postpartum at five minute intervals (Table V). The initial five minute value was positive after which the coefficient became increasingly negative. A Page's L test, calculated for the first forty minutes postpartum, found this increasingly negative trend immediately following

TABLE IV: Comparison of six weekly mean Hinde coefficients on land and in water.

BLOCK NUMBER/ DATE	N (L)	HINDE COEFFICIENTS LAND		WATER	N (W)	STATISTICAL MEASURES (T-tests)
1) May 23- May 29	27	-50.8	=	-44.5	19	t=0.47 df=33 p=0.64
2) May 30- June 7	73	-61.3	*>	-24.3	76	t=5.01 df=135 p=0.00
3) June 8- June 14	47	-58.0	*>	-15.1	53	t=4.66 df=96 p=0.00
4) June 16- June 22	131	-69.9	*>	-22.0	69	t=7.45 df=129 p=0.00
5) June 23- June 29	69	-70.3	*>	-51.2	29	t=2.02 df=48 p=0.02
6) July 1- July 2	14	-73.9	*>	-25.0	6	t=2.51 df=8 p=0.02

Significantly greater weekly means indicated by "*>"

Not significantly different weekly means indicated by "="

Number of daily hinde indices (each from a single pair) used to derive block mean value indicated by "N"

TABLE V: Hinde coefficients immediately postpartum

Age (min)	0	5	10	15	20	25	30	35	40	45
Hinde Coeff.	+22	-6	-15	-33	-15	-17	-14	-48	-55	
No. Pairs Observed	9	9	9	9	9	9	9	9	7	

The mean Hinde coefficients for all pairs in each interval are denoted by "Hinde Coeff."

birth to be significant ($L=1550$, $r=9$, $k=8$, $p < .05$).

Concurrent observation revealed that in most cases there were a larger number of nose-to-nose contacts per unit time between mothers and their pups during this period than later in the season (one mother nosed her pup 39 times during the third minute after its birth).

(C) Behaviour During Periods of Nursery Disturbance

On 29 percent of the days of observation, a major flush of seals from the nursery occurred following the approach of vehicles, low-flying aircraft and weather conditions such as sudden rain squalls. Occasionally the mothers and pups were flushed from the nursery by the approach of thick, localized fog banks on otherwise sunny days. Following these disturbances the mothers and their pups rarely returned to the original nursery site (disturbed days are labelled in Tables II and III (*****)).

The effect of disturbances on pair interactions was determined by comparing Hinde coefficients for movement on normal and disturbed days. On land the overall mean Hinde value for normal days (-69.26; 24 days) was significantly more negative than for disturbed ((-45.82; 10 days) ($t=3.864$, d.f.=14, $p=0.0009$)). Similarly, the mean Hinde value for normal days (-36.00; 18 days) in water was significantly more negative than on disturbed days ((-17.40; 10 days)($t=2.977$, d.f.=23, $p=0.0034$)). The overall average Hinde indices for land were still significantly greater than those for water during disturbed periods on the nursery ($t=4.020$, d.f.=18, $p=0.0008$) despite the fact that there were lower land

Hinde values during the early portion of the season (section A; page 21). When the nursery was disturbed mothers remained closer to their pups and were more likely to wait for or return to them if they fell behind during a rapid escape to the sea.

(D) Responses to Distance Changes, Nose-to-nose Contacts and Vocalizations

The responses of mothers and pups to the others' distance changes, nose-to-nose contacts and pup vocalizations were also measured. These responses were recorded as either increasing or decreasing the distance separating the two animals, or no movement.

(i) Distance changes

The overall percentages of the mother's response to distance increases or non-following by pups in both media, as well as the mean daily frequencies, are summarized in Table VI. On the nursery a mother was more likely to follow than to stay in one place ($t=1.954$, $d.f.=49$, $p=0.0282$) or move away ($t=6.660$, $d.f.=34$, $p=0.0000$) from the pup if it moved away from her. The mothers also had a significantly greater propensity to follow when the pups moved away than when they did not follow as their mothers led the way through the nursery ($t=5.385$, $d.f.=38$, $p=0.0000$). If the pup did not follow its mother (a rare event), she demonstrated no predictable response (as determined by the lack of statistically significant differences between the mean daily

TABLE VI: Responses of mothers to their pups' distance increases or non-following

	LAND						WATER					
	N= 35 days						N= 28 days					
	Pup Increases			Pup Stays			Pup Increases			Pup Stays		
	Md	Mi	Mst	Md	Mi	Mst	Md	Mi	Mst	Md	Mi	Mst
No.	133	1	93	26	20	41	52	2	11	5	0	1
F.	3.8 *> 0.03 <* 3.0			0.7 = 0.6 = 1.2			1.8 *> 0.1 <* 0.4			0.2 *> 0.04		
%	59	0.4	40.6	30	23	47	80	3	17	83	0	17

Md:Mother decreases Mi:Mother increases Mst:Mother stays

Significantly greater responses indicated by "*>"

Not significantly different responses indicated by "="

Mean daily frequencies of each response indicated by "F"

Total occurrences of each response are indicated by "No."

frequencies of each response type). If the pup began to move away when the pair was in the water the mother was again more likely to approach her pup rather than stay ($t=4.458$, $d.f.=44$, $p=0.0000$) or move away ($t=6.025$, $d.f.=31$, $p=0.0000$). If she did not follow her pup she usually remained stationary rather than swim away on her own ($t=8.043$, $d.f.=30$, $p=0.0000$). This was similar to the situation on land where the mother was much more likely to follow her stray pup (mother decreases 59 percent) where it was subject to attacks by other females.

Pups responses to distance changes initiated by their mothers were divided into two catagories; pups could respond to mothers moving away or to mothers approaching. These responses, presented as overall mean daily frequencies, are found in Table VII. If the mothers moved away, both on the nursery and while swimming, the pups were more likely to follow their mothers than stay still ($t=7.807$, $d.f.=39$, $p=0.0000$ (land); $t=10.679$, $d.f.=29$, $p=0.0000$ (water)) or move in the opposite direction ($t=9.913$, $d.f.=34$, $p=0.0000$ (land); $t=11.209$, $d.f.=28$, $p=0.0000$ (water)). The pups were more likely to not move than move in an opposite direction on land ($t=6.444$, $d.f.=35$, $p=0.0000$). If the mother swam away from its pup, and it did not follow, the pup was as likely to stay as move away ($t=-1.906$, $d.f.=30$, $p=0.0662$).

If the mother crawled towards her pup on land the pup was more likely to remain in place than crawl away ($t=6.380$, $d.f.=34$, $p=0.0000$) or approach ($t=6.427$, $d.f.=34$, $p=0.0000$); pups were equally likely to crawl away as towards their mothers ($t=-0.240$, $d.f.=6$, $p=0.8111$). When the mother approached her pup in the water, the pup was as likely to stay in one spot as approach its advancing mother ($t=1.935$, $d.f.=54$,

Table VII: Responses of Pups to Mothers' Distance Changes on Land and in Water

LAND (N=35 days)

Mother Increases			Mother Decreases		
Pd	Pi	Pst	Pd	Pi	Pst
31.2 *>	0.3 <*	5.9	0.23 =	0.26 <*	6.03
*>			<*		

WATER (N=28 days)

Mother Increases			Mother Decreases		
Pd	Pi	Pst	Pd	Pi	Pst
9.7 *>	0.03 =	0.34	1.9 *>	0.07 <*	1.2
*>			=		

Pd: Pup decreases Pi: Pup increases Pst: Pup stays

Significantly greater values are denoted by "*>"

Not significantly different values are denoted by "="

p=0.0583). Both staying still and approaches were more probable occurrences than swimming away (t=-1.971, d.f.=30,p=0.0000 and t=6.754, d.f.=29, p=0.0000).

(ii) Nose-to-nose contacts

Nose-to-nose contact between mothers and their pups was one of the most common types of interaction observed on the nursery and in the water. Even though the pairs were in close proximity a distance "decrease" could occur after a nose-to-nose contact (the actual contact was not recorded as a decrease). In many cases the initiator had stretched its neck out to make the contact (Figure 3). The recipient could then approach by crawling in front of, or alongside, the initiator. Also, in the water, a nose-to-nose contact by the mothers usually resulted in the pups swimming onto the mothers' backs or under their chins.

Data on the mothers' and pups' responses to their partners' nose-to-nose contact initiations are summarized as overall totals, percentages and mean daily frequencies in Table VIII. A test for seasonal order was not carried out as it was apparent that there were no trends in these behavioural responses.

Mothers nosed their pups significantly more than vice versa both on land (t=6.957, d.f.=37, p=0.0000), and in the water (t=3.052,d.f.=40, p=0.0000). On land, mothers were more likely to stay in response to a nose-to-nose contact by their pups than approach (t=4.450, d.f.=39, p=0.0000) or move away (t=5.864, d.f.=35, p=0.0000). The pups were also

TABLE VIII: Distance changes due to nose-to-nose contacts

		Mother Noses Pup				Pup Noses Mother			
		Pd	Pi	Pst	Total	Md	Mi	Mst	Total
LAND	No.	254	17	570	841	34	10	121	165
	Freq	7.9*>	0.5<*	16.8	24.7	1.0*>	0.3<*	3.5	5.47
	%	30	2	68	84	21	6	73	16

		Pd	Pi	Pst	Total	Md	Mi	Mst	Total
WATER	No.	123	2	54	179	21	6	26	53
	Freq	4.4*>	0.1<*	1.9	6.39	0.8*>	0.2<*	0.9	1.89
	%	69	1	30	77	40	11	49	23

Pd:Pup decreases Pi:Pup increases Pst:Pup stays

Md:Mother decreases Mi:Mother increases Mst:Mother stays

A significantly greater response is indicated by "*>"

Not significantly different response are indicated by "="

more likely to remain following a nosing bout initiated by their mothers than to approach (t=4.025, d.f.=49, p=0.0001) or move away, (t=8.361, d.f.=33, p=0.0000). Nonetheless, if the pups did respond with a distance change, they would approach their mothers more frequently than they would move away (t=7.184, d.f.=32, p=0.0000).

