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Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance?

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Abstract We investigated the possibility that male harassment of lactating females differed in relation to time of birth in the grey seal, *Halichoerus grypus*, on Sable Island, Nova Scotia. This was done by comparing the frequency of male disturbances, maternal performance and pup growth for females that either gave birth during the peak of the pupping season or after the peak. Of the females, 58% gave birth in a 7-day period near the beginning of the pupping period, when the operational sex ratio was 2–4 females per male. Late in the pupping period the operational sex ratio reversed to about 1 female for every 2 males. The relative frequency of disturbances by males was significantly greater for late-pupping mothers than for peak-pupping ones (1.9 vs. 1.4 encounters/h). Females that gave birth late also were disturbed by males 3 times more often than females that gave birth during the peak (3.4 vs. 1.1% of observation time). Late-pupping mothers spent 22% less time suckling (4.0 vs. 5.1% of observation time), had 30% slower growing pups (1.7 vs. 2.4 kg/d), and weaned pups that were 16% lighter (45.6 vs. 54.0 kg). The effect of birth time on pup mass gain and weaning mass was not attributable to factors such as maternal mass, pup birth mass or pup sex. We conclude that the reduced maternal performance is likely the result of the increased male harassment. As

reduced weaning mass can lead to reduced juvenile survival, male harassment may have contributed to the enhanced reproductive synchrony in this species.

Key words *Halichoerus grypus* · Male disturbance · Late pupping · Pup growth · Reproductive synchrony

Introduction

Many animals and plants that live in seasonally varying environments synchronize their reproduction (Ims 1990a). The primary factor suggested to explain birthing synchrony is food availability and suitable weather to enhance offspring survival (e.g., Darling 1938; Sadleir 1969; Sekulic 1978). However, synchrony is often much greater than would be expected from environmental seasonality alone (Emlen and Demong 1975; Rutberg 1987; Ims 1990a). Several factors have been suggested as contributing to enhanced synchrony in various birds and mammals, including: predation (Darling 1938; Yom-Tov 1975; Kruuk 1964; Patterson 1965; Bergerud 1974; Estes and Estes 1979; Rutberg 1987; Ims 1990b; Harcourt 1992), cooperative feeding on unpredictable food (Emlen and Demong 1975; Bertram 1975), communal care of offspring (Rood 1980; Boyce and Boyce 1988), and improved mate choice (Emlen and Oring 1977; Knowlton 1979).

Pinnipeds (seals, sea lions, and walrus) breed seasonally, most returning from dispersed foraging locations at sea to give birth and subsequently mate in colonies at traditional sites. Retention of the ancestral pattern of producing young on land (or ice), along with the temporal linkage between pupping and mating, has undoubtedly played a major role in the evolution of synchrony in birthing and mating. An embryonic diapause, in which implantation of the blastocyst is delayed until triggered by stimuli that are not entirely clear, but include environmental factors, facilitates

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birthing synchrony (Daniel 1981; Sandell 1990; Boyd 1991). However, there is considerable variation in the degree of birth synchrony among species, ranging from periods of pupping of about 10 to about 180 days (see Table 2 in Oftedal et al. 1987).

This variation may reflect differences in the selective forces which have contributed to the evolution of synchrony among species. For example, species breeding on pack ice may have a shortened pupping period to take advantage of breeding at a time when the ice is beginning to break up. Thus, in the hooded seal (*Cystophora cristata*) pupping occurs over about 2 weeks and lactation is extremely abbreviated at only 4 days long (Bowen et al. 1985, 1987b). The seasonal formation of ice around the rookery, limiting access to the rookery and food resources at sea, has likely contributed to the high level of reproductive synchrony in the polar northern fur seal, *Callorhinus ursinus*, and Antarctic fur seal, *Arctocephalus gazella* (Duck 1990; Trites 1992). Predation, a factor often cited as contributing to synchrony in reproduction, may have been a factor in the synchrony of the South American fur seal, *Arctocephalus australis* (Harcourt 1992; Majluf 1992). In moderately to highly polygynous species (see Le Boeuf 1991; Boness 1991), where sexual selection may have led to higher levels of spatial clustering among females (McLaren 1967; Bartholomew 1970), sexual and natural selection may also have sharpened breeding synchrony (Miller 1975).

