

The social development of a captive Grey Seal (*halichoerus grypus*) pup for the first six months

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Abstract

The social development of a female grey seal (*Halichoerus grypus*) pup born at the National Zoo, Washington DC was chronicled for six months after birth. Also present in the grey seal enclosure were the mother and three other females. The father was present only until weaning. Until weaning, records were taken of maternal care, nursing bouts, activity cycle of the pup, and social interaction between mother and pup. After weaning, the pup did not begin to eat fish for nearly six weeks, and during this fasting period she interacted very little with any other seal, reacting in an alarmed or defensive manner to any approach. During this period the mother-pup relationship appeared gradually to be totally severed.

After the fasting period, the pup increasingly initiated social exploration of the other individuals, usually by following and attempting to nose the hind-flipper region. From three months of age she also sometimes initiated nose touching. In this way she developed limited social relationships first with the two smaller females, then her mother, and finally the other large female. Her relationship with her mother at this time appeared not to differ in quality from her relationships with the other three seals; during months 4-6, however, the pup oriented to her mother and sister a little more than to the two unrelated seals.

These observations are discussed in relation to our current knowledge of grey seal pups in their natural environment.

Introduction

The aim of this study was to chronicle the social development of a newborn grey seal (*Halichoerus grypus*) through the stages of nursing, weaning and independence.

We are familiar from earlier field studies with the general picture of a grey seal's social experience from birth until weaning during the third week of

age (Davies 1949; Lockley 1966; Fogden 1971). Most pups remain on the beach during this period. At breeding sites where the mother-pup population is sparse and mothers have easy access to the water, the mothers spend much time hovering offshore. They may spend little time with their pups except for just before, during and after nursing, which seems to occur at irregular intervals of 2-6 h. However, Davies (1949) and Wilson (1970) have highlighted the individualistic behaviour of several mother-pup pairs on Ramsey Island, Wales, which varied considerably from this general pattern. Also, Davies (1949) and Fogden (1971) have pointed out that on crowded beaches mothers spend more time lying beside their pups between nursing bouts. The variations seem to suggest considerable flexibility in maternal care according to prevailing conditions, and also according to the 'personality' of mother and pup. Most healthy pups spend most of the time between nursing bouts sleeping, and do not interact with one another. Some pups on Ramsey Island, however, do enter the sea, and may swim around or play with the mother at the water's edge.

During the third post-natal week, the mother usually disappears from the beach, leaving the pup behind, and does not return. Such apparently abrupt weaning behaviour also occurs between the more aquatic mother-pup pairs of the common and harbour seals (*Phoca vitulina vitulina* and *P. v. concolor*), in which species the dynamics of the mother-pup relationship have been studied in more depth (Wilson, 1974a; Renouf *et al.*, 1983).

After their mothers' final departure, most grey seal pups remain on the natal beach for several more days while they complete their moult (Davies, 1949; Lockley, 1966). Some pups may move around the beach and swim in the shallows, but healthy pups still do not interact at this time. Lockley (1966) comments that 'The grey pup remains unsociable and hostile to all other seals on first becoming independent...' In this respect they differ from pups of *Phoca vitulina* and *Mirounga angustirostris* (the elephant seal), who do associate and interact with

one another immediately after weaning (Wilson, 1978; Rasa, 1971; Reiter *et al.*, 1978). After moulting, the pup leaves its natal beach, and is thought to spend much of the next six months at sea, wandering locally or considerable distances (Lockley, 1966; Hewer, 1974).

Despite the grey seal pup's inauspicious start in social life, field observations during the spring, late summer and early autumn have indicated that young seals from a year old up to fully grown males are extremely social, contact-prone, and engage in prolonged non-aggressive interaction with one another. Most of such interaction is dyadic, between two males or a male and female (Backhouse, 1960; Lockley, 1966; Wilson, 1970; 1974b).

We know, therefore, that during their first year, pups must enter a period of peer socialization. Lockley (1966) notes that moulted pups haul out with older seals, but remain socially aloof from them and other pups. Six-month old pups 'are still shy of the older seals and to some extent of each other', but two pups will occasionally play together in the sea. Lockley suggests that most peer socialization probably occurs during the second six months of the pup's first year.

The main purpose of this longitudinal study of a single captive-born pup in a group of older females was to explore the pup's post-weaning shyness and subsequent overcoming of this shyness. The study did not continue beyond the first six months because the lack of a young male or another pup in the group meant that the pup's opportunities for peer socialization were in any case extremely limited. Nevertheless, by monitoring the pup's curiosity towards the other seals in the group, we hoped to obtain some idea of a grey seal pup's internal timetable of social disposition. Observations on maternal care are included here in order to assess how close our pup came to having a 'normal' infancy (compared to field observations) and to help refine our knowledge of progressive changes in the mother-pup relationship. The latter is treated as the start of the continuum of the pup's social development.