The situation was different in the water where the pups were more likely to approach their mothers following a nose-to-nose contact rather than to stay or move away (t=2.928, d.f.=51, p=0.0025 and t=7.219, d.f.=26, p=0.0000). If the pups did not approach their mothers, they were more likely to remain at the same distance than move away (t=3.118, d.f.=26, p=0.0022).

(iii) Responses to vocalizations

Quantitative records of the mothers' responses to their pups' calling were recorded during 1982. The mothers could either approach, remain still or move away in response to a call. Overall percentages for each of the three categories of movement by the mother following her pup's cries were calculated by dividing the sums of the daily average percentages by the total number of sample days (35 on land and 28 in water). The percentages and mean daily frequencies of maternal responses to pup cries during the season are contained in Table IX. On land the pups' cries did not produce a reliable distance change from the mothers. The mothers were as likely to stay or decrease (t=0.869; d.f.=53, p=0.3885) as they were to move away (t=0.503, d.f.=51, p=0.6168 (mother increases = mother stays) and t=0.869, d.f.=53, p=0.1943 (mother

TABLE IX: Distance changes by mothers in responses to pups' cries on land and in the water.

	LAND			WATER		
	Md	Mi	Mst	Md	Mi	Mst
No.	60	81	74	62	25	17
Freq	1.7 =	2.3 =	2.1	2.2 *>	0.9 =	0.6
%	32.3	33.3	34.4	47.0	30.2	22.8
	N=362 Pairs			N=262 Pairs		

Total numbers of each distance change are denoted by "No."

Md:Mother decreases Mi:Mother increases Mst:Mother stays

Significantly greater values indicated by "*>"

Not significantly different values indicated by "="

Mean daily frequencies of response types denoted by "Freq"

increases = mother decreases)). In the water, the mothers were more likely to approach the pup in response to its cry than to stay (t=4.044, d.f.=35, p=0.0001) or move away (t=3.047, d.f.=42, p=0.002).

(E) Entries and Exits to and From the Nursery

Examination of data involving haul-out and exit to and from the nursery showed that the mother was leading during most pair movements between water and land (Table X). Seasonal mean daily frequencies and overall percentage values of mothers leading, pups leading or both moving together showed that during haul-out onto the nursery the mothers led significantly more often than the pups (t=7.909, d.f.=34, p=0.0000) which occurred more often than mothers and pups coming out together (t=7.160, d.f.=35, p=0.0000). Mothers and their pups hauled out side by side more frequently than pups led the pair (t=2.438, d.f.=60, p=0.0089). There were no changes in this haul-out pattern during the four-week nursing period. The same was true for leaving the nursery; mothers led more often than the pups did (t=7.977, d.f.=40, p=0.0000). On the infrequent occasions when the mother did not lead the pair from the nursery, the pairs were as likely to leave side by side as with the pup leading (t=1.373, d.f.=67, p=0.1742).

(F) Interactions During Swimming

The mothers were also the leaders when swimming with their pups.

TABLE X: Leading during haul-outs and exits from the nursery.

	Haul Out			Exit		
	No.	%	Freq	No.	%	Freq
Mother leads	278	82	7.9 * V	212	79	7.4 * V
Pup leads	21	6	0.6 * Λ V	22	8	0.8 * Λ V
Move together	42	12	1.2 * Λ	36	13	1.3 * Λ

Total number of leadings and haul-outs are denoted by "No."

Significantly greater mean values are indicated by "*>"

Mean daily frequencies of leading are denoted by "Freq"

Overall seasonal percentages are indicated by "%"

The pups' responses were catagorized as pups following, pups staying and pups swimming away from their mothers ("increasing"). A comparison of overall season means for surface submergence and emergence shows that the mothers initiated most dives (t=7.281, d.f.=35, p=0.0000), with the pups typically following rather than remaining at the surface (t=8.409, d.f.=29, p=0.0000). In only one case during 1982 did a pup swim away rather than follow its mother or remain at the surface. Statistically, pups were more likely to follow or stay at the surface after their mothers dove than to swim away {t=9.563, d.f.=27, p=0.0000 (pup following > pup increasing) and t=3.973, d.f.=30, p=0.0000 (pup staying > pup increasing)}. If the pups submerged first their mothers would dive after them more often than they would remain at the surface (t=2.942, d.f.=33, p=0.003). The mothers also led during emergences more often than the pups (t=3.767, d.f.=38, p=0.0003). (see Table XI).

Piggybacking was seen most often during the early part of the pupping season (see Table XII). There was a significant decreasing trend in the frequency of piggybacking over the course of the season with the pups carried most frequently during their first week of life and tapering off towards weaning (L=7964, k=29, r=1, $p < .01$; Figure 12). Slightly more than 68 percent of piggybacking occurred during the first two weeks of the pups' lives.

(G) Nursing Behaviour

I was able to record 512 nursing bouts. Both mothers and pups could initiate and terminate nursing. Mothers initiated nursing by

TABLE XI: Overall emergence and submergence data

	Mother Emerge		Pup Emerge	Mother Submerge			Pup Sub.		
Resp.	Pf		Mf	Pf	Pst	Pi	Mf	Mst	Mi
No.	165		80	257	17	1	50	16	0
Freq.	5.7	*>	2.8	9.2	*> 0.6	*> 0.04	1.7	*> 0.6	
%	67.3		32.7	93	7	0	76	24	0
Overall Daily Mean Frequencies (submergence)				9.8	*>		2.4		

M=Mother P=Pup f=follows st=stays i=increases

Significantly greater values are indicated by "*>"

Response to partners' emerge or submerge denoted by "resp."

Number of occurrences for each response denoted by "No."

Mean daily frequencies of leading are denoted by "F."

Overall percentages for leading are denoted by "%"

TABLE XII: Frequencies and daily ratios of aquatic piggybacking

	MAY					JUNE							
DATE	23	26	29	30	31	1	3	4	6	7	8	9	10
N =	2	5	12	8	14	9	14	13	6	12	6	7	9
Freq	3	5	4	4	8	11	5	4	4	3	2	1	2
Prop	1.5	1.0	.33	.50	.57	1.2	.36	.31	.67	.25	.33	.14	.22

	JUNE (Cont.)												
	11	12	13	14	16	17	18	19	20	22	23	24	25	29
	11	8	5	7	16	13	11	6	12	11	12	5	7	5
	2	0	0	3	6	4	3	2	3	2	1	1	1	1
	.18	0.0	0.0	.43	.38	.31	.27	.33	.25	.18	.08	.20	.14	.20

JULY	
1	2
3	3
0	0
0.0	0.0

"N" = the number of pairs observed in the water per day.

"Freq" = number of piggybacking bouts recorded in a single day.

"Prop" = number of piggybacking bouts / number of pairs recorded.

rolling onto their sides with their nipples, seen to protrude approximately one centimeter, close to the pups' faces. While watching the pups they would then swing their hindquarters (and nipples) towards the pups. If the pups moved away from the mothers, or did not seem aware of the initial nursing solicitation, the mothers would lightly pat and push the pups' heads towards the nipples with their foreflippers. Pups initiated nursing bouts by pressing their noses repeatedly into the mothers' sides until she rolled over to expose the nipples. If females did not immediately comply with the pups' attempts the latter would often cry. Rejection by the mothers was previously described on page 18.

From observations of the pups suckling, data regarding the number of nursing initiations and terminations for mothers and pups were used to calculate a modified Hinde index. This index provided a means for determining whether the mother or the pup was responsible for prolonging suckling. A negative value indicated that the pup was the member of a pair primarily interested in nursing. Table XIII contains these modified Hinde indices for the major portion of the nursing period. The Hinde index for nursing revealed that the pup was increasingly responsible for maintaining nursing bouts prior to complete weaning by initiating a greater proportion of nursing bouts and a smaller proportion of the terminations. A Page's L test for predicted order indicated that there were increasingly negative values for the index over the season ($L=11,697$, $k=33$, $r=1$, $p < .01$). As weaning approached the mothers initiated fewer nursing bouts and began to reject the pups' efforts.