The grey seal (*Halichoerus grypus*), a moderately polygynous species, forms colonies that are highly variable in size and density. At most sites females develop poorly defined clusters, exhibiting little activity other than nursing and protecting their pups, and mating near the end of lactation (Boness et al. 1982; Anderson and Harwood 1985). Males either compete directly to establish and maintain positions among the clusters of females, or roam throughout the colony, attempting to seize an opportunity to mate (Anderson et al. 1975; Boness and James 1979). At other colonies there is little evidence of direct competition among males. Instead, one or two males patrol off the beach where females are located with their pups (Davies 1949).

Coulson (1981) described variation in birth synchrony among grey seals, with standard deviations about the mean date of birth ranging from 6 days at Sable Island, Nova Scotia to 14 days at Ramsey Island, Wales. The distribution of births at most rookeries consists of a rapid increase in births to a peak followed by a gradual decline with an extended tail, although at Ramsey Island (Davies 1949), births are more uniformly distributed over the pupping period.

During a study of lactation in this species on Sable Island, we noted that females which gave birth late in the reproductive period appeared to be "harassed" by males more frequently and apparently departed the rookery earlier than those which gave birth during the

peak. The main forms of disturbance to females involved aggressive interactions resulting from approaches by males, attempts to mount females before they become receptive, and fighting among conspecific males. Based on this we hypothesized that maternal performance would be poorer for females which gave birth late in the season than for those which gave birth during the peak. We further expected that maternal performance would correlate negatively with levels of male harassment as described above. Our findings are discussed in terms of male harassment as a potential selective force for enhanced birth synchrony in this population.

Methods

In 1991 we constructed an observation blind overlooking a grey seal rookery at an area known as No. 4 on Sable Island, Nova Scotia (43°55'N; 60°00'W). This rookery is separated from adjacent breeding areas by tall dunes.

Upon our arrival at the study site on 5 January, 18 pups were present. From evidence of blood on females and pups, and from fresh placentas, 7 of these pups were estimated to be newborns. Using body shape and coat coloration (see Kovacs and Lavigne 1986), 6 pups were estimated to be 1 day old, 5 to be 2 days old and 2 to be 3 days old. These pups were paint-marked for potential use in the behavioral study. Each day until 9 January, females that gave birth within view of the observation blind and their newborn pups were also paint-marked. On the basis of the birth distribution from previous years, we intended these pairs to represent a group giving birth during the peak of pupping, i.e., the "peak group". Pups were not captured in the first few days after birth because prior experience had revealed that during this time females may abandon their pups while the pup is being weighed. On 13 January we weighed to the nearest 100 g the 15 marked pups in the peak group that were being included in the behavioral study. Additional marked pups of known age but not within view of the observation blind were weighed until we had a sample of 10 pups of each sex (one pup initially recorded as a female was in fact a male).

On 13 January we also began marking a second set of females and newborn pups to make up the "late group". All pups born between 13 and 24 January ($n=18$) were weighed for the first time on either 21, 23 or 29 January within 3–9 days of birth. We weighed pups on these 3 days to avoid daily disturbance in the study area. Initially, 14 of the late-born pairs were visible from the blind and incorporated in the behavioral study.

In both pupping groups, a second weight was obtained within 0.5 days of weaning to provide both a measure of mass gain and an estimate of weaning mass. For most pups there was at least 6 days between the first and second weights. In the peak group, two pups and their mothers, disappeared during a storm on 11 January before the pups were weighed a second time. Thus neither a rate of mass gain nor weaning mass was obtained for them. A third pup in this group was weaned at 12 days, only 3 days after its initial weight. The rate of mass gain of this pup was only 0.4 kg/day, more than 4 times lower than any other pup in this group and twice as low as any pup in the late-born group. Thus, this pup was excluded from the analysis of rate of mass gain. In the late-born group, one pup could not be weighed in the first 9 days postpartum because it resided on a little island created by flooding during the January storm. A weaning mass was obtained for this pup, however. Thus for analysis of mass gain there were 17 pups in each group and for weaning mass there were 18 pups in each.

Not all mother-pup pairs that were initially visible from the blind remained so throughout the course of the study. A combination of low lying dunes obscuring vision from the blind and movements of females and pups around the study area resulted in only partial behavioral data being collected for some pairs. Furthermore, the part of lactation not observed was variable, and as lactation stage can affect suckling parameters and the behavior of males towards females (Ofstedal et al. 1987; Boness and James 1979), the data to be included in the final analysis were selected by a two-stage process. First, only those females for which observations were obtained on days covering 80% or more of lactation were included. Thus three females in the peak group and two females from the late group were excluded. Second, to avoid the confounding effects of lactation stage, for each female in the peak group, we included only the comparable portion of lactation from a randomly selected female in the late group.

Each day for between 3 and 7 h, the same observer continuously recorded the interactions of all visible marked females with each other and with other animals, using The Observer (Ver. 2.0, Noldus) software and a laptop computer. Since the number of hours of observation varied from day to day, durations and frequencies of the recorded behavioral interactions were converted to daily total duration (as a percentage of observation time) and daily relative frequencies (number per hours of observation) for each animal. Although it is possible that our daytime samples do not reflect night activity, evidence from the Farne Islands revealed no differences between day and night activity of male grey seals (Anderson 1978). The average number of observation hours for individual animals was 90.

The behavioral interactions recorded included:

1. *Suckling*: time spent by a pup on its mother's teat
2. *Interrupted suckles*: suckling that was terminated in response to the activity of males
3. *Female-female threats*: vocal threats, flipper slapping, lunging or biting of another female, usually caused by movement of females or pups in close proximity to one another
4. *Female-male threats*: vocal threats, flipper slapping, lunging or biting of a male; these were classified as to whether they were induced by a male approaching a female (*approaches*), a male forcibly attempting to mount and copulate with a female (*mounts*), or two or more males threatening one another or fighting in close proximity to a female and her pup (*male-male interactions*)

Although we planned to study equal numbers of male and female pups, the various factors which resulted in attrition of animals in the study yielded imbalanced sex composition of the two groups compared in the various analyses. The sex composition (M:F) of the peak and late pups were as follows for the various analyses: mass gain – peak 10:7, late 8:9; weaning mass and lactation duration – peak 11:7, late 9:9; and suckling parameters – peak 8:4, late 6:6. A two-way analysis of variance, incorporating time of birth and pup sex, was used to analyze measures that were potentially affected by the sex of pups. In fact there were no significant sex effects on pup mass gain ($F=0.51$, $P=0.48$), weaning mass ($F=0.55$, $P=0.46$), lactation length ($F=1.64$, $P=0.21$) or daily suckling duration ($F=3.62$, $P=0.07$). Consequently, sex was not incorporated in the final analysis.

A number of studies have indicated that time of birth is related to other factors (e.g. maternal mass, maternal age, pup birth mass), which could contribute to or even account for the differences in pup mass gain and weaning mass associated with time of birth (Coulson and Hickling 1964; Reiter et al. 1981; Anderson and Fedak 1987; Boyd and McCann 1989; Lunn and Boyd 1993). Because we wanted to minimize interference with maternal behavior in our initial study, we did not obtain weights on females in 1991. We did at least weigh pups early in lactation to determine whether pups in the two periods were comparable in size at the beginning of lactation. The number of known age females in the 1991 study was too small to permit a statistical analysis of possible confounding effects of maternal age (or experience).

In 1992, we conducted a further study to test the alternate hypothesis that maternal size and age accounted for the differences in maternal performance as a function of time of birth. To investigate whether birth time was influenced by maternal age, we chose a larger study area than in 1991 and recorded the birth dates of all branded females, which were of known age. For younger females (5–7 years, $n=18$) and for older females (>7 years, $n=31$), we separately determined whether the frequency of births during the first and second halves of the pupping period deviated from that expected based on the overall distribution of births.

To examine the possible confounding effects on maternal performance of maternal mass, initial pup mass and pup sex, we weighed a sample of 30 mothers and pups in the study area at three days postpartum. As in 1991, we also weighed pups a second time within 0.5 days of their mother's departure, which provided a weaning mass and a rate of mass gain. A SAS General Linear Models analysis of pup mass gain and weaning mass was run in two stages. In the first stage, initial maternal and pup mass, and pup sex were included in the analysis, along with date of birth, to determine whether these variables affected pup mass gain and weaning mass and whether they interacted with date of birth in their effects. The analysis was run such that each variable was evaluated having already entered all other variables. As in 1991, there was no effect of sex on pup mass gain and weaning mass ($F=0.02$, $P=0.88$; $F=2.09$, $P=0.17$). Also, initial pup mass did not affect pup mass gain ($F=2.53$, $P=0.13$), but it did influence weaning mass ($F=5.21$, $P=0.03$). In the second stage of the analysis, those variables which had no significant effect on the dependent variables were dropped so that the final analysis of time of birth on pup mass gain controlled only maternal mass, and of time of birth on pup weaning mass controlled maternal mass and pup initial mass.

In analysis of the 1991 data, the equality of sample variances were tested (SAS TTEST procedure) because sample sizes were small. When the variances were not equal, a Wilcoxon two-sample test, with a t -test approximation (SAS procedure NPAR1WAY) was used to assess the differences between the peak and late groups. Since most analyses of the behavioral data presented in Table 1 had unequal variances, a Wilcoxon test was used to analyze all variables. SAS Version 6.03 was used for statistical tests. As we had *a priori* expectations for the direction of differences in analyses, one-way tests were used unless stated otherwise.

Results

Distribution of births

The distribution of births at our study rookery showed a rapid rise to the peak followed by a gradual decline with an extended tail (Fig. 1). Of the births in the study area, 58% occurred over a 7-day period between 3 and 9 January. Most (39%) of the remaining births were distributed over a 22-day period, except for 3% at the beginning before the peak of pupping. This distribution of births indicates that our *a priori* choice of dates for peak and late groups did reasonably reflect the peak and tail of pupping in the study area.

Disturbance to females in relation to time of birth

The mean daily relative frequency of disturbances to lactating females and the mean daily percent of observation time spent responding to the disturbances

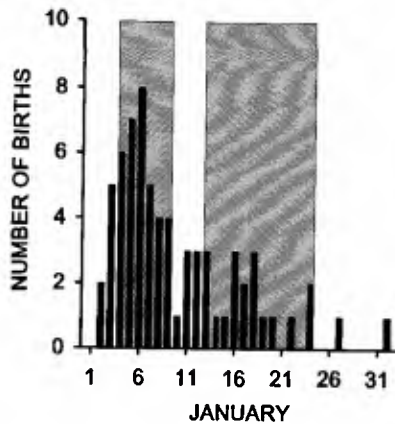


Fig. 1 Distribution of grey seal births in the study site at Sable Island, Nova Scotia in 1991. Shaded areas represent the periods from which the peak and late groups were derived

were significantly greater for females that gave birth late in the pupping period than for females that pupped during the peak [daily duration: $3.9 \pm 1.33\%$ vs. $1.8 \pm 0.18\%$, $P = 0.011$; frequency (number/h): 2.0 ± 0.21 encounters/h vs. 2.3 ± 0.14 encounters/h, $P = 0.023$]. This difference was attributable to interactions involving males, but not to interactions with other females (Table 1). All three categories of interactions between males and females that were recorded (i.e., approaches of females, attempts by males to copulate (mounts) and male-male aggressive encounters which triggered a response by the female) showed the same trends. The most notable differences occurred in the mean daily percentage of time females were harassed by males mounting them and the frequency and daily duration of responses by females to male-male aggressive encounters. The amount of time females spent rejecting premature attempts to copulate was 17 times greater on average in the late group, although there was considerable variation in the amount of attention paid to different females, as indicated by the large standard

error (Table 1). The relative frequency of mounting of females in the late group was about 50% greater than in the peak group. Incidental disturbances due to male-male encounters were three times more frequent and consumed a greater amount of a female's time, on average, for females that gave birth late than for ones that pupped during the peak.

A possible factor that contributes to the greater disturbance by males to late-pupping females is a change in the operational sex ratio. The number of females per male decreased from about 3.5 at the beginning of the pupping period to less than 1 female per male near the end of the pupping period ($r = 0.970$, $F = 11.9$, $P = 0.002$; Fig. 2). This change was due to a combination of the departure of females and an increase in transient males.

Disturbances resulting from interactions with other females were not more prevalent in the late group (Table 1). In fact, the relative frequency of female-female interactions was slightly lower for late-pupping females than for peak-pupping ones, as was the percentage of time spent interacting aggressively with other females although neither difference was significant.

Reproductive performance in relation to time of birth

Indices of maternal performance of late-pupping mothers were substantially lower in association with the greater levels of male harassment (Table 2). Suckling among late-pupping females was interrupted more than twice as frequently as that among females which gave birth during the peak of pupping (Table 2). Similarly, the mean percentage of time spent suckling by pairs in the late group was significantly less than that of pairs in the peak group. Consistent with these differences in suckling behavior, late-born pups gained weight 30% (0.7 kg/day) more slowly on average and had an

Table 1 Mean daily relative frequency and duration (as a percentage of observation time) of disturbances to grey seal mothers in 1991 by male and female conspecifics as a function of time of birth

	Time of birth relative to breeding season		
	Peak <i>n</i> = 12	Late <i>n</i> = 12	<i>P</i>
Total male disturbances			
% Of observation time	1.1 ± 0.12	3.4 ± 1.36	0.001
Frequency (no./h)	1.4 ± 0.14	1.9 ± 0.11	0.023
Approaches			
% Of observation time	0.8 ± 0.08	1.2 ± 0.08	0.01
Frequency (no./h)	1.1 ± 0.12	1.2 ± 0.06	0.18
Mounts			
% Of observation time	0.1 ± 0.06	1.7 ± 1.30	0.03
Frequency (no./day)	1.0 ± 0.14	1.5 ± 0.31	0.12
Male-male encounters			
% Of observation time	0.2 ± 0.04	0.6 ± 0.09	0.001
Frequency (no./h)	0.2 ± 0.07	0.6 ± 0.03	0.006
Total female disturbances			
% Of observation time	0.7 ± 0.11	0.4 ± 0.13	0.037
Frequency (no./h)	0.6 ± 0.09	0.4 ± 0.12	0.074

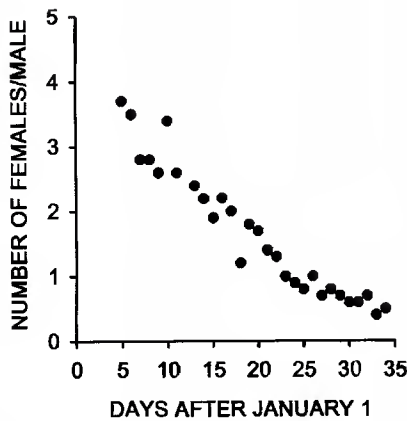


Fig. 2 The relationship between operational sex ratio and date in grey seals on Sable Island, Nova Scotia in 1991

average of 16% (8.4 kg) lower weaning weights than pups born during the peak (Table 2). The minimum rate of mass gain in the late group was 0.8 kg/day compared to 1.8 kg/day for the peak group. Lactation length did not differ between females of the two groups, however (Table 2). There was no pup mortality in our study prior to the time of weaning.

Possible factors confounding male harassment effects

Since we did not measure maternal mass in 1991 to avoid undue disturbances to females, we could not assess the influence of maternal mass on maternal performance, or control for its effects statistically. We did obtain the initial mass of pups and can at least examine whether initial mass, controlling for age of pup at initial weighing, differed between the peak and late part of the season. An ANCOVA showed that there was no difference ($P > 0.05$).

In 1992 we attempted to corroborate our 1991 findings and address more fully the alternate hypothesis that the difference between peak and late pupping was due to older, larger females giving birth earlier and younger, lighter females giving birth later. Using a general linear models analysis, we examined pup mass gain and weaning mass of peak and late-born pups while statistically controlling for initial maternal and pup mass (only necessary for pup weaning mass, see Methods). This analysis showed a significant effect of birth time on pup mass gain and

weaning mass when the possible confounding effects of maternal mass were removed (Table 3), corroborating the 1991 results. Figure 3 illustrates the negative relationship between these pup growth measures relative to maternal mass and birth date. It is apparent that while time of birth does influence pup growth, there is still variability in pup growth that is not accounted for by date of birth.

For both pup mass gain and weaning mass there was a significant interaction between date of birth and initial maternal mass. This interaction appears to have resulted from a tendency for lighter females to have given birth earlier in the pupping period ($r = 0.320$, $P = 0.09$) and for these light females to have slower growing pups than the few light females that pupped later. Females pupping during the peak were no larger and even tended to be lighter (179.8 ± 5.9 kg) compared to those pupping after the peak (190.5 ± 7.8 kg), however, because of the high variance this difference was not significant (t -test, $df = 28$, $P = 0.281$). These results are contrary to those reported in other seal studies, although harbor seals, *Phoca vitulina*, on Sable Island also show no trend in maternal mass over the birth season (Bowen et al. 1994). Thus in our study the effect of maternal mass on pup mass gain and weaning mass in relation to birth time should operate to mask the effect of male harassment, not confound it. In fact the tendency of light females with small pups to give birth during the peak may be part of the reason why the least squared means of pup mass gain and weaning mass in the peak and after the peak only differed by about 4% in 1992 (pup mass gain: 2.4 ± 0.07 and 2.3 ± 0.09 , respectively and pup weaning mass: 50.9 ± 0.73 and 48.9 ± 1.21 , respectively).

To test the alternate hypothesis that young females give birth later in pupping and older females earlier, 49 known-age females from 1991 and 1992 were divided into two groups, females at least 8 years old and females less than 8 (the youngest being 5 years old). Based on the distribution of births, for each group an expected frequency of births in each half of the distribution was calculated, and a G -test performed to determine whether the observed frequencies deviated from the expected. For the older females ($n = 31$) there was no significant deviation from the expected (71% observed in the first half vs. 84% expected, $G_{adj} = 2.49$, $P > 0.10$). However, for the younger females ($n = 18$) there was a

Table 2 Proximate consequences of producing offspring during the peak and late in the pupping period in 1991. Values are means \pm SEs. Arcsine transformation was performed on percentages before analysis. The number of animals in each group was 12 for the suckling measures, 17 for mass gain and 18 for weaning mass and lactation length

	Time of birth relative to pupping season		
	Peak	Late	P
Interrupted suckles (no./24 h)	1.2 ± 0.24	2.6 ± 0.39	0.003
% Time spent suckling	5.1 ± 0.38	4.0 ± 0.29	0.049
Mass gain (kg/day)	2.4 ± 0.09	1.7 ± 0.12	0.0001
Weaning mass (kg)	54.0 ± 1.34	45.6 ± 2.54	0.004
Lactation duration (day)	15.8 ± 0.39	15.6 ± 0.58	0.037

Table 3 Summary of General Linear Models analysis (SAS) of pup mass gain and weaning mass of grey seals in 1992 in relation to time of birth (*Tob*), statistically controlling for maternal (*Mmass*) and pup mass (only for weaning mass) at three days postpartum. Sample size for pup mass gain is 30 and for weaning mass is 27. Statistical tests are two-tailed analyses

Variable	<i>b</i>	<i>t</i>	<i>P</i>
Pup mass gain			
Time of birth	0.223	2.90	0.0075
Maternal mass	0.021	4.12	0.0003
<i>Tob</i> × <i>Mmass</i>	-0.001	-3.15	0.0041
Pup weaning mass			
Time of birth	3.23	3.52	0.0019
Maternal mass	0.39	6.16	0.0001
Pup mass	0.64	3.19	0.0043
<i>Tob</i> × <i>Mmass</i>	-0.02	-3.96	0.0007

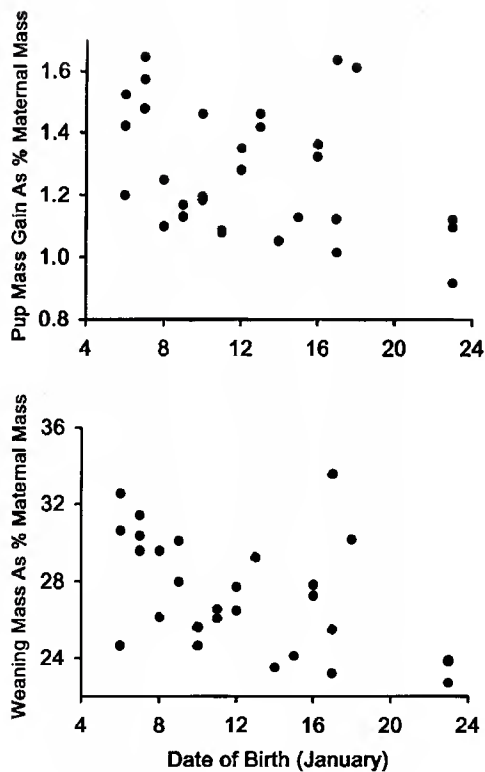


Fig. 3 The relationship between date of birth and pup mass gain and weaning mass as percentages of maternal mass for grey seals on Sable Island in 1992

non-significant tendency to give birth in the first half of the pupping period (100% observed vs 84% expected, $G_{adj} = 3.60$, $P = 0.06$). These results are consistent with the tendency reported above for lighter females to give birth earlier in the pupping period.

Discussion

Male harassment and time of birth

The behavioral data from 1991 on interactions between males and females confirm our hypothesis based on previous casual observations which suggested that late-pupping females are harassed by males more than are peak-pupping females (Table I). Our study also shows that giving birth late may be costly to grey seal females as a consequence of the harassment. Pups born late suckled less frequently, gained mass more slowly and were lighter at weaning, although harassment was not sufficient to cause females to prematurely abandon lactation as lactation length did not differ between peak and late-pupping females (Table 2). In 1992, the relationship between birth time and pup mass gain and weaning mass was apparent only after controlling for maternal mass. This appears to be due to the tendency for lighter and younger females to give birth during the peak of pupping in that year. As we did not weigh females in 1991, we do not know if this relationship between maternal mass and birth time was an anomaly or typical. However, the fact that all of the seven known-age young females in our 1991 sample gave birth during the peak of pupping suggests that the results of 1992 are typical.

A second possible explanation for a weaker relationship between time of birth and pup mass gain and weaning mass in 1992 could be that the study area in 1992 had a lower density of seals than that in 1991. The study area in 1991 covered 2328 m² and had 68 births, whereas that in 1992 was twice as large, covering 4900 m² and had only 77 births. The daily mean number of males in the smaller area in 1991 was 25 compared to only 16 in the larger area in 1992. The importance of the effect of colony density on male harassment of females in relation to time of birth warrants further investigation.

Possible confounding effects of maternal age or body mass

Despite evidence from other studies of grey seals and other seals which shows that large and experienced females tend to give birth during the peak of pupping and small and inexperienced females do so later in the pupping period (Reiter et al. 1981; Anderson and Fedak 1987; McCann 1982; Boyd and McCann 1989; Sydeman et al. 1991a, b; Lunn and Boyd 1993), we found no indication of this on Sable Island. In fact, the direction of the relationships between both maternal mass and maternal age and birth date was the opposite of that reported in the literature. Younger females on Sable Island tended to give birth earlier in pupping rather than later. Thus maternal mass effects in our

1992 study would not confound the effect of male harassment on pup growth in relation to time of birth, but would tend to mask it. Indeed, when we statistically controlled for the influence of maternal mass on pup mass gain and weaning mass, we found a significant negative relationship between time of birth and pup mass gain and weaning mass. Moreover, this relationship in the 1992 study is consistent with our 1991 findings and our hypothesis that increased male harassment leads to reduced maternal effort and pup growth late in the pupping period.

We do not know why grey seal females on Sable Island show a different relationship between date of birth and maternal mass and age from that reported for other grey seal colonies and several other phocids. However, the purported interrelationship between maternal mass, mass gain of pups and time of birth for grey seals on North Rona (Anderson and Fedak 1987) is confounded with differences in the sex ratio of pups over the pupping period. Anderson and Fedak found that male pups are born earlier than female pups and that males are larger and grow faster than the females. In contrast, Bowen et al. (1992) found no evidence of sex differences in birth mass, rate of mass gain or weaning mass in a larger study of grey seal pups on Sable Island.

Male harassment and birth synchrony

The shape of the distribution of births in our rookery on Sable Island (Fig. 1) is comparable to that reported at other grey seal rookeries (e.g., Farne Islands, Coulson and Hickling 1964; North Rona, Summers et al. 1975). In both of these colonies there was a rapid climb to a peak and a gradual decline, with a small percentage of births being distributed over an extended period at the end. The reasons for the asymmetry in the tails of the distribution are not understood, but a high degree of synchrony is clear. Both of these distributions are for substantially larger colonies than the relatively small rookery observed in our study, suggesting that we might expect to find a similar distribution for the entire colony on Sable Island as well.

We suggest that our data are consistent with an hypothesis that male harassment may be a contributing factor to this high reproductive synchrony of births in grey seals. Although our argument would be stronger if all data sets had been collected in a single season, we have shown that male harassment is greater after the peak of pupping and that maternal performance and pup growth is diminished for females and pups giving birth and being born during that period. We have also provided evidence to indicate that the relationship between maternal performance and pup growth and time of birth is not explained by the differences in maternal mass or age during the peak and after the peak of pupping.

The reduced growth rates and weaning mass of late-born pups, in association with male harassment, likely affects juvenile mortality. This may provide the means by which selection for increased synchrony could occur. Grey seal pups, like other phocids, undergo a post-weaning fast in which fat stores are critical (Ortiz et al. 1978; Bowen et al. 1987a; Worthy and Lavigne 1987). On average, grey seal pups may be expected to lose about 25% of their mass at weaning during this fast (Bowen et al. 1992). Pups with lower growth rates gain proportionately less fat than those growing more rapidly, and thus have smaller energy reserves at the beginning of the fast (Iverson et al. 1993). Furthermore, during the fast, lighter pups may lose mass more rapidly than heavier ones (Bowen et al. 1992).

Coulson and Hickling (1964) have shown for grey seals at the Farne Islands, United Kingdom, that there is a strong correlation between pup growth rate and survival of pups to 5 weeks of age. The slowest growing pups (0.8 kg/day) in our sample of late-born pups would have a less than 50% chance of survival based on Coulson and Hickling's data. Evidence of increased mortality associated with low birth mass or juvenile body mass has been reported in other species of seals and other mammals (Guinness et al. 1978; Clutton-Brock et al. 1982; Murie and Boag 1984; Calambokidis and Gentry 1985; Small and Smith 1986; Iason 1989; Majluf 1992).

Comparative data from other grey seal colonies lend further support to an hypothesis that male harassment may contribute to birth synchrony. A birth distribution lacking a peak has been shown for grey seals on Ramsey Island, Wales, which also has a more extended pupping period (about 10 weeks) than other colonies (Davies 1949; Coulson 1981). Given the lack of a peak in pupping at this colony, according to our hypothesis, we might expect male harassment at Ramsey Island to be low. Davies (1949) describes a situation at Ramsey very different from that on Sable. Males at Ramsey Island spend most of their time in the water off the beach where suckling occurs. Thus, males rarely approach or try to mount females on land and also rarely interrupt suckling. Interestingly, in unpublished data on suckling behavior from Ramsey Island in 1975 by one of us (D.J.B), there was no difference in the percent of observation time spent suckling between females that gave birth in the first half of pupping compared to the second half ($n = 20$ females, $4.9 \pm 0.59\%$ vs. $4.6 \pm 0.60\%$, respectively) in contrast to our findings on Sable Island.

At North Rona, Shillