Grey seal maternal attendance patterns are affected by water availability on North Rona, Scotland.

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Abstract

Previous studies on grey seals (*Halichoerus grypus*) have shown that pools of water influence female distribution within inland breeding colonies. This study reveals that the availability of pools also affects maternal attendance patterns and may have implications for breeding success. An atypical dry period at the start of the 1998 breeding season on North Rona, Scotland, followed by a normal wet period, provided a natural experiment that allowed us to examine female behaviour in relation to the availability of pools. During the dry period, lactating grey seals (1) travelled long distances to gain access to water; (2) had significantly greater rates of locomotion towards water and as a result of interactions between conspecifics; (3) spent significantly less time close to their pups. Long distance locomotion and reduced time with the pup often lead to permanent mother/pup separation, resulting in starvation of the pup. However, the immediate need to gain access to water outweighed the potential costs of reproductive failure, emphasising the importance of water for lactating grey seals even during the relatively cold and damp UK breeding season.

Introduction

The grey seal (*Halichoerus grypus*) breeds in a variety of habitats: on land-fast and floe ice, in caves, along sandy beaches or rocky shores, and at grassy inland sites (see Hewer 1960; Bonner 1981). These differing environments influence broad scale aspects of their breeding biology such as female distribution, social systems and the amount of time females spend at sea (Stirling 1975; Anderson and Harwood 1985; Caudron 1997). Around the UK, grey seals use two of these habitats predominantly; open beaches (e.g. the Monach Islands) and inland sites (e.g. North Rona). At open-beach colonies, access to the sea is unrestricted and females may spend more than 50% of their time resting at sea within sight of the beach, reducing the time available for direct mother-pup contact (Fogden 1971; Hewer 1974; Anderson and Harwood 1985; Kovacs 1987). It has been suggested that mothers that exhibit this behaviour decrease their risk of predation, mainly from humans, as well as reducing aggressive encounters between conspecifics (Fogden 1971). At island colonies, where grey seals breed far inland and access to the sea is very restricted, mothers tend to remain with their pups throughout lactation and instead cluster around pools of water (Boyd *et al*. 1962; Anderson *et al.* 1975; Twiss *et al.* 2000). While these different maternal attendance patterns indicate that access to fresh or salt water is important, the explanations offered by Fogden (1971) for such behaviour are not convincing. The use of isolated islands as breeding colonies affords grey seals protection from terrestrial predators, but clustering around small pools (often only large enough to accommodate a single seal) is not an effective way to reduce predation risk. Furthermore, clustering around pools increases local density, which is likely to increase the number of aggressive encounters between conspecifics rather than decrease them. Therefore the reason for the importance of water to lactating grey seals remains unclear.

Factors that influence maternal attendance patterns in different environments include energy conservation, thermoregulation and water balance. Beach breeding seals have continual access to a nearby source of water, reached by moving over low elevation land, with a low cost of locomotion. At inland sites, the high cost of travelling to the sea, resulting from locomotion over difficult terrain, interactions with conspecifics and the risk of permanent mother/pup separation, explains why mothers remain with their offspring throughout lactation (Twiss *et al.* 2000). Mothers using inland sites normally only use areas that contain pools and have a tendency to use the same areas for pupping year after year (Pomeroy *et al.* 1994). However, when water availability is limited, mothers must choose between attendance patterns that favour either direct contact with their pup or access to water, even if this incurs a comparatively long journey. Manipulations of seal breeding habitat are difficult to carry out, but this study took advantage of an atypical weather pattern to conduct a natural experiment. An unusually dry start to the 1998 breeding season on North Rona, Scotland which was followed by a more typical wet period, allowed us to investigate changes in maternal behaviour in response to water availability on the breeding colony. We compared rates of locomotion, time spent with pup and number of suckling bouts for lactating grey seals during consecutive periods where access to freshwater pools was at first restricted and later unrestricted.