TABLE XIII: Modified Hinde Indices For Nursing Behaviour

	MAY									JUNE				
DATE	23	24	25	26	27	28	29	30	31	1	3	4	6	7
N =	2	2	2	8	4	4	4	4	10	23	9	13	6	9
% Mi	43	20	0	59	100	80	100	50	67	56	75	82	67	64
% Pi	57	80	100	41	0	20	0	50	33	44	25	18	33	36
% Mt	33	100	0	91	75	100	100	75	100	100	70	90	89	100
% Pt	67	0	100	9	25	0	0	25	0	0	30	10	11	0
H.N.	+10	−80	0	−32	+25	−20	0	−25	−33	−44	+5	−8	−22	−36
Rej.	2	2	2	0	0	0	0	0	0	1	0	1	0	0

	JUNE (cont.)													
DATE	8	9	10	12	13	14	16	17	18	19	20	21	22	23
N =	8	9	13	3	4	10	25	17	20	22	18	21	8	16
% Mi	50	57	29	50	67	33	31	12	44	11	17	8	13	5
% Pi	50	43	71	50	33	67	69	88	56	89	83	92	87	95
% Mt	75	93	65	86	100	83	94	85	84	91	90	81	100	76
% Pt	25	7	35	14	0	17	6	15	16	9	10	19	0	24
H.N.	−25	−36	−36	−36	−33	+16	−63	−73	−90	−80	−73	−73	−87	−71
Rej.	0	0	0	1	1	0	1	5	20	21	15	7	5	22

	JULY						
DATE	24	26	27	28	29	1	2
N =	13	8	7	5	21	9	5
% Mi	3	0	36	0	2	3	9
% Pi	97	100	94	100	98	97	91
% Mt	87	58	86	67	81	89	86
% Pt	13	42	14	33	19	11	4
H.N.	−84	−58	−80	−67	−79	−86	−77
Rej.	10	8	3	10	26	10	4

Number of pairs for each day denoted by "N"

"REJ." denotes the frequency of nursing rejections by mothers

The modified Hinde nursing index is denoted by "H.N."

The daily proportion of nursing rejections (refused nursing solicitations) by the mothers, derived by dividing the number of observed maternal nursing rejections by the total number of suckling bouts, over the nursing season significantly matched a predicted increasing value; that is, the mothers rejected their pups' nursing attempts more frequently as weaning approached ($L=13,681$, $k=35$, $r=1$, $p < .01$). In fact, the mothers accounted for 97.8 % of the recorded nursing rejections. I observed pups rejecting their mothers' solicitations only four times (by ignoring their mothers or crawling away slightly).

(H) Inappropriate responses

Although pups were only rarely observed to follow, approach or accept the attentions of strange females, there were enough data to compare the overall seasonal means. Approaching still, or following moving strangers were equally likely to occur ($t=0.905$, $d.f.=32$, $p=0.3720$) and both were significantly more probable than pups accepting advances of females other than their mothers ($t=3.227$, $d.f.=21$, $p=0.002$ and $t=3.187$, $d.f.=25$, $p=0.0019$ respectively). Sixty-six percent of these episodes happened during periods of disturbance.

(I) Play

The comparison of mean play bouts initiated by mothers or pups throughout the season revealed that the pups initiated significantly

more play during the season than their mothers ($t=5.763$, $d.f.=30$, $p=0.0000$). The pups initiated 84 percent of the play bouts whereas they terminated only 37 percent. Also, over 70 percent of all play occurred during the last half of the nursing period (from two weeks of age until weaning).

CHAPTER FOUR: DISCUSSION

Discussion

An amphibious lifestyle confers both advantages and problems on the Harbour seal. A problem arises from the fact that, like all pinnipeds, Harbour seal mothers must return to land to give birth to and nurse their pups (Peterson, 1968). Atypically, however, the pups spend as much time in water as on land prior to weaning. The ability of the mothers and pups to remain together in both places is advantageous since it permits this species to occupy environments from which other seals with land-bound pups are excluded by tidal flooding. As well, the fact that the Harbour seal pups follow their mothers' movements in and out of water provides a better means of escape from predators or disturbance than in the case of sedentary young. However the cost of these advantages is that the mothers and pups must recognize and remain in constant contact with each other during the brief four to five week nursing period in order for the pups to survive. This must be achieved in spite of the fact that the nurseries are often crowded and featureless with nearby waters providing poor visibility, strong currents and problematic noise levels (Renouf, 1980). Data from this thesis suggest that Harbour seal mothers and infants behave in ways to ensure that separation does not occur in either environment. The study indicates that, contrary to suggestions in the literature, pups not only recognize their mothers but soon after birth show a strong tendency to follow and nurse from only their own mothers. It remains for the

mothers to ensure that these predispositions on the part of her pup are functioning until she decides to terminate the relationship. This then implies the existence of a bilateral bond between the pair which exists until weaning.

All but two of the Hinde coefficients for land and water (Tables II and III) were negative indicating that the pups were responsible for actively staying with their mothers for the entire nurturant period. The pups were specifically attracted to their own mothers and were rarely seen to approach other females, even during weaning. However, it was not only the pup which was responsible for keeping the pair together since other measures indicated that the mothers played a role which became obvious during periods when the likelihood of separation increased, that is, when the pairs were swimming and during commotions.

An indication of the mothers' increased concern while swimming derives from the fact that the mothers were as likely to initiate distance decreases in the water, where the pups' were more mobile and the risk of separation greater, as the pups (Table I). On land, with the pups' mobility reduced compared to water, the pup instituted a majority of the decreases; the mothers only initiating 24.6 percent. This difference between land and water was further evident in the fact that regardless of whether or not the data were analyzed in one week blocks or as overall means, the Hinde indices, although negative in both media, were less so in water (Tables II-IV). That is, the pups were responsible for staying with their mothers in both places, but there was a significant shift towards overt maternal intervention while the pairs were swimming.

The negative Hinde values in water are contrary to Wilson's (1974) findings, which were positive. This might be explained simply on the basis of my shorter observation range and greater sample size. Alternatively, her positive Hinde coefficients could be a result of some need for increased maternal control and attentiveness in the waters around the Shetland Islands.

On land, mothers displayed greatest concern for their offspring during the early stages of life after which they presumably relied on the pups' increasing strength and experience to ensure propinquity. It might be expected that up to one week of age the pups required as much attention from their mothers on land as they did for most of the season when in the water. Consistent with this suggestion is the fact that the Hinde indices for the first week of the pups' lives were not significantly different in land and water.

Apart from the difficulties of staying together in water, another potential source of separation was the many disturbances near the nursery which resulted in panic-driven rushes to the water and frequent mixing of pups. The Barachois is located between two French settlements popular to tourists, and is itself a local attraction when the seals are pupping, so there were frequent disturbances of the nursery and surrounding area. During extreme commotions the mothers led their pups from the nursery out to the deeper waters near the Goulet de Langlade (Figure 1) or to another haul out area which had not been disturbed. If their pups fell behind, the mothers would usually return to them and encourage following. Hinde index values during these times of upheaval were significantly less negative than during undisturbed periods,

suggesting that the pups were proportionately less involved in maintaining proximity with their mothers during such disruptions. Increased involvement by the mothers in keeping the pairs together became obvious in that they would return to their pups if they fell behind, nosing them frequently when swimming away from the disturbed nursery. This may have been in part a response to the fact that sixty-six percent of the recorded inappropriate approaches and following by pups occurred during periods of turmoil on, or near, the nursery. The mothers' behaviour probably made it easier for the pups to keep up. I made six underwater approaches to the nursery while snorkeling and caused the mothers to interpose themselves between their pups and me. The mothers continuously displayed threat gestures to me and rapidly guided their pups away with nudges of their flippers and noses.

Other terrestrial and aquatic comparisons support the hypothesis that there are modifications of mother and pup behaviour in situations in which the hazard of separation is greatest. The mothers were more responsive to pups' cries in the water as they were significantly more likely to return to crying pups than they were to swim away or maintain the same distance (Table IX). By contrast, on the nursery the mothers exhibited no overt reaction to their pups' cries. Presumably the greatly reduced mobility of the young on land and the concurrent reduction in the risk that the pups could become separated from their mothers reduced the need for active maternal reponses to cries. This supports Hart et al.'s (1965) contention that the mothers' care-giving patterns are adapted to the limited locomotor abilities of the offspring. However, in water, frequent cries may act as locational

"beacons" since they are propagated in air and water simultaneously and appear to have features which make them unique to the pup which is vocalizing (Renouf, personal communication).

Mothers usually led during haul-out or exit to and from the nursery (Table X) at which times there might be increased chance of becoming separated because of intermingling with others as yet unsettled at the water/shore interface. The females were alert and responsible for leading the pups to a location on the beach and thereafter defending the pups. Similarly, they usually led their offspring during submergence and emergence while swimming (Table XI) also presumably times of increased likelihood of separation because of poor visibility underwater and across the air/water interface. The mothers perhaps also ensured that their pups did not stray by frequently piggybacking the initially-weak neonates which progressively decreased in frequency until the pups were weaned (Table XII; Figure 11).

Though mothers and pups could not be observed when they went to sea, it seems likely that they stay together at all times, considering the short maturation period of this species to weaning, the dynamic nature of the haul-out site and the specificity of the mothers' attentions. Lone pups were rarely seen. A mechanism whereby mothers and their pups could recognize and stay in close proximity with each other would be highly adaptive and could involve the formation of some form of bond. Whether or not the mother bonds to the young, or vice versa, or both, depends on the social structure of the breeding group and the degree of offspring mobility.