Animals and methods

The female pup (Kara) was born at the National Zoo on Dec 4, 1983. Her birth and weaning weights were 16 kg and 50 kg respectively. The pup fasted from final weaning on Dec 24 until she first began to tear and chew fish on Feb 1. Her mother (Selkie) and father (Gunnar) were both about 10 years old at the time of the study; both had been captured in Iceland as six-month old pups. Kara was Selkie's fourth pup (her first was still-born), and her second by Gunnar; Selkie had been a successful mother with her two surviving earlier pups. Gunnar

remained in the enclosure until Kara was 19 days old, when he was removed (for zoo management reasons) for the remainder of the study period. The other seals in the enclosure were all also *H. grypus*: Chandrie (2 yrs), daughter of Selkie and a full sister of Kara; Keltie (5 yrs), a small, nulliparous female collected as an 'orphaned pup' from the New England coast; and Lila (3 yrs), an adult-sized female born in San Francisco Zoo (Lila gave birth in Oct, 83, but did not care for the pup, which drowned).

The topography and dimensions of the enclosure are shown in Fig. 1. Most of Kara's time on the beach was spent in the 'cave'. After weaning, Kara spent much time resting submerged at the 'top' end of the pool.

Observations were made between 7.00 am and 5.00 pm from Dec 5, 1983 until the end of May, 1984. The authors (and supplementary observers from FONZ during the first three post-natal weeks) observed in shifts usually lasting about two hours. Observers were asked to record certain behaviours and positions of animals, but unfortunately inter-observer reliability could not be tested. The total number of hours of observation during each month of the study are given in Fig. 3.

For the first five post-natal weeks, behaviour records were made on a 15-min check sheet divided into one-min intervals: in each interval the positions and behaviour of pup, mother and other relevant seals were recorded. Observers were asked to note all activity by or directed towards the pup, including nursing, social and solo behaviours. Initiation, duration and termination of nursing bouts were recorded, and any nosing contacts between the pup and any other seal were specifically noted. After five weeks of age, a narrative record of behaviour was made, with a time check noted beside each behavioural event.

Since interactions between the pup, her mother and the other seals tended to be occasional, slow-moving and brief, they were easy to see and describe in layman's terms. Some observers may not have fully described nosing contact exchanges; the frequency of these may therefore be slightly underestimated. Where the first author (S. Wilson) was unable to reconstruct with reasonable certainty all the behavioural events from a particular record, that record was discarded from some or all of the behavioural frequency calculations.

Results

(a) Pup nursing and activity cycle during the nursing period

Nursing was virtually always initiated by the pup calling and terminated by the pup detaching from

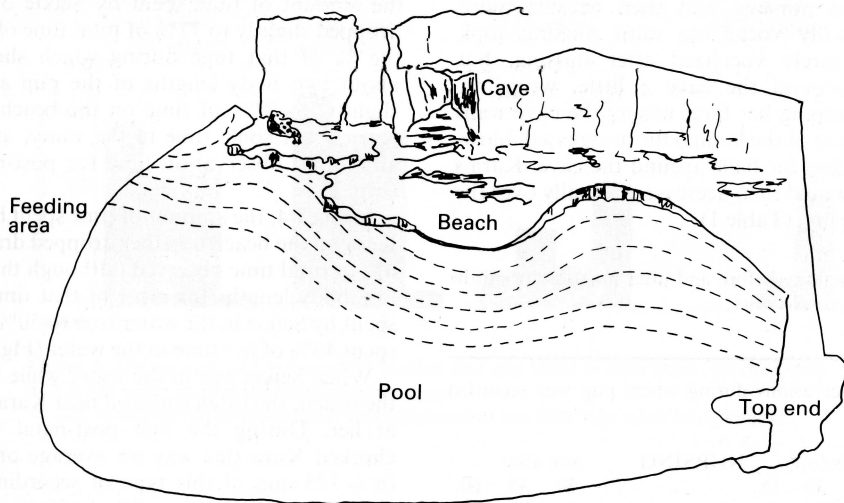


Figure 1. The grey seal enclosure at the National Zoo, Washington DC. Detail is given of the 'cave' area inhabited by the pup during the nursing period. The pool is about 25 m long, 3 m deep, and has a sloping side indicated by the broken lines.

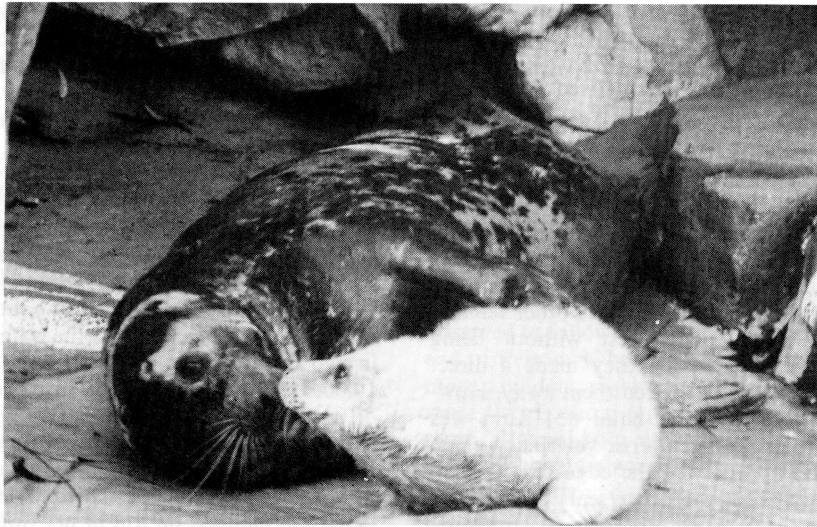


Plate 1. Mother and pup touch noses; mother strokes pup (photo—L. Miller).

the nipple and moving away, often towards the mother's head. The pair often interacted then by nosing one another, and Selkie would often pat or stroke Kara (Plate 1; detailed in (c) below).