Materials and methods

Study Colony

North Rona (59°06′N, 05°50′W) is situated approximately 75km NNW of Cape Wrath, Scotland. The island covers an area of 120 hectares, rising to a height of 108m above sea level, although the majority of seals breed on the relatively low-lying northern peninsula of Fianuis (Boyd *et al.* 1962). The main area used in this study lies within the southern part of Fianuis, covering an area of approximately 0.38km^2 (Twiss *et al*. 1994). Access to this area is by way of a few narrow gullies on the east side of the island. These gullies allow restricted access from the sea, but then lead to an open grassy slope where animals are relatively free to move around.

Behavioural Observations

Seals were observed between September 29th 1998 and October 25th 1998, encompassing the period of peak pupping which occurs around 8th October each year (Hiby *et al*. 1996). Focal observations were made (simultaneously on each day) on two groups within the main study area on the Fianuis peninsula. Each group was defined according to locality using permanent landmarks that encompassed an area approximately 20m x 20m. During the study, group size varied from three to 12 females and their pups. The study groups were observed from a hide at a distance of approximately 150 metres and an elevation of approximately 40 metres. Continuous observations were made during daylight hours, with a maximum observation period of nine hours per day. Two observers carried out observations on 16 days, spanning a period of 26 days (a total of 172 hours), with observers alternating between groups each day. The behaviour of the animals was observed using binoculars and recorded on data sheets. Individual females were identified from pelage markings and scars that were recorded on prepared outline sheets to aid daily identification.

There were two distinct distance categories for locomotion – long-distance and short-distance. ‘Long-distance’ locomotion consisted of movement over a distance greater than ten adult body lengths (approximately 20m). This type of locomotion generally involved movement of the mother between the pup and the sea or a pool outside of the study area (females were observed returning from these excursions with wet pelage). ‘Short-distance’ locomotion was typically less than two adult body lengths, although movements up to five adult body lengths were recorded. In the majority of cases, a cause was identified for these movements. Therefore short-distance locomotion was classified further - as movement made in relation to local pools, or as movement related to interactions between conspecifics. An indication of maternal attendance was given by the number of suckling bouts observed per female each day, and the percentage of time each female spent in close proximity (within two adult body lengths) to her pup.

Natural Experiment

In 1998, an atypical weather pattern was experienced during the breeding season on North Rona. The early autumn and first few weeks of the breeding season were unusually dry, with the result that pools were extremely scarce and small throughout the breeding colony. About halfway through our study period, the weather returned to normal wet conditions and pools were abundant throughout the colony (Table 1). Meteorological data was obtained, with permission from the British Atmospheric Data Centre, from a fixed weather station, positioned approximately 50 metres above and 180 metres SW of the study area on North Rona. This weather station provided information on temperature, wind speed, wind direction and mean sea level pressure, but did not provide rainfall data. Records of relative precipitation strength and frequency were collected from daily field observations. The frequency and extent of locomotion made by individually identifiable females was examined in relation to the contrasting conditions which occurred during the 1998 breeding season on North Rona. We tested the hypotheses that females would travel further to water when pools were scarce and that females travelling long distances would spend less time with their pups (Twiss *et al.* 2000). The effects of the observed attendance patterns are reported.

Data analysis

For each observation day, females were included in the data set if they conformed to the following criteria:

1) The female was individually identifiable, so that if she travelled to the sea she could be recognised on her return. Very few females were excluded by this criterion alone.
2) The female was observable for the duration of the observation period. Mothers that travelled to the sea were also included in the data set if their pup remained within the study group location, as this allowed us to obtain information about the length of time each female left her pup unattended.
3) The female had a live pup. Females that remained in the study group after their pup had died were excluded from the data set as they were not subject to the same constraints as lactating females.
4) Females with pups born during an observation period were omitted from that day's data set as they frequently spent a prolonged period of time in behaviours associated with birth.