The probability of maternal bonding is greatest when the young are

single, precocial, highly mobile and the social structure (at least during breeding) is gregarious (Ewer, 1968; Gubernick, 1981). Phoca vitulina precisely fit these criteria with perhaps the most precocial young and autonomous maternal diads. Strong behavioural bonds on the part of the mothers forged at birth have been proposed for Grey seals (Smith, 1968; Fogden, 1971), Elephant seals (Petrinovich, 1974) and Weddell seals (Tedman and Bryden, 1979). Such a maternal bond would be of obvious importance to the cows returning to nurse their pups in the rookeries. However since Harbour seals pups are never far from their mothers, the need for a maternal bond likely stems from the precarious position the pair finds itself in in water. The pup also bonding to its mother would help compensate for the pup's increased mobility in water.

The behavioural records presented in this thesis indicate the existence of, and some of the properties of some form of mutual bond. The mother had a clear preference for her own pup since she would nurse only it and launched attacks on any other seals, particularly pups, which might inadvertently approach too close. The main reason for this specificity is probably energy-related. Mothers rejecting approaches by other pups prevent these unrelated offspring suckling and consequently depriving their own young of milk. The milk, with its extremely high fat content (43 percent; Jelliffe and Jelliffe, 1976), is undoubtably costly for the mothers to produce. Even with a single pup nursing, by the time the pups were two weeks old their mothers had taken on a gaunt appearance with protruding hips. Single females were never observed to accept the attentions of a strange pup and in only one unique case amongst more than 200 Harbour seal maternal diads were two females

observed to nurse the same pup (page 16 and Figure 6). The pup seemed to prefer one female over the other but was seen to suckle both. Perhaps the two females gave birth in close spatial and temporal proximity and both became convinced of their ownership of the one pup. In one incident, two Harbour seals were observed to whelp within inches of each other simultaneously (Ben Davis, personal communication).

The mothers prevented the approach of other adults as well. Keeping other bellicose females away probably minimized the number of potential attacks on the pup. Aggression directed at pups may be a potential source of injury and may even result in a pup becoming separated from its mother and perhaps orphaned. Several of these attacks caused the recipient pups to flee to the water in panic necessitating pursuit by their own mothers to retrieve them.

The development of the pup's bond to its mother is evident in the Hinde coefficients calculated for the first forty minutes postpartum (Table V) which revealed a significant transition from initial positive values (the mothers actively maintaining proximity with their newborn pups) to the negative values common on the nursery subsequently (the pups sustaining proximity with their mothers). The positive values during this early period were not simply due to the immobility on the part of the pups since they could, and usually did, approach virtually any object, such as afterbirth. Three of these newborns even followed strange females that happened to move past in front of the pups. However, by the age of thirty minutes, before which the pups' own mothers belligerently prevented the approaches of other seals and continually initiated nose-to-nose contacts, the pups oriented towards

and stayed with their own mothers. From this point on the pups would rarely approach or follow strange females.

These events suggest early formation of a bond by the pup to its own mother which was rapidly acquired and analogous in some respects to imprinting characteristic of many nudifigous bird young (Lorenz, 1937) and the rapid bonds formed by goats (within five minutes after birth; Klopfer et al., 1964). Inherent in imprinting models is an "unbonded" condition prior to the critical period at which the bond is formed (Lorenz, 1937; Hess, 1973; Poindron et al., 1979). The early positive Hinde values and the pups' indiscriminate interest in objects other than their own mothers indicate that this might also be occurring with the Harbour seal pups prior to their developing a strong filial bond. After approximately 15 minutes the pups began to react noticeably to the attentions of their own mothers as indicated by their orientation and active responses to nose-to-nose contacts. By the time that the tide returned to flood the nursery, the pups would follow their mothers reliably.

It is possible that, at least early in the pups' life, instead of a specific bond pups responded to generalized stimuli such as mothers' bouncing hindquarters as she crawled on land, or the mothers' head while swimming, regardless of whether or not the hindquarters or head belonged to the pups' own mothers. In this event, the onus would be on the mother to ensure that she was the closest individual to her pup. This notion is supported by the fact that at least during the first few days following birth pups were occasionally observed to approach or nose nearby females other than their mothers. From the second week of life

the pups would infrequently tolerate a stranger's attentions, perhaps having learned that approaching other mothers always resulted in aggressive attacks.

A bilateral bond between Harbour seal mothers and their young is a strategy by which the mothers and pups could ensure necessary contact and reduce identification errors which might result in attacks on the pups. This bond would also act in conjunction with the media-dependent behavioural modifications by the mothers to even further reduce the risk of separation.

Data regarding weaning provide a somewhat different picture than previously described for Phoca vitulina. An important behavioural change occurred slowly during the season in which the mothers became decreasingly solicitous towards their pups by initiating fewer nursing bouts, piggybacking the pups less and increasingly rebuffing their attempts to suckle. The pups responded by becoming increasingly intent on approaching (indicated by the significant increasingly negative value for the terrestrial Hinde coefficient; Table II). This is contrary to a study of another phocid, the Weddell seal (Leptonychotes weddelli), by Tedman and Bryden (1979) in which the pup gradually initiated more haul-outs, and exits and maintained a greater intrapair distance as weaning approached. This may stem from the Weddells' static birth and haul-out sites where the mothers remain after the pups are weaned. The Harbour seal pups' behaviour is more akin to the normal mammalian pattern. This contention is supported by a modified Hinde coefficient (Table XIII) which became increasingly negative from birth until the pups were weaned at four to five weeks of age, suggesting that the pups

assumed an increasing responsibility for nursing. The pups were certainly initiating a greater proportion of nursing bouts, and had to tolerate increasing rejections by the mothers (Table XIII). This pattern differs from that reported by Wilson (1974). In her Irish group mothers never rejected the approaches by pups and continued to initiate all nursing bouts until weaning.

These findings by Wilson corroborated a captive pair study by Finch (1966), which suggested that Harbour seal pups wean themselves. Contrary to these studies, Lawson (1982), Renouf and Diamand (1983) and Renouf et al. (1983) postulated that the mothers were responsible for weaning the pups, and that it was an abrupt event rather than the normal mammalian pattern in which the mother gradually weans its offspring through increasing aggressive rejections to nursing initiations (e.g. Hinde and Atkinson, 1970; Barash, 1974; Clark, 1977) and the young strive to maintain the maternal relationship (Rosenblatt and Lehrman, 1963; Hoff et al., 1981). The apparent abruptness of weaning concluded from these earlier Miquelon works, compared to this 1982 study, was probably a function of the smaller sample size and use of primarily one measure (distance changes). The data in this thesis, which encompass a wider range of behavioural measures and contain more detail, provide strong evidence that, like most other pinniped species (LeBoeuf and Briggs, 1977; Reiter et al., 1978; Ronald and Dougan, 1982), the Harbour seal mothers weaned their pups. Further, this weaning process parallels the aforementioned mammalian pattern.

It is probable that lactation is followed shortly by ovulation and mating with delayed implantation until several months later (Fisher,

1954; Bigg and Fisher, 1974; Bigg, 1981). Since this is the case, why are the pups weaned after such a short nurturant period ? There are two possible explanations.

The mothers may wish to wean their pups during mid summer so that they can take advantage of the relative abundance of food in the sea at this time to recover the significant amount of fat that they have lost during nursing. Fat stores accumulated for the following winter provide a crucial insulating layer, energy for warmth and development of the fetus for the following spring. Secondly, if the pups are weaned so rapidly, they can also take advantage of the summer abundance to learn to feed for themselves. It is thought that pups feed on bottom-dwelling crustaceans for one and one-half to three months after weaning (Bigg, 1973); these, and caplin, are plentiful in the Barachois during July and August. Both mothers and pups can rapidly develop fat stores during the warm air and water temperatures of late summer.

The Harbour seal weaning pattern conforms to that predicted by the parent/infant conflict model developed by Trivers (1974). Trivers proposed that there would be conflict between an infant and its parent during weaning if the offspring's behaviour demanded more parental investment than that which the parent was selected to give in terms of its own future reproductive success.

The costs to the mother of feeding her pup, gauged by significant body fat loss, may be augmented by the assumption that she did not feed during the lactation period (Boulva and McLaren, 1979). Selection may have produced a strategy such that mothers terminated nursing rapidly in order to minimize this energy expenditure for her own sake, and as

mentioned previously, to provide energy for the development of her next offspring. Pups, on the other hand, may have evolved behaviour to attempt prolonged suckling (further parental investment) in order to further improve their chances of surviving their critical first winter. These opposing strategies regarding further parental care may have caused the weaning conflict I observed, as predicted by Trivers' model.

Conclusions

As would be expected there are differences in the Harbour seal mothers' and pups' behavioural responses to the dissimilar demands of land and water. The behavioural adaptations unique to this species' maternal interaction are linked to the unusually precocious offspring and the environmental necessities forcing these pups to remain with their mothers continually during an extremely short nursing period. By assuming greater (or more overt) vigilance and control during periods of disturbance, and when the pairs are in the water, Harbour seal mothers can reduce the risk that they will become separated from their pups. Pups too can modify their behaviour by becoming more responsive to nose-to-nose contacts in the water and by emitting almost constant vocalizations with which their mothers can locate and perhaps identify them. By establishing a mutual bond mother and pups further enhance the likelihood of their remaining together until the pup has gained sufficient weight to survive after the short nurturant period.

It appears that the Harbour seal mothers become decreasingly solicitous towards the pups as the latter mature and become proficient

in the water. Despite protests by the pups, their mothers wean them at a time when it is presumably easiest for the pups to learn to feed and for both mothers and pups to establish sufficient fat stores to survive the following winter.