Nursing bouts were evenly distributed between 7.00 am and 5.00 pm. The amount of time devoted to nursing increased slightly from week to week during the three-week lactation period (\bar{X} nursing time was 1.2, 2.0 and 3.7 min/h for weeks 1, 2 and 3 respectively). The mean frequency of nursing bouts

similarly increased (one bout per 4.6 h, 3.9 h and 2.4 h for each of the three weeks), and so did the mean duration of nursing bouts (5.5, 8.9 and 9.6 min respectively; 2-tailed $P < 0.02$, comparing the first and second 10d periods by the Mann-Whitney U test). Nursing was last observed on d 20 (Dec 24), but no obvious avoidance or rejection of the pup by Selkie was seen. The final day of nursing was the day after Kara first entered the water.

Kara tended to be relatively inactive until about

30 min before nursing, and then became more active, eventually vocalizing until nursing took place. Kara rarely vocalized after nursing, but would shift around the cave a little, wriggling, rolling over, wiping her face, nosing the cave walls and, as moulting of the lanugo fur progressed, blowing and pursuing fur balls around the cave. Kara's activity level would then decrease gradually over the hour after nursing (Table 1).

Table 1. Pup activity before and after nursing during the first three post-natal weeks

| wk | % min of observations during which pup was recorded active | | | | | | | | |
|----|--|----|----|----|---------|-----------|----|----|----|
| | min before | | | | NURSING | min after | | | |
| | 60 | 45 | 30 | 15 | | 15 | 30 | 45 | 60 |
| 1. | 0 | 0 | 20 | 42 | 98 | 98 | 56 | 52 | |
| 2. | 14 | 18 | 20 | 35 | 37 | 29 | 18 | 27 | |
| 3. | 0 | 0 | 2 | 37 | 63 | 60 | 67 | 20 | |

(b) Maternal care

(i) While the pup was on the beach (weeks 1-5)

Throughout the first 19 days after birth, the pup moved little from the 'cave', and the mother was vigilant and defensive of her. The male, Gunnar, persistently hauled out on the beach, and Selkie repeatedly drove him away by hooting, flipping and lunging at him. She often looked back at Kara while attending to Gunnar, and occasionally nudged the pup out of his way. The other females occasionally hauled out to rest without being repelled by Selkie, but when they made a direct approach to Kara, Selkie chased them away. However, on one occasion (post-natal d5) Kara was returned to the enclosure after a veterinary exam and (unusually) approached the edge of the pool, Selkie at her side. All the other seals approached Kara from the water, and took turns at stretching out of the water towards her and touching noses. Selkie tolerated the females' approaches, but when Gunnar touched the pup's nose, she snapped at the pup, nudging it away from Gunnar. When Gunnar approached a second time, she dived in the water to chase him away. The last occasions when Selkie chased another seal away from Kara were post-natal d18 and d23.

During the first week, Selkie spent most (85%) of her time on the beach, and most of that time (88%) she lay within about two adult body lengths of the pup. The remainder of the time she spent in the water (Fig. 2). During the second and third week,

the amount of time spent by Selkie on the beach dropped slightly to 77% of total time observed, and the % of that time during which she lay within about two body lengths of the pup also dropped slightly, to 77% of time on the beach. From d19, Kara spent some time in the water, amounting to 10% total observation time for post-natal week 3 (Fig. 2).

In week 4, the amount of time spent by Selkie and Kara on the beach together dropped dramatically to 6% of total time observed (although they lay within two body lengths for most of that time). The time spent by Selkie in the water rose to 50%, while Kara spent 45% of her time in the water (Fig. 2).

When Selkie was in the water while Kara was on the beach, she often surfaced near Kara, and looked at her. During the first post-natal week, Selkie checked Kara this way on average once a minute ($n = 125$ min of this type of recording), and also spent some of that time (19 of 125 min) gazing continuously at the pup from the water. During the second week, Selkie checked Kara on average only once every two min ($n = 291$ min), and spent very little time (less than 5 min) gazing continuously at her. During the third week, Selkie checked Kara only once every 5 min on average ($n = 116$ min). During the fourth and beginning of the fifth week, she still occasionally looked at Kara from the water. Kara was last seen resting in the cave on d30; thereafter she was always in the water.

(ii) Maternal care while the pup was in the water

Kara first entered the water on post-natal d19. Selkie and Kara consorted together (continually swimming around each other, touching and following) on d19 and some of d20 but not thereafter.