Calculation of Locomotion Rate and Suckling Rate

To compensate for differences in observation effort per day, the rate of locomotion for each female was standardised as a rate per hour. For each female fulfilling the four criteria above, the rate of locomotion per hour (L) was calculated using the equation

$$L = (n/t)*60$$

Where n = number of movements observed, and t = length of observation period in minutes.

L was calculated separately for four categories of locomotion:

1) long distance (>10 adult body lengths)
2) short distance to local pools
3) short distance in relation to interactions between conspecifics
4) total locomotion in relation to water (1 and 2 combined).

The number of suckling bouts observed for each female was also calculated as a rate per hour and the amount of time spent in close proximity to the pup was calculated as a percentage of the observation period.

Tests of Observer and Location Difference

As our main aim involved looking at the difference in locomotion between the dry and wet periods, the data was first divided into two groups (see also table 1):

1) observations during the dry period (30th September to 7th October, n = 6 observation days)
2) observations during the wet period (10th October to 25th October, n = 10 observation days).

These two groups were tested separately for observer and location difference. Data were not normally distributed and were therefore analysed using non-parametric tests. The statistics package Minitab for windows (version 10.5) was used for all analysis, except for Wilcoxon signed-ranks tests, which were performed according to Sokal and Rohlf (1995).

A series of Mann-Whitney U tests were used to test the standardised data sets collected by each observer. There were no significant differences between the two observers for any category of locomotion, for the number of suckling bouts per hour or for the percentage time spent near to the pup. Therefore the results from the two observers were pooled.

Differences between the two study locations were also tested using Mann-Whitney U tests. There were no significant differences within any category during the wet period.

However, during the dry period, the rate of movement (per hour) to local pools was different at the two study group locations (Mann-Whitney U test: U=87, N_1=12, N_2=6, P=0.008). This can be explained by differences in the availability of local pools in each study group location. In area 1, two small pools were present throughout the dry period and each female was within 10 adult body lengths of one of these pools. In area 2, there were no pools within the study group location. However, a few females at the eastern edge of this area could travel to pools that were within 10 adult body lengths. Movement to pools by the rest of females in area 2 involved travelling a greater distance and was classified as long distance locomotion. All other categories of locomotion were similar in the two study locations during the dry period. Data were not pooled for data sets pertaining to the rate of locomotion to local pools, although data were pooled for all other categories of locomotion. Suckling bout rate (per hour) and the percentage time spent with the pup were not significantly affected by study location, and these data sets were also pooled.

Pseudoreplication

The manner in which observations were conducted resulted in many females being observed over a number of consecutive observation days. To avoid the problem of pseudoreplication and obtain independence, the average rate (per hour) for each behavioural category (four categories for locomotion, one for suckling behaviour and one for time spent in close proximity to pup) was calculated for each female over the period in which she was observed. Before this was done, a series of Friedman tests for randomised blocks were performed for each category using a sub-sample of females that were present over a period of several days. The tests indicated that individual day within the dry period or the wet period did not significantly affect behaviour.

The process described above, resulted in a data set with n = 19 females during the dry period and n = 34 females during the wet period. Of these, eight females were present in both the dry and wet periods. The behavioural categories for these eight females were analysed separately using Wilcoxon signed-ranks tests to compare paired data (dry period v wet period for each female). The remaining data, which consisted of independent data points (n = 11 females during the dry period and n = 26 females in the wet period), were analysed using Mann Whitney U tests (dry period v wet period).

Results

All median rates, percentages and interquartile ranges are presented in table 2 (for females that were present in either the dry period or the wet period) and table 3 (for females that were present in both periods).

Affect of Pup Age on Behaviour

Due to the temporal scale on which behaviour was observed, an increase in pup age between the dry and wet periods may have influenced behaviour rather than the absence or presence of pools. During the dry period at the start of the breeding season, all pups were classified as stage ‘I’ or ‘II’, whereas during the wet period, pups were classified as stages ‘I’ through to ‘V’ (based on the descriptive age classes of Boyd and Campbell 1971). As data were not normally distributed, a general linear model could not be used to determine whether pup age had a greater effect on behaviour than the availability of water. Therefore female behaviour according to pup age, was compared for each of the dry and wet periods using a series of Kruskal-Wallis tests. Pup age was not found to significantly affect locomotory behaviour of any kind, or the time spent in close proximity to the pup. However, older pups had a greater median number of suckling bouts than younger pups during the wet period (Kruskal-Wallis test: H_4=19.86, P=0.001).

Long Distance Locomotion

Females made more long-distance movements per hour during the dry period than during the wet period (Mann-Whitney U test: U=320, N_1=11, N_2=26, P<0.001). There were insufficient data to perform the Wilcoxon signed-ranks test for females that were present during both the dry and wet periods because four females did not make any long distance movements during either period. The remaining females all made long-distance movements during the dry period but not during the wet period.

In total, 13 out of 19 mothers made at least one long-distance movement during the dry period, with six mothers travelling in excess of 200m to the sea on one or more of their trips. During the wet period, three out of 36 mothers made long-distance movements. Only one of these females did so on a regular basis, travelling to a pool within one of the study group locations from an outlying area that had no pool until late in the wet period. No mothers travelled between their pup and the sea when pools were abundant.

Short-distance locomotion to local pools

Location influenced the median rate of locomotion towards local pools, therefore the two study groups could not be pooled. In area 1 (where all females were within 10 adult body lengths of a pool during the dry period) the median rate of locomotion to pools was significantly lower in the wet period than in the dry period (Mann-Whitney U test: U=25, N_1=2, N_2=11, P=0.035,). N_1 is very small as most of the females present here during the dry period were included in the subset of females present during both the dry and wet periods. In area 2 (where a few females were within 10 adult body lengths of a pool during the dry period) there was no significant difference between the median rates of locomotion to local pools during the dry and wet periods (Mann-Whitney U test: U=82.5, N_1=9, N_2=14, NS). It is likely that the result obtained in area 2 was confounded by the fact that, during the dry period, most females in this group had to travel more than 10 adult body lengths (classified as long-distance locomotion) to their closest pool. There were insufficient data to perform Wilcoxon signed-ranks tests for females that were present during both the dry and wet periods after the two study groups had been separated.

Short-distance locomotion due to interactions between conspecifics

The median rate of locomotion due to interactions between conspecifics was significantly greater during the dry period than during the wet period (Mann-Whitney U test: U=283, N_1=11, N_2=26, P=0.012). This was also the case with females that were observed in both the dry and wet periods (Wilcoxon signed-ranks test: T=2, N=8, P=0.025).

Total Locomotion to Water

The median rate of locomotion to water (long distance and to local pools combined) was significantly greater during the dry period than during the wet period (Mann-Whitney U test: U=293, N_1=11, N_2=26, P=0.005). Females that were present during both the dry and the wet period also showed a significantly greater median rate of locomotion to water during the dry period (Wilcoxon signed-ranks test: T=3, N=8, P=0.025).

Time Spent with Pup

Females spent significantly more time in close proximity to their pups (within two adult body lengths) during the wet period than during the dry period (Mann-Whitney U test: U=108.5, N_1=11, N_2=25, P<0.001). When pools were scarce, females spent a median of 40%

of their time in close proximity to their pups. This increased to a median of 100% of their time when pools were abundant. Females that were present during both the dry and wet periods also spent significantly more time close to their pups during the wet period than during the dry period (Wilcoxon signed-ranks test: T=0, N=7, p=0.01; medians = 81% and 97% for dry and wet periods respectively).

Suckling Rate

The median number of suckling bouts per hour was the same during the dry and wet period (Mann-Whitney U test: U=194.5, N_1=11, N_2=24, NS). Females that were present during both periods also showed no significant difference in the median number of suckling bouts per hour (Wilcoxon signed-ranks test: T=13, N=8, NS).

Discussion

The availability of pools of water has been suggested as an important factor in determining the distribution of females within grey seal breeding colonies (Boyd *et al*. 1962; Anderson *et al*. 1975; Pomeroy *et al*. 2000; Twiss *et al*. 2000). Here, evidence is provided for a direct link between the spatial and temporal availability of pools and daily maternal behaviour patterns. Female grey seals on North Rona moved more frequently, travelled greater distances and left their pups unattended for longer periods of time when pools were scarce.

Long-distance locomotion and short duration pup attendance are potentially costly for female grey seals at inland sites, as such behaviour may affect their chances of raising a pup to weaning successfully. Both behaviours increase the risk of permanent mother/pup separation, which results in starvation of the pup (Anderson *et al*. 1979; Baker and Baker 1988; Pomeroy *et al*. 1994). Furthermore, unprotected pups are prone to attacks from adult conspecifics. Bites and trauma can result in fatalities, but, depending on the environment in which they are raised, pups are probably at greater risk of dying from infection of the wounds (Anderson *et al*. 1979; Baker and Baker 1988). Infection and starvation are the major causes of pup mortality on North Rona (Baker 1984; Baker and Baker 1988) and at least one of the pups in this study died after its mother travelled to the sea, because the two failed to reunite on her return. At this colony, greater black-backed gulls (*Larus marinus*) attack young pups, particularly when mothers fail to protect them, and the injuries that gulls inflict can result in pup mortality (Seddon, Garner and Pomeroy unpublished data). Long-distance locomotion also affects the female directly, as movement through the colony leads to increased harassment from males and a greater number of aggressive interactions with conspecifics (Caudron 1998; Twiss *et al*. 2000). The energy used for locomotion and during interactions is effectively ‘lost’, and this may have repercussions on the weaning weight of the pup or the extent to which a female depletes her body reserves. Whereas the former may affect the pup’s chances of survival, the latter may dictate whether or not the female has a pup the following year. Therefore, the distances that these females travelled in order to obtain access to water, and the potential costs of their behaviour suggest that water is of critical importance during lactation.

There are two major reasons why water may be important for lactating grey seals – firstly, to maintain a positive water balance and secondly, as an aid to thermoregulation. Grey seals must conserve water during the breeding season as they spend around 20 days ashore during lactation without eating. Fasting phocids are believed to obtain all their water requirements from the metabolism of fat reserves (Irving *et al*. 1935; Ridgway 1972 and references therein; Ortiz *et al*. 1978), at the same time utilising physiological adaptations to help conserve water (Huntley *et al*. 1984; Folkow and Blix 1987; Baker 1990; Reilly 1991; Skog and Folkow 1994). Evidence from a study on grey seals breeding on Sable Island, Canada, suggests that fat metabolism provides enough water to meet the added demands of milk production (Schweigert 1993). However, Reilly *et al.* (1996) showed that female grey seals on North Rona undergo a negative water balance whilst feeding pups. Furthermore, lactating females have been observed drinking from fresh water pools at this colony (personal observations, this study; Reilly *et al*. 1996). The mean daily temperature at Sable Island during the January breeding season is around 7°C colder than the mean daily temperature during the autumnal breeding season on North Rona[1]. This is a conservative comparison as wind chill and the longer nights at Sable Island probably produce a much harsher temperature regime than in the UK. It is likely that this temperature difference between the breeding seasons at the two colonies is sufficient to affect the water requirements of lactating seals.

In addition to their physiological adaptations, pinnipeds can alter their behaviour to help conserve water and aid thermoregulation. For example, phocids often spend large periods of time inactive, apparently asleep; this may be as much as 80% of the time in female grey seals (Anderson and Harwood 1985; Twiss *et al*. 2000). During sleep, apneustic breathing can reduce oxygen consumption (and hence heat output) by as much as 50% (Worthy 1987; Boily and Lavigne 1996). In addition, grey seals often spend long periods of time immersed in pools (personal observations, this study, but see Hewer 1960; Twiss *et al*. 2000 for examples at other sites). Pinnipeds in warmer climates also regularly use the sea or pools for behavioural thermoregulation (e.g. Gentry 1973; Campagna and Le Boeuf 1988) and even fur seals move into water if the ambient temperature gets too warm (Bartholemew and Wilkie 1956; McCann 1980). During this study, mothers also made trips to the sea when pools were scarce, which is unusual as females on North Rona normally move an average of only 10 metres around their pupping site (Pomeroy and Aust unpublished data). It is not known whether mothers drank

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[1] Sable Island data obtained from http://www.wunderground.com/global/stations/71600.html; North Rona data obtained from the British Atmospheric Data Centre (http://www.badc.rl.ac.uk/)

seawater on these trips, although it is physiologically possible for phocids to restore their water balance by mariposia (Reilly 1991). However, the thermoregulatory function served by lying in the sea or in pools probably alleviates some of the need for extra water.

Although the thermoneutral zone of adult grey seals has not been measured, for grey seal pups it extends from around -7°C to 23°C (Hansen and Lavigne 1997). The upper critical temperature would appear to be substantially higher than the mean daily temperatures experienced by the animals on North Rona during our study. However, these laboratory measurements do not take into account the affects of solar radiation, which can have a major impact on thermal balance (Watts 1992). In addition, the heat output of lactating grey seals has been calculated to be about 2.3 times BMR (Reilly *et al.*, 1996). Therefore, the unique combination of heat output due to lactation, an unusually warm and sunny start to the breeding season and limited availability of water once ashore may have brought the females in this study close to their upper thermal limit and produced the stimulus to seek out water.

The fact that lactating grey seals require access to water gives rise to a situation where the habitat contains a defendable resource. Higher rates of movement in relation to conspecifics during the dry period may arise due to competition for pools, whilst variation between animals is likely to reflect their ability to monopolise such resources. Although the number of suckling bouts observed for each female was not significantly affected by pool availability, time spent with the pup and long-distance locomotion were highly variable. These results demonstrate that all females fulfilled the essential demands of nursing their pup, but those with restricted access to water spent less time in other mother/pup interactions. Although differences in pup attendance due to the availability of pools may not necessarily lead to detectable differences in pup growth rates, they may be reflected by less predictable chance events which lead to mother/pup separation, pup injury and even death. Evidence for this comes from comparative pup mortality studies. Although total pup mortality levels recorded at open beach and inland breeding sites were similar, a greater proportion of pups died as a result of starvation on the beach sites (Baker 1984; Baker and Baker 1988).

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Table 1. Precipitation strength, frequency and mean air temperature for observation days at North Rona during the 1998 breeding season

Observation day	Precipitation strength[1]	Precipitation frequency[1]	Mean Temperature[2] (°C)	Abundance of pools[1]
30th September 1998	Light	Occasional	11.9	Area 1 = Scarce Area 2 = None
1st October 1998	Dry	None	11.7	Area 1 = Scarce Area 2 = None
2nd October 1998	Dry	None	11.6	Area 1 = Scarce Area 2 = None
4th October 1998	Light	Occasional	10.1	Area 1 = Scarce Area 2 = None
6th October 1998	Dry	None	10.9	Area 1 = Scarce Area 2 = None
7th October 1998	Dry	None	10.5	Area 1 = Scarce Area 2 = None
10th October 1998	Moderate	Occasional	8.7	Water present in most hollows
11th October 1998	Heavy	Frequent	8.7	Water present in most hollows
13th October 1998	Moderate	Constant	10.1	All hollows filled – pools abundant

15th October 1998	Light	Occasional	7.2	Abundant
17th October 1998	Moderate	Occasional	5.2	Abundant
19th October 1998	Moderate	Occasional	5.0	Abundant
21st October 1998	Moderate	Frequent	11.5	Abundant
22nd October 1998	Heavy	Frequent	10.6	Abundant
24th October 1998	Moderate	Constant	8.3	Abundant
25th October 1998	Moderate	Occasional	5.6	Abundant

[1] Precipitation frequency, precipitation strength and pool abundance obtained from field observations.

[2] Mean temperature calculated as the average of hourly values over 24 hours. Data obtained, with permission from the British Atmospheric Data Centre, from a weather station on North Rona.

Table 2. Summary and comparison of frequencies of locomotion (rate per hour), suckling bouts (rate per hour) and time spent with pup for lactating female grey seals during dry and wet periods[1]

	Dry		Wet		Difference between dry and wet periods[2]
	median	Q1-Q3	median	Q1-Q3	
Long-distance locomotion (rate per hour)					
	0.20 (n = 11)	0.13-0.27	0.0 (n = 26)	0-0	P<0.001
Short-distance locomotion (rate per hour)					
To local pools (area 1)	0.33 (n = 2)		0.06 (n = 11)	0-0.13	P=0.035
To local pools (area 2)	0.0 (n = 9)	0-0.07	0.11 (n = 14)	0-0.14	NS
Interactions with conspecifics	0.21 (n = 11)	0.07-0.27	0.04 (n = 26)	0-0.13	P=0.012

Total locomotion to water (rate per hour)					
Long distance and to local pools combined	0.27 (n = 11)	0.14-0.44	0.11 (n = 26)	0-0.14	P=0.005
Pup Attendance					
Number of suckling bouts per hour	0.14 (n = 11)	0-0.24	0.13 (n = 24)	0-0.33	NS
Time spent with pup (%)	40% (n = 11)	26-82	100% (n = 25)	97-100	P<0.001

[1] Each female was observed in either the dry period or the wet period, not both. Rates were calculated for each female over the total time period in which she was observed. Note: area 1 had two pools in the area throughout the dry period whilst area 2 only had pools near its eastern edge during the dry period. N = number of females. ‘Area’ had no significant effect on locomotion rates (other than to local pool), number of suckling bouts per hour or time spent with pup, so areas were pooled for all other comparisons between the dry and wet periods.

[2] Differences tested by Mann-Whitney U.

Table 3. Summary and comparison of frequencies of locomotion (rate per hour), suckling bouts (rate per hour) and time spent with pup for lactating female grey seals observed during both dry and wet periods[1]

	Dry		Wet		Difference between dry and wet periods[2]
	median	Q1-Q3	median	Q1-Q3	
Long-distance locomotion (rate per hour)					
	0.07 (n = 8)	0-0.19	0.0 (n = 8)	0-0	Insufficient data due to ties
Short-distance locomotion (rate per hour)					
To local pools (area 1)	0.08 (n = 5)	0.05-0.20	0.0 (n = 5)	0-0.04	Insufficient data due to low ‘n’
To local pools (area 2)	0.0 (n = 3)	0-0.20	0.04 (n = 3)	0-0.08	Insufficient data due to low ‘n’
Interactions with conspecifics	0.21 (n = 8)	0.10-0.25	0.06 (n = 8)	0.03-0.11	P=0.025
Total locomotion to water (rate per hour)					

Long distance and to local pools combined	0.24 (n = 8)	0.06-0.33	0.03 (n = 8)	0-0.07	P=0.025
Pup Attendance					
Number of suckling bouts per hour	0.20 (n = 8)	0.14-0.38	0.24 (n = 8)	0.17-0.42	NS
Time spent with pup (%)	81 (n = 8)	66-92	97 (n = 8)	93-100	P<0.01

[1] Each female was observed in both periods. Rates were calculated for each female over the total time period in which she was observed. Note: area 1 had two pools in the area throughout the dry period whilst area 2 only had pools near its eastern edge during the dry period. N = number of females. ‘Area’ had no significant effect on locomotion rates (other than to local pool), number of suckling bouts per hour or time spent with pup, so areas were pooled for all other comparisons between the dry and wet periods.

[2] Differences tested using Wilcoxon signed-ranks test.