The key, then, to successful raising of pups rests with continuous propinquity while living on land and in the water to ensure rapid maturation and weaning at a propitious time. The Harbour seal has evolved mechanisms which ensure this.

Future Considerations

While extensive observation has provided a wide variety of behavioural measures to assess the roles of the Harbour seal mothers and pups during the lactation period, there are several field manipulation studies which might yield further information. Of primary value would be a marking program such that individual mother/pup diads could be repeatedly identified during the entire nursing season. Attempts at marking the Miquelon seals in 1982 failed as the substances tested did not adhere to the seals' wet fur for prolonged periods and it was virtually impossible to approach the group close enough to administer the marking solution. I did not attempt to throw marking materials from the blinds for fear of making the seals avoid these observation points thereafter. With marked seals information about site tenacity and interpair behavioural difference could be gained. This marking program would also be a valuable precursor to any physical manipulations designed to study the sensory modality(s) used by the mothers and pups

to identify each other.

Harbour seal mothers searching for their pups often approached various youngsters before finding their own. Since lone pups were usually crying, the mothers may have been able to distinguish their own pups' cries from others', much like the acoustic cues used by female horseshoe bats to find their offspring in crowded caves (Matsumura, 1979) or the calf calls used by female reindeer to locate young in dense herds (Espmark, 1971). Auditory signals undoubtedly would have advantages over visual cues on the crowded nursery where the pups were often obscured by other nearby pairs and in the water where the bulk of the pups' bodies were below the water's surface.

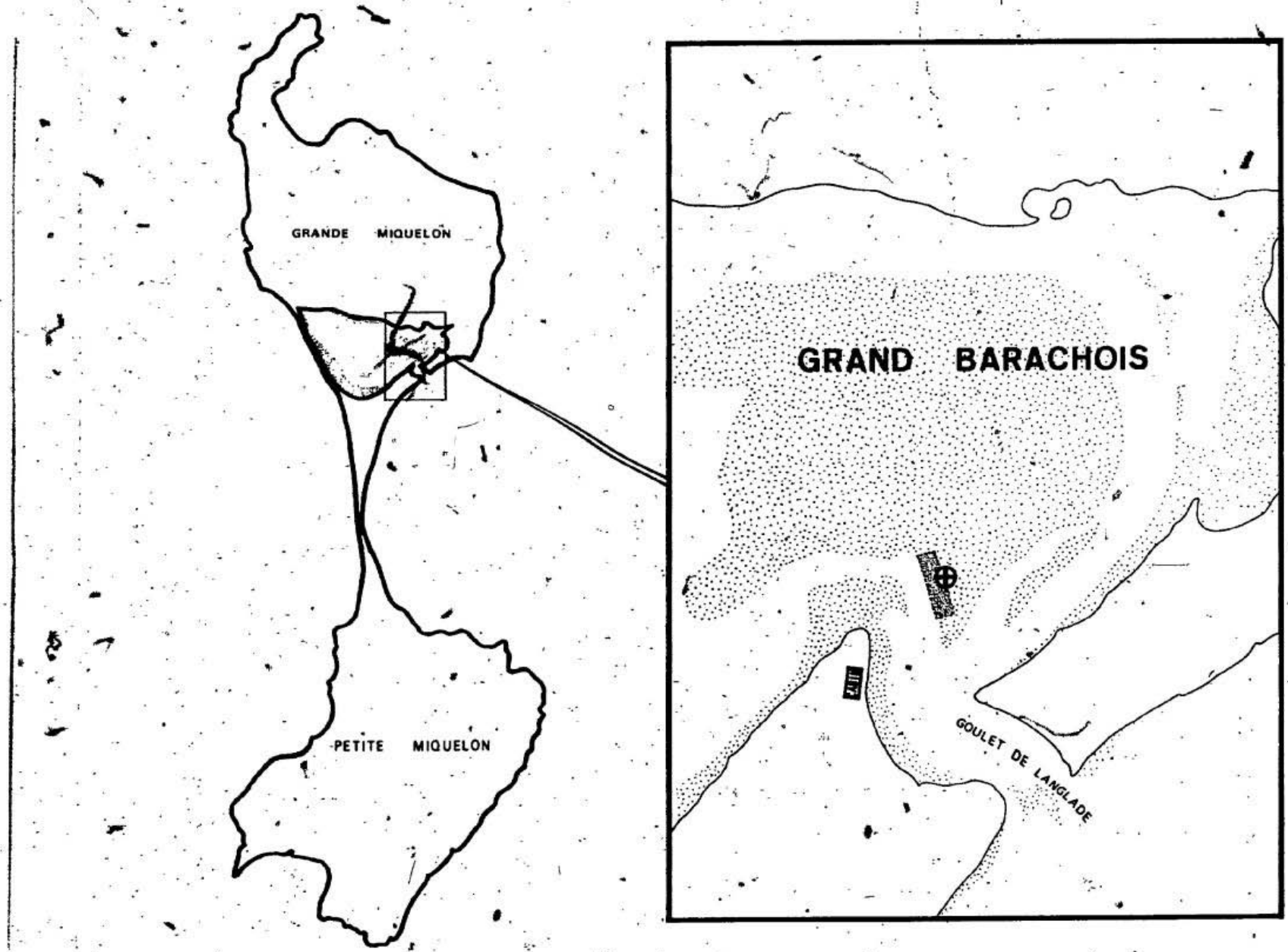
The pups' calls likely did not have an attraction function per se on land as the mothers were as likely to remain still as to move away or approach following a call (Table IX). Preliminary sonographic analyses suggest that pup calls display individual uniqueness which the mothers could use to identify their offspring (Renouf, personal communication). Further collection of a large number of individual pup cries, preferably from marked pups, would enable statistical comparisons of the harmonics of each call to determine if there are perhaps vocal "signatures".

Although mothers nosed their pups more frequently than vice versa (Table VIII) while on land, both mothers and their pups were NOT predisposed to approach each other as a result of nose-to-nose contact. Only in the water were nose-to-nose contacts likely to result in the pups swimming closer to their mothers. Having reached a pup, the mothers' final confirmation of ownership seemed to come following nose-to-nose contact during which either olfactory or tactile

information might have been exchanged. Since nasal contacts rarely resulted in distance changes on the part of either mothers or their pups, except when the mothers nosed their pups in the water (Table VIII), it is likely that this behaviour might be used primarily as an aid to identification on land. By rendering mother Harbour seals temporarily anosmic (techniques for which are well developed), the role of olfaction in pup identification might be better assessed.

South of Miquelon, on the rocky coast of Langlade (Figure 1), there are several other colonies of Harbour seals. The seals whelp in these locations and can be observed for extended periods of time (albeit not as closely as in the Grand Barachois). The substrate and wave action of these other locations are similar to those described for Wilson's (1974) study group. A quantitative study of the Langlade colonies, using some of the same techniques as presented in this thesis, might provide evidence to suggest whether or not the behavioural differences seen on opposite sides of the Atlantic are substrate-related.

Figure 1: A map of the islands of Miquelon and Langlade with an enlargement showing details of the Grand Barachois and nursery haul-out sites. The nursery area is denoted by the stipled area. The location of the observation blind (+) and elevated observation point (cabin) are indicated.


GRANDE MIQUELON
PETITE MIQUELON
GRAND BARACHOIS
GOULET DE LANGLADE

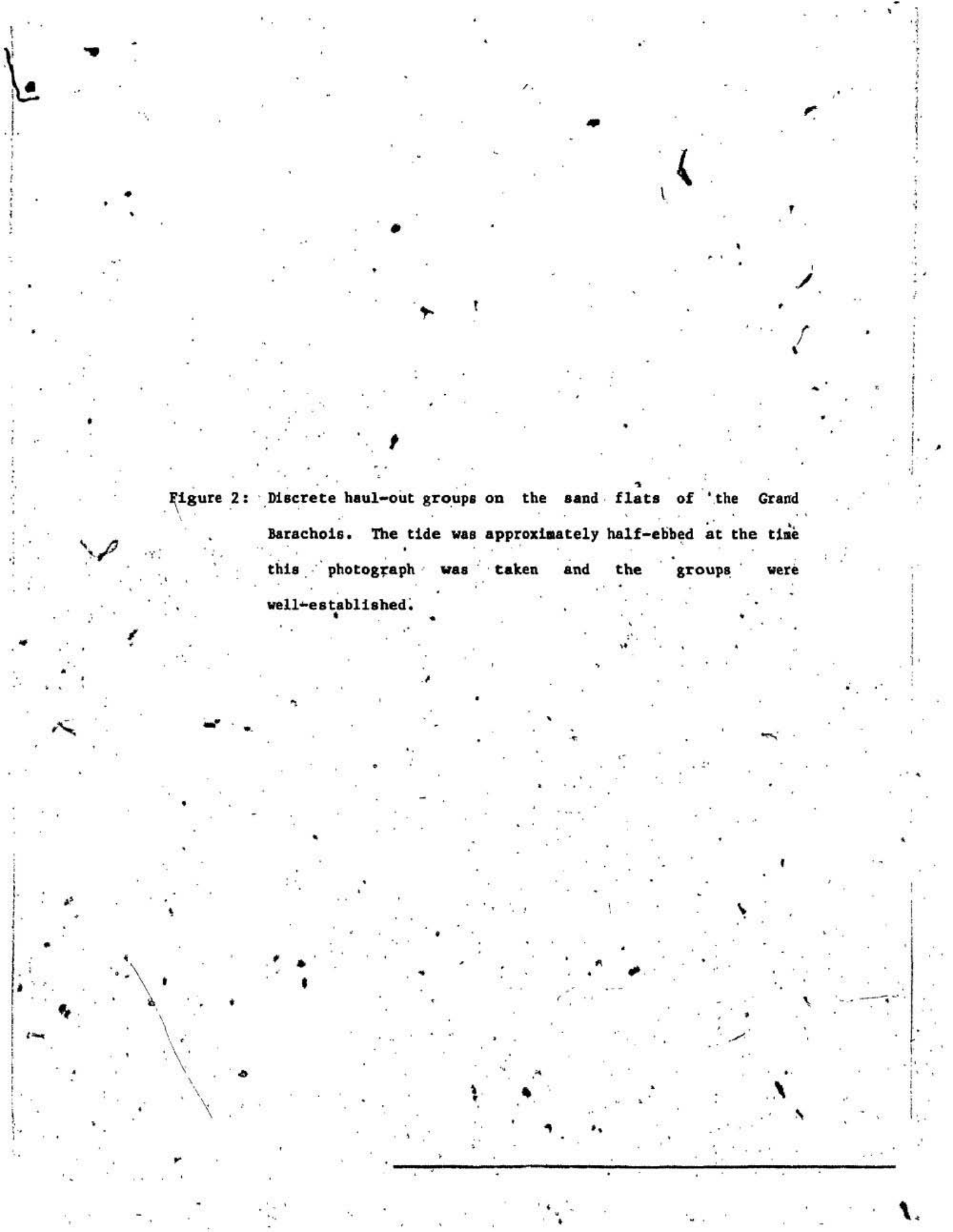


Figure 2: Discrete haul-out groups on the sand flats of the Grand Barachois. The tide was approximately half-ebbed at the time this photograph was taken and the groups were well-established.

Figure 3: Characteristic posture adopted by Harbour seals about to give birth. Note this female's proximity to other females.

Figure 4: A mother and her pup involved in nose-to-nose contact. The nostrils of both are dilated and their vibrissae are protracted.

Figure 5: Diagram of the typical position occupied by a pup while "piggybacking" on its mother while swimming. The pups' foreflippers were seen to clasp the mothers' backs.

Figure 6: A pup accompanied by two females both of which acted as its mother (indicated by -->). Both were observed to nurse it and initiate nose-to-nose contacts. Neither female directed aggressive behaviour at the other but would repell the advances of strange mothers and pups.

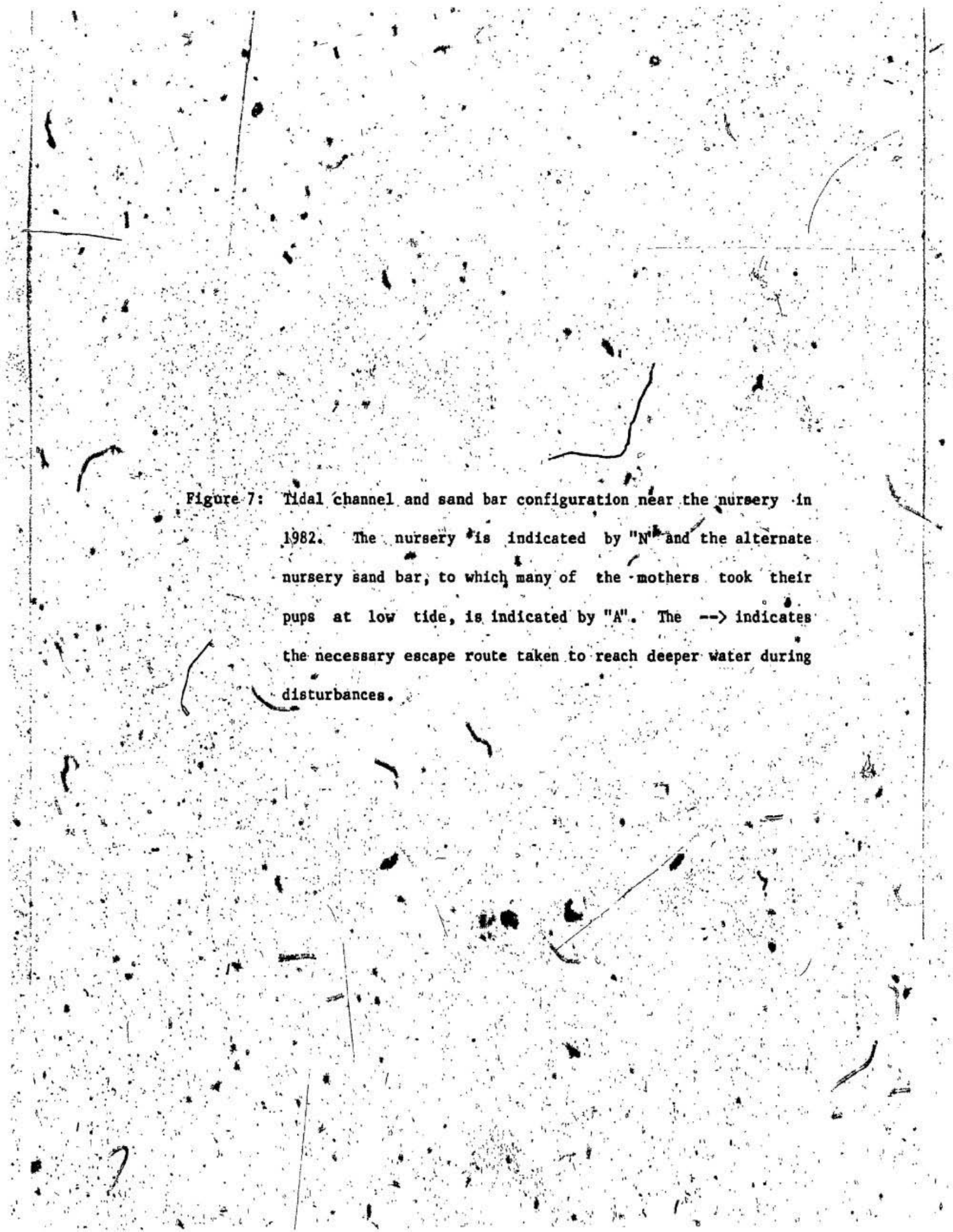


Figure 7: Tidal channel and sand bar configuration near the nursery in 1982. The nursery is indicated by "N" and the alternate nursery sand bar, to which many of the mothers took their pups at low tide, is indicated by "A". The --> indicates the necessary escape route taken to reach deeper water during disturbances.

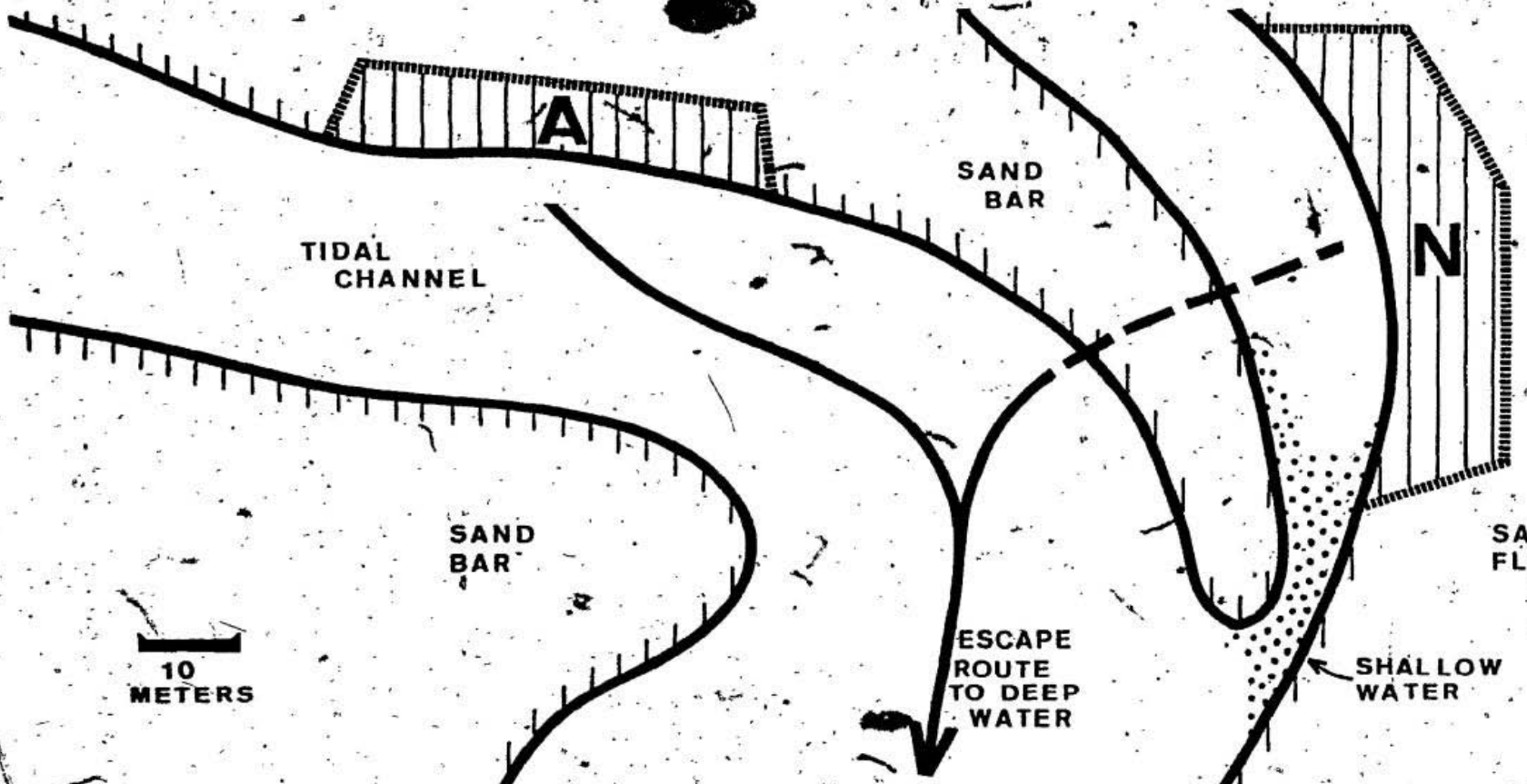

A
SAND
BAR
TIDAL
CHANNEL
N
SAND
BAR
SAND
FLATS
10
METERS
ESCAPE
ROUTE
TO DEEP
WATER
SHALLOW
WATER

Figure 8: A pup (male; indicated by a ★) about to attempt to nurse from a female already suckling her own pup (indicated by N). The "sneaking" pup usually approached the nursing females from behind them and did not cry. The intruding pup would then push the rightful pup from its mother's nipple and begin suckling.


N

Figure 9: A female with two pups she had suckled frequently for several hours. She had initiated numerous nose-to-nose contacts with both pups. Note the disparity in the pups' sizes; the female eventually left the nursery accompanied by the smaller of the two pups (indicated by S).

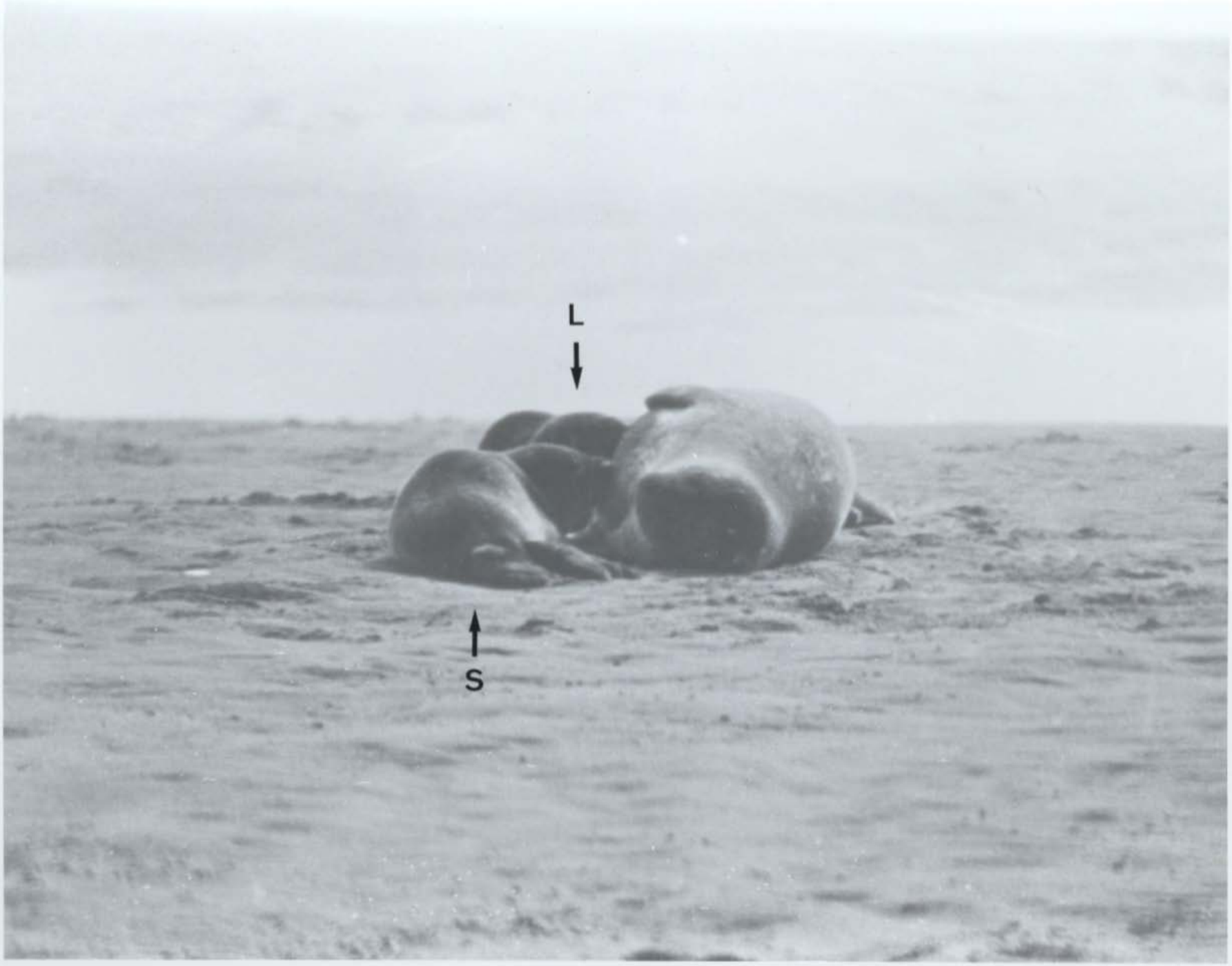

L
S

Figure 10: Elevated canvas observation blind.


1 METER

Figure 11: Graph of daily, weighted frequencies of aquatic piggybacking behaviour. Individual vertical scale values were calculated by dividing the number of piggybacking bouts recorded on a day by the total number of pairs recorded that day. A Page's L test revealed a significant decreasing daily frequency over the nursing season. A regression line has been plotted onto the graph.

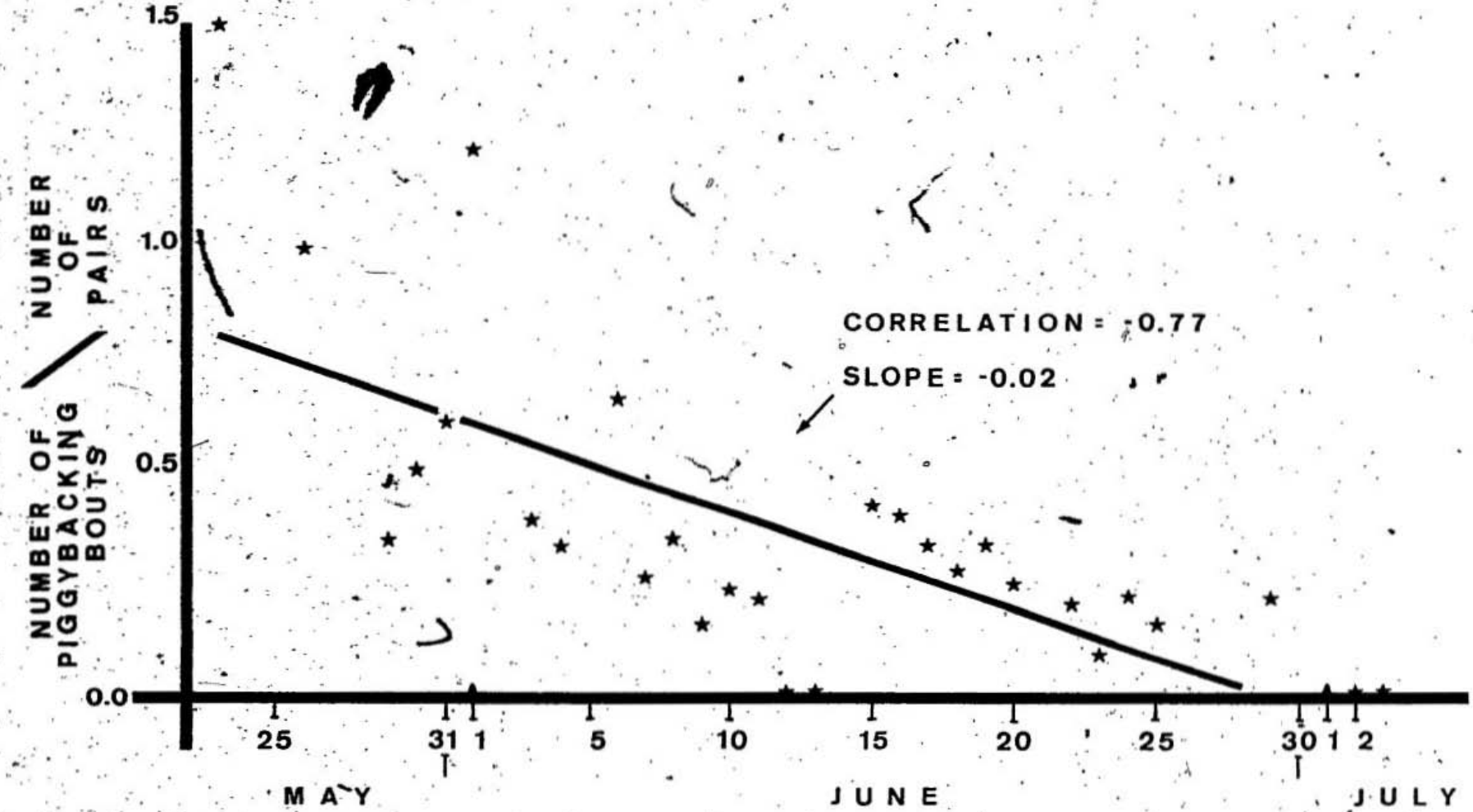

1.5
1.0
0.5
0.0
NUMBER OF PAIRS
NUMBER OF PIGGYBACKING BOUTS
CORRELATION = -0.77
SLOPE = -0.02
25
31
1
5
10
15
20
25
30
1
2
MAY
JUNE
JULY

Figure 12: Graph of daily proportions of distance decreases by the pups during the nursing season. Not shown, for clarity, are the proportions of distance decreases by the mothers (since their values are such that they sum with the pups' decreases to equal 100 percent).

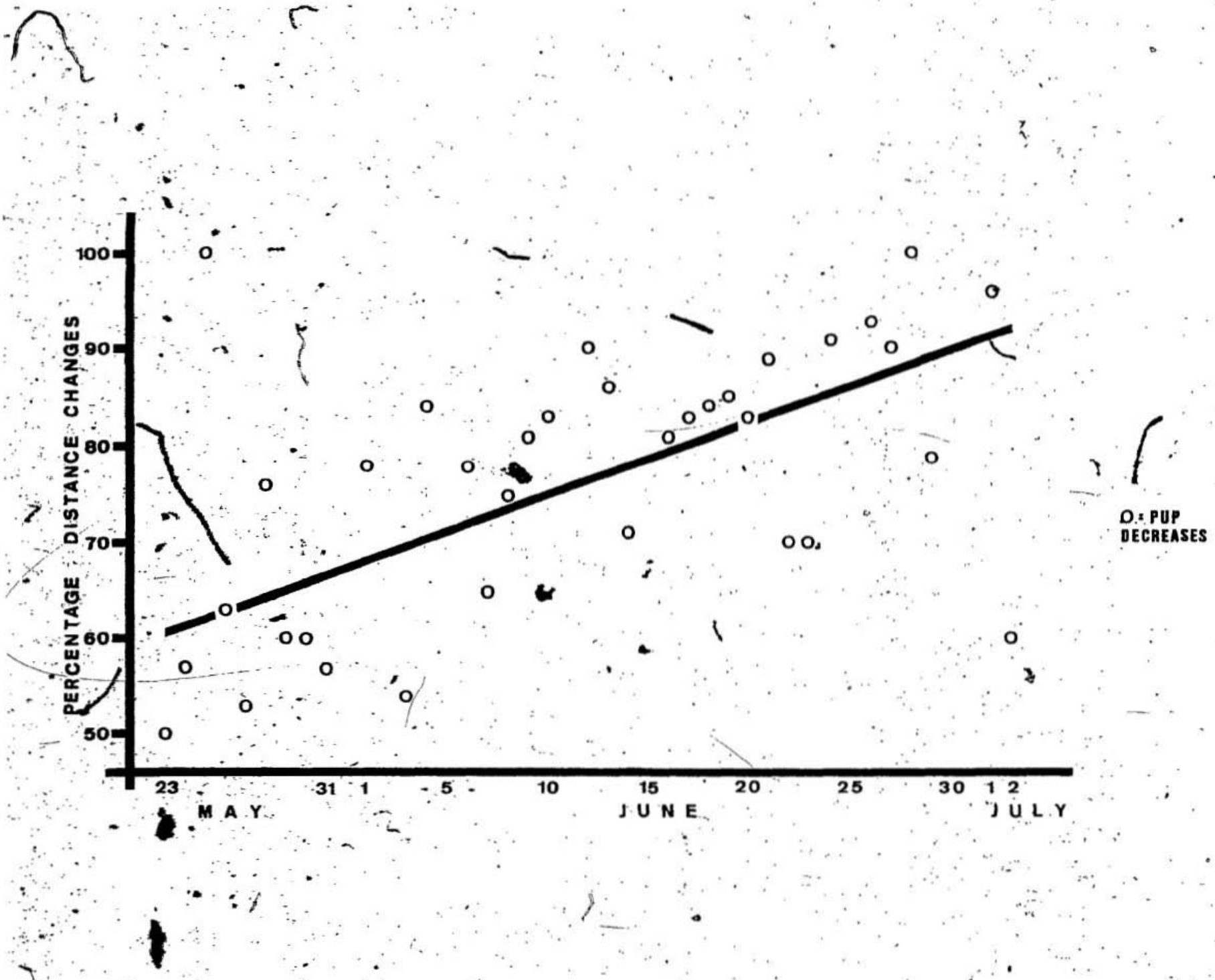
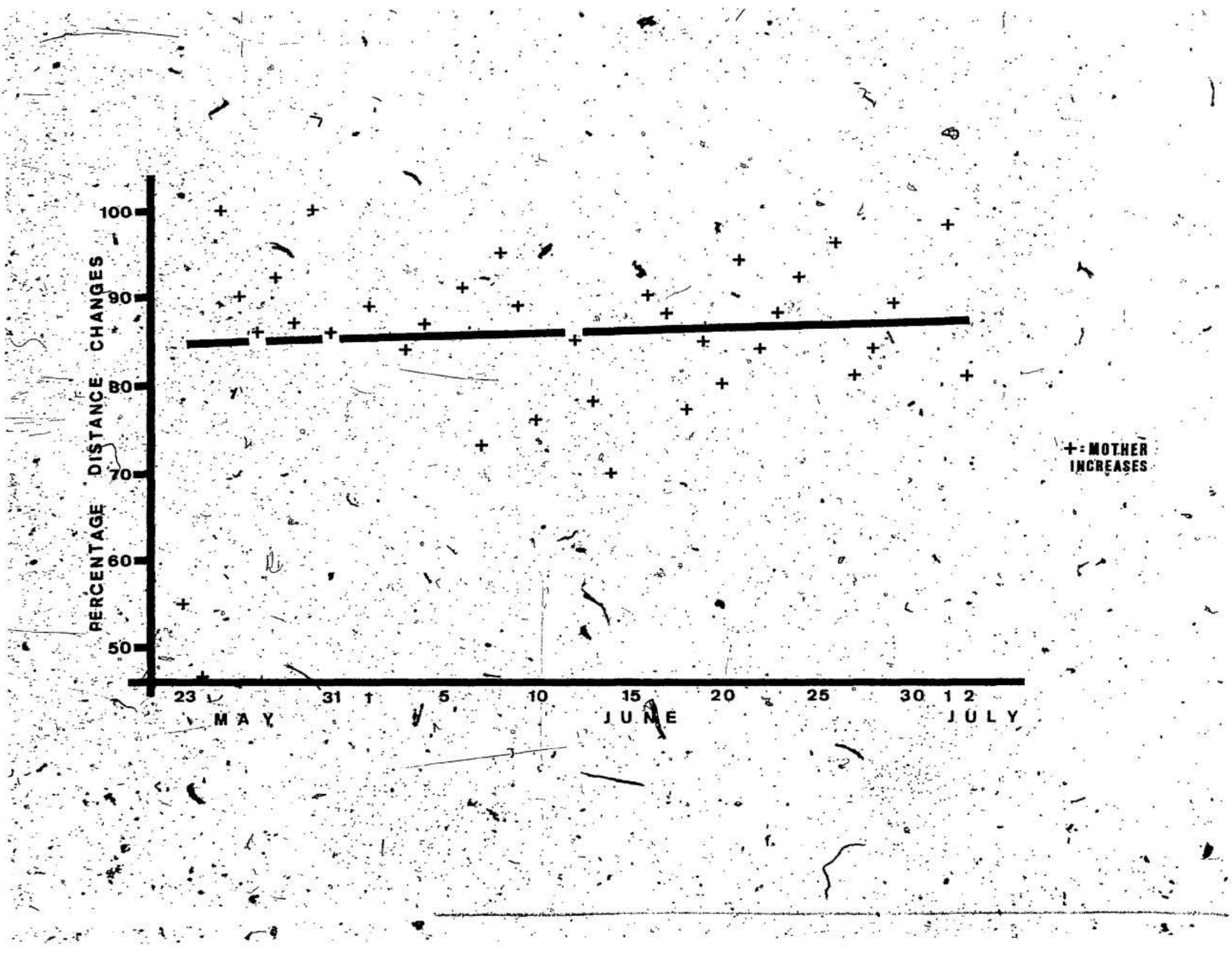

PERCENTAGE DISTANCE CHANGES
100
90
80
70
60
50
O: PUP DECREASES
23
31
1
5
10
15
20
25
30
1
2
MAY
JUNE
JULY

Figure 13: Graph of daily proportions of distance increases by the mothers during the nursing season. Not shown, for clarity, are the proportions of distance increases by the pups (since their values are such that they sum with the mothers' increases to equal 100 percent).


PERCENTAGE DISTANCE CHANGES
100
90
80
70
60
50
23
31
1
5
10
15
20
25
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MAY
JUNE
JULY
+: MOTHER INCREASES

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