On d19 their behaviour in the water was recorded in two 45-min bouts as they swam together. From 10.00-11.15 am there were 39 instances of following or approaching by Selkie and 19 by Kara. There were 27 instances of mutual nose touching, 14 other nosing contacts made by Selkie to Kara, and also 14 by Kara to Selkie. Selkie leaned her head over Kara twice and climbed on top of her three times. There were five occasions when Selkie swam along, and Kara did not follow her. From 12.30-1.15 pm Selkie was apparently encouraging Kara to haul out with her. There were 18 instances of following and approaching by Selkie and 8 by Kara. There were 19 mutual nose touches, 2 other nosing contacts by Selkie and 6 by Kara. Selkie hauled out fully at 1.05 pm, but Kara did not follow. Selkie returned to the water at 1.08 when Chandrie was following Kara and nosing her hind flippers; Selkie chased Chandrie away.

On d22 Selkie watch Kara for nearly half an hour while Kara attempted to haul out on the ice-covered

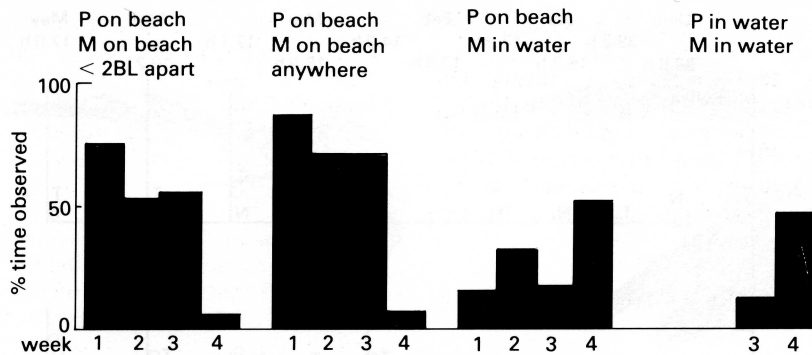


Figure 2. The amount of time spent by mother and pup close to each other, on the beach and in the water during the first four post-natal weeks.

< 2BL indicates the distance apart was estimated at less than two adult body lengths.

shore. Selkie then swam under Kara, seemingly attempting to push her up, though unsuccessfully. On other occasions Selkie seemed to be trying to prevent Kara from hauling out. On d27 Selkie approached and touched Kara, who was hauling out. Kara flipped and splashed at Selkie, and swam away. Later on, Kara tried again to haul out. Selkie approached, nosed Kara's nose and neck, leaned over her, and dragged her back into the water. Kara snorted and swam away. Similar behaviour was seen again twice in January (d32 and d40).

From d22 onward, Kara spent much time submerged in a corner at the top end of the pool (Fig. 1); this corner was rarely disturbed by the other seals as they swam around, and was the corner remotest from the turbulence created during feeding.

(c) The development of social interaction between the pup and the other seals in the group (months 1-6)

In sections (a) and (b) above on nursing and maternal care, social interaction between mother and pup has been described as it occurred in those care-giving contexts. The present section brings together from all contexts social behaviour patterns such as approaching, following, body nosing, touching, and play, and chronicles the occurrence of these behaviours as they related to the pup through the nursing, weaning and post-weaning period until the pup was six months old.

We will begin here with an outline of the pup's social responsiveness during this period, and then proceed to a profile of her developing social relationship with each of the four other females in the group, starting with her mother.

During the nursing period, mother and pup interacted often, the pup responding to the mother's

contacts with apparent enthusiasm. The other seals displayed considerable curiosity towards Kara, but were rarely able to approach her because of Selkie's protective behaviour (with the exception of the incident described in section (b) (i)).

During the first two months after weaning (January and February), Kara appeared to be shy of any social contact, even with her mother (Fig. 3). She approached other seals very seldom, followed them only at a distance, and if another seal approached her, she usually swam away or responded defensively by splashing or snorting. Her post-weaning period of virtual social isolation coincided with her post-weaning period of not accepting fish. Her renewed socializing, beginning in February, coincided with the onset of feeding on fish.

February 27 was the first day when Kara was observed to follow other seals persistently. From the end of February, her approaches gradually became more confident as she approached the other animals more closely and more often, and sometimes incorporated lateral body movements, splashing and fast swimming that appeared to be skittish.

The pup oriented to (i.e. approached or followed) the other seals increasingly often with the passing months (Fig. 3). Typically, she followed another seal, orienting towards its hind-flippers; sometimes Kara's nose actually touched the other's hind-flipper/tail region (Fig. 4). Nose-to-nose touching occurred frequently between mother and pup before weaning, but rarely between weaning and 3 months of age (March onwards). Nosing of other body regions occurred often between mother and pup during the nursing period, but so rarely after then that such nosing contacts are excluded from Fig. 3. Nosing occurred both underwater and above the surface. Hind-flipper nosing was especially common underwater; mutual nose touching occurred

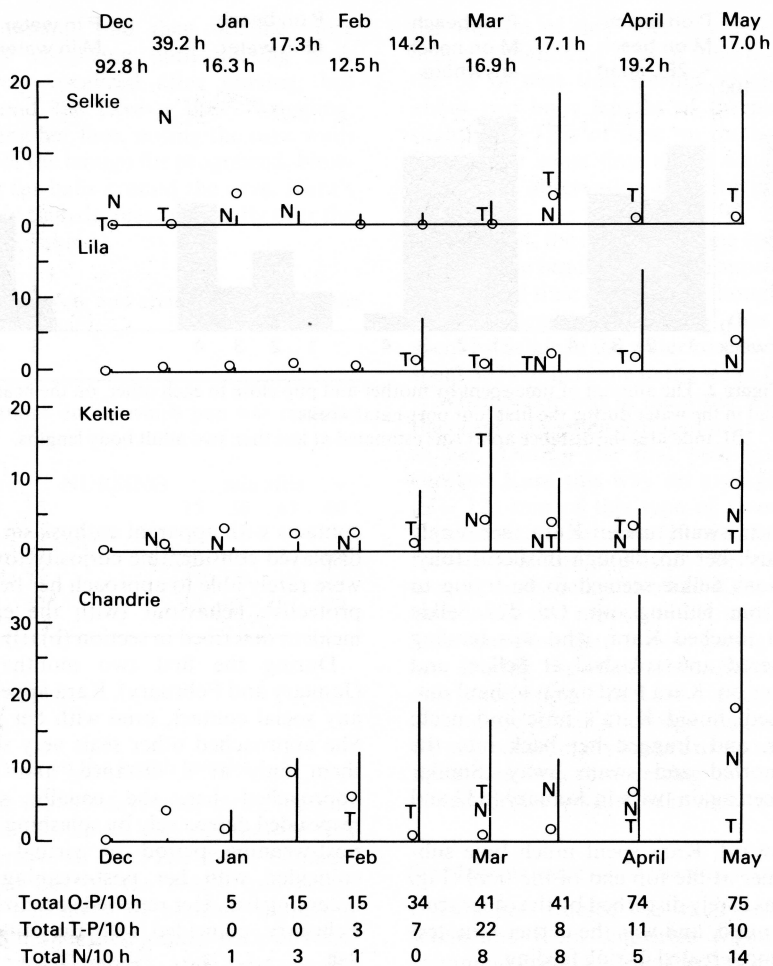


Figure 3. Social interaction between the pup (Kara) and each of the four other females.

Total observation hours are given for each half month for December to March, and for the whole months of April and May.

The vertical scale indicates the number of occurrences per 10h of Kara's approaching and touching of each of the other females. The vertical lines are the number of orientations (approach or follow) by Kara to the named individual;* the small circles are the number of orientations towards the pup by the named individual;* T is the number of hind-flipper nosings by the pup, and N is the number of nose touches. Total O-P is the total orientations by the pup to all individuals in each time period, and Total T-P is similarly the total hind-flipper nosing by the pup.

*Excluding those between mother and pup during the Nursing period

more commonly in the air, but also took place underwater.

Kara tended to focus on one other seal at a time, repeatedly following that individual for a few days. The others seals in the chronological order in which Kara focussed on them were: (1) Chandrie (peaking at the end of February); (2) Keltie (peaking at the beginning of March); (3) Selkie (peaking at the end

of March); and (4) Lila (peaking at the beginning of April). Kara approached all the seals rather frequently during April and May, but Chandrie was most often approached. Chandrie was also approached more consistently than the other seals during the earlier months (Fig. 3).

A 'social haul-out' was recorded on March 24, and again on March 29, for two hours on each



Figure 4. Illustrations of types of orientation by the pup (Kara) and juvenile (Chandrie) towards the other seals

Top 3 on left: Chandrie orientating to Selkie (note nosing of the back of the head by Chandrie); Kara watches them (3rd down).

Top 3 on right: Nose touching between pup and Chandrie; Chandrie approaches Kara and Kara blows bubbles (1st); mutual nose touch (2nd); Chandrie on shore, moulting, and Kara initiates nose touch from the water (3rd).

Bottom 3: Kara following and hind-flipper nosing; Kara noses hind-flipper region (underwater) of Keltie (upper) and Chandrie (lower); Kara follows Lila's hind-flippers as Lila swims slowly in circles underwater (bottom right).

All drawings from photographs.

occasion (3.00–5.00 pm). The seals repeatedly porpoised, oriented to one another, and jumped in and out of the water before finally hauling out in turn to rest. On March 24 there were 21 brief haul-outs (averaging 5 per individual), and 46 on March 29 (averaging 11 per individual). For these brief haul-outs, a seal sometimes came out of the water only partially, sometimes perched on the ledge with the hind-flippers dangling in the water, and sometimes turned round, dipping the nose in the water. On both days the seals made their final haul-out in the same order: first Chandrie, then Keltie, Selkie, and finally Lila. Selkie was the only one of the four who was not seen to follow and nose another's hind-flippers, but she actively participated in porpoising and repeated haul-out. On March 24, Kara occasionally watched the haul-out activity, but did not participate. On the 29th she once partially hauled out briefly, but otherwise did not join in this group behaviour.

(d) Social interaction profiles (Fig. 3)

(i) Selkie (mother) and pup

During the nursing period, social interaction between mother and pup consisted of touching noses and nosing one another on various parts of the body, mainly the neck, rump and hind-flipper/tail/anal region. Interaction involving such nosing was observed before nursing (19 different occasions), after nursing (20 occasions), and after a separation or disturbance caused by Zoo staff (18 occasions). Interaction also occurred at other times, notably when Kara was moving about restlessly, and when Selkie approached her after spending some time in the water.

Selkie also patted, stroked or scratched the pup with her fore-flipper (Plate 1) usually after nursing (36 occasions), sometimes before nursing (12 times) and occasionally unrelated to nursing (6 times), including once after a disturbance.

Eleven brief instances of 'play' were seen. Selkie and Kara would touch each other with a fore-flipper, lean their heads over each other in turn, push at each other's noses, and bite gently. Seven of these bouts occurred shortly after nursing, and three shortly before nursing.

Apart from the 'mutual' touches of nose-to-nose contact, Selkie nosed Kara (81 times) very much more than Kara nosed Selkie (15 times) while the pair was on the beach during the first three weeks. While they were in the water together on d19, however, Kara nosed her mother just as much as Selkie nosed her (16 times for Selkie nosing, and 20 times for Kara). On the beach, the pup's nosing contacts towards her mother included only four occasions of neck nosing, two of rump nosing, and four of hind-flipper nosing during the entire three-week period.

In the water on d19, however, during only a 90 min period the pup nosed her mother's neck 5 times, her rump 9 times and her hind-flipper region 5 times.

Social interaction between Selkie and Kara fell almost to zero during January (weeks 5–8). A close approach by Selkie often caused the pup to splash and swim rapidly away (seen 6 times). On three occasions of Selkie approaching, however, Kara responded by following her a little way.

During February (the pup's third month), there were only three recorded interactions between Selkie and Kara: there was one instance of brief following by Kara, and two instances of Kara stretching towards Selkie's hind-flippers without actual contact.

During the second half of March, there was a dramatic increase in the extent to which Kara oriented to Selkie, mainly by following her and sometimes actually nosing her hind-flippers (Fig. 3). This interest in Selkie continued through April and May, as manifest by approximately constant frequencies of orienting towards Selkie and nosing her hind-flippers (Fig. 3).

Immediately after Kara was weaned, Selkie was frequently followed by her two-year-old daughter, Chandrie, who would try to ride her back and nose the back of her head. Selkie tolerated this behaviour, and Kara appeared to ignore it through the end of December and all of January. From the end of February, however, Kara sometimes followed and watched them, e.g. on Feb 27th:

'Chandrie approaches Selkie and stretches up to her; Kara approaches Selkie and stretches up to her. Kara leaves with a "whoosh" and a splash. Chandrie approaches Kara; Kara dives with a small porpoising movement. Lila follows Chandrie underwater. Kara dives with a splash, swims fast, and surfaces under Selkie.'

A year later, L. Miller and S. Wilson noticed during visits to the seal enclosure that Kara stayed near Selkie and Chandrie for much of the time.

(ii) Chandrie and pup

Chandrie (2 yrs old) was the smallest and youngest of the females, and was Kara's full sister.

During the pup's fourth week of age, Chandrie would follow her, nose her hind-flippers, approach her face-to-face, and attempt to make nosing contact. Kara responded defensively to these approaches by snapping, splashing, snorting, or blowing bubbles in a defensive manner. She continued to respond defensively during the first half of January. Twice during this period, however, Chandrie swam closely past Kara, who then followed her at a distance. Kara also initiated follow-

ing at a distance on several occasions (Fig. 3). During the second half of January, Kara followed Chandrie more often, and first nosed her hind-flippers on Jan 17. She responded defensively to only 2 of 17 approaches by Chandrie. On Feb 16, Kara made her first prolonged nose-to-hind-flipper touch while following Chandrie underwater.

Chandrie began her moult in the second week of March, spending much time on the beach. Kara often approached her, stretched up to her, and attempted to touch noses (Fig. 4). Chandrie was generally tolerant of these approaches except on one occasion (March 15) when Kara hauled out and persisted in following her into a recess on the beach and trying to nose her. Chandrie reared up and lunged at Kara, who then jumped back into the pool, swimming fast with splashing.

During April and May, there were many approaches between Kara and Chandrie (Fig. 3). Neither seal tended to respond defensively, but neither did any interaction involving body contact develop out of their approaches. The following excerpt from our notes records the only instance of a 'play' approach between Kara and Chandrie that we observed (May 17):

'Kara approaches Chandrie with 2 splashes. Chandrie swims round her, and Kara splashes a lot at Chandrie. Kara blows bubbles and splashes. Chandrie stretches towards Kara. Kara continues to splash, opening and shutting mouth. Chandrie swims up pool, and Kara shoots after her . . .'

(iii) Keltie and pup

Keltie (5 yrs old) was little bigger than Chandrie; she was genetically unrelated to Kara or any of the other seals.

During the immediate post-weaning period in December, January, and the first half of February, Keltie occasionally approached Kara and tried to initiate nose touching (Fig. 3). Kara rarely approached Keltie, and responded to her approaches defensively, sometimes by snorting, bubble blowing, or splashing. Kara began to approach Keltie more often towards the end of February, and her approaches to Keltie peaked during the first half of March (while Chandrie was hauled-out, moulting). Kara repeatedly followed and nosed Keltie's hind-flippers during this period (Fig. 3; Fig. 4) in a persistent and occasionally playful manner, e.g. (March 5):

'Kara high dives behind Keltie, noses her hind-flippers. Both separate. Kara swims fast to Keltie, noses Keltie's hind-flippers under water, surfaces, rotates, swims fast away, splashes, dives backwards after Keltie's tail, noses her hind-flippers, and Keltie

leaves. Kara dives alone with large splash, swims fast and surfaces alone . . .'

Keltie did not begin her moult until the end of March. During April and May, Keltie and Kara continued to orient towards each other without defensive behaviour. Kara often manoeuvred sticks, stones, sandwich bags, etc., that found their way into the pool. Keltie occasionally approached Kara when she was thus occupied, and displayed interest in Kara's object.

(iv) Lila and pup

Lila (4 yrs old) was similar in size and body markings to Selkie; she was not genetically related to Kara or the other seals.

Lila was the first seal to moult, beginning in the second week of February (Selkie began her moult a few days later). There were virtually no interactions at all between Lila and Kara until the second half of February. Eight of the nine orientations by Kara to Lila noted in the second half of February (Fig. 3) occurred on Feb 27 (the pup's first day of persistent social approaches); Kara followed Lila closely on this day, but only nosed her hind-flippers once. After that date, Kara and Lila rarely interacted until the beginning of April, when Kara for a few days displayed intense interest in Lila. Whereas the other females usually continued swimming in a straight line when Kara followed them, Lila tended to swim slowly in circles with Kara following after her tail (Fig. 4). Kara rarely actually touched Lila's hind-flippers (Fig. 3). Lila seemed to be very tolerant of the pup's persistent following. Orientation between Kara and Lila continued into May, although less often than between Kara and any other seal (Fig. 3).

Conclusions

From our six-month observations of the pup, Kara, we conclude that she was social and contact-prone with respect to her mother until weaning. Immediately after weaning she became shy of any social contact. This period of contact-shyness coincided with her post-weaning period of fasting; she gradually emerged from her shyness over the next four months, but even then she engaged in almost no body contact or play behaviours.

We believe that the development of Kara's social behaviour, including her limited post-weaning sociality, should be discussed with the assumption that Kara and all the other study animals behaved in a normal way for their species within the obvious constraints of their captive condition (such as small pool size and lack of young males in the group). Our justification for this assumption is as follows:

Kara appeared to be healthy, and grew normally. Her nursing frequency was similar to that reported for wild grey seal pups (see Introduction), and her mean nursing duration of 5–10 min approximated that reported for wild pups by Fogden (1971).

Social interaction between mother and pup was also similar to that described for naturally occurring *H. grypus* by Wilson (1970) and Fogden (1971). Our pup's tendency to sleep on the beach for two weeks after weaning followed by her permanent entry into the water also tallies with field observations of grey seal pups outlined in the introduction. Her period of fasting after weaning is believed to be characteristic of grey seal weanlings in the wild.

Selkie's maternal care and protectiveness was typical of wild grey seals, although this study has focussed on some details of maternal care not easy to quantify in the wild. The mother's care-giving behaviour ceased quite abruptly, as in the wild: the only overt maternal behaviours to show a gradual waning towards the time of weaning were time spent on the beach with the pup (this decreased only slightly) and the frequency of checking the pup from the water by approaching or looking at it.

The persistent approaching of the mother and pup by the male (Gunnar), his repeated repulsion by Selkie, and their eventual attempt at mating were all normal behaviours, commonplace in the wild. Gunnar also consorted and mated with Lila using bubble blowing, body nosing and fore-flipper touching and holding techniques typical of the species.

The two social haul-outs recorded at the end of March are significant in our interpretation of our seal group as consisting of normally socializing individuals: 'social haul-out' is believed to be typical of a cohesive group of seals (Wilson, 1974: 1978).

Discussion

(a) social responsiveness between mother and pup

The pup only interacted closely with another individual during the nursing period, when she interacted with her mother. The touching and nosing between mother and pup undoubtedly enhances the short-term bond between them necessary for mutual recognition, filial responsiveness and maternal care (studied in harbour seals by Wilson & Kleiman 1974). For a wild grey seal pup, the sensory input received from its mother may be virtually the only social memory the pup has to carry through the ensuing months of individual wandering at sea.

We observed that pup wakefulness and bouts of mother-pup stroking, body nosing and play occurred mainly just before and just after nursing (Results (a) and (d iii)). Since we know that wild grey seal mothers in optimum pupping habitat (i.e. uncrowded and with easy access to the sea) prefer to

spend much of the interval between nursing bouts in the water, it makes sense for the pup to be awake and receptive to social interaction before and after feeding, while the mother is available. Selkie spent more time on the beach with the pup than might be expected in uncrowded, undisturbed habitat. She may have been protecting the pup from Gunnar's persistent approaches (wild males would have several mother-pup pairs to visit, thus relieving any one female from continual pressure); she may also have been guarding her from the keepers, who were often waiting for an opportunity to take her for a vet exam. It is interesting that Selkie and Kara adhered to the pattern of interacting just before and after nursing, even though Selkie was available on the beach for much of the time between nursing.

The increased nosing seen between mother and pup in the water on d19 may help to focus the pup's attention on its mother, thereby promoting its following response. It should also enhance the 'olfactory image' each has of the other, which should encourage searching behaviour (particularly by the mother) if they were to become separated at sea.

The social dynamics of the weaning period remain imperfectly understood. Our rather scanty observations (due to abnormally cold weather and the Christmas holiday) suggested that the greatest change in social responsiveness was in the pup rather than in the mother. The pup spent much of the week after weaning asleep either on the beach or in the water, and made no attempt to solicit nursing, to contact Selkie, or to follow her in the water. The day after the last nursing bout was seen (i.e. d21), she responded passively to three nose touches initiated by Selkie in the water, and thereafter she responded negatively. It seemed to us that the pup withdrew into herself, and that this withdrawal was probably determined internally, since the other seals did not attempt to intimidate her. One possible mechanism might relate to the link early in ontogeny between nursing and social interaction (discussed above): when nursing behaviour ceases, perhaps the 'trigger' for social responsiveness on the part of the pup disappears. Kara was not unresponsive to the physical environment during this period: our records indicate much sniffing round the edge of the pool, and manoeuvring of a frisbee and various stray objects in the pool.

(b) The post-weaning period

The choice made by Kara to sleep in the water after the first month of age may possibly correspond to a winter pelagic period in the wild, when weanlings may wander locally or far afield (Hewer, 1974). In fact, it is thought that grey seals of all ages may spend much of the winter at sea. During the end of

December and January, Kara slept for long periods during the daytime, and showed very little curiosity towards the other seals when she was awake. However, observations on more pups are certainly needed before we can be sure that this post-weaning asociality is typical of grey seal pups.

(c) Socialization from the post-weaning period onwards

Kara's post-weaning social responsiveness developed very gradually. The beginnings were discernible in January, with a few occasions of Kara following Chandrie a little way, but no physical contact. The coincidental timing of Kara's beginning to eat (after a five week fast) and marked increase in curiosity and boldness towards the two smallest seals, first Chandrie and then Keltie, hints again at a possible connection between feeding and social interaction, already noted in the context of nursing and weaning. Certainly in wild common or harbour seals of all ages there is a clear pattern of seals returning from feeding at the start of the ebb, and then interacting socially before finally hauling out to rest (Wilson, 1974b; 1978). There may also be a feeding-socializing link, perhaps less obvious, in grey seals. Our two recorded instances in the present study of a social haul-out both occurred just after feeding.

Kara's attention towards another seal was most often focussed on the other's hind-flipper region, which is the site of a large anal gland (Ortmann, 1967). Face-to-face encounters initiated by the other animals in the post-weaning period appeared stressful to Kara; she was three months old before she was again able to engage in nose-to-nose touching. Continual repetition of body nosing among juveniles, such as we witnessed between Kara and Chandrie, is common in species from diverse mammalian orders (Muller-Schwarze, 1971; Wilson, 1973; 1982; Wilson & Kleiman, 1974). Particularly interesting in this close-up study of a grey seal were the many instances of body nosing underwater, when the nostrils are closed. No doubt the seals benefit from the tactile and visual stimuli of underwater nosing, but it seems possible that olfactory stimuli were also perceived. Nosing of the hind-flippers (the site of the anal gland) was especially common underwater. It has sometimes been assumed that grey seals are not perceiving olfactory stimuli when the nostrils are closed (Fogden, 1971), but our seal keepers at the National Zoo have noticed the male grey seal, Gunnar, 'tongue-flicking' quite often while nosing their hands with closed nostrils (L. Moore, personal communication). It seems possible that seals may use a vomero-nasal organ when nosing with closed nostrils.

Although Kara seemed to have, by the end of the

study period, quite overcome her post-weaning shyness of the other seals, and engaged in many amicable nosing contacts with them, no more intimate contact (such as occurs in grey seal juvenile play; Wilson, 1974b) was ever seen to occur. Possible reasons for this may have been (i) there was no other pup or juvenile male in the group (see Introduction), (ii) Kara was still too young at six months of age (see Introduction), or (iii) Kara was more 'self-contained' than Selkie's other pups have been (K. Cover, personal communication). All three of these factors may have contributed to the lack of play, but we suspect that the lack of another pup or juvenile male may ultimately be the major factor in limiting Kara's socialization.

There appeared to be no continuity in the mother-pup relationship between weaning and late March, when Kara began once more to approach Selkie. From March, Kara approached and followed Selkie in the same way that she approached and followed the other three females: there were no behaviours indicative of any lingering mother-pup bond, or recognition by the pup of Selkie as her mother. However, Kara did orient towards her mother and her sister, Chandrie, slightly more often overall than towards the two unrelated females, and after the end of the official study, she was often seen maintaining a position in the water near Selkie and Chandrie. Chandrie quite clearly stayed closer to Selkie than to any other seal. These observations generate a hypothesis for future study, that there might be an affinity between related females based not on a lingering mother-infant relationship, as in some mammal species (Horwich *et al*, 1970), but on kinship recognized, probably by smell, during nosing contacts.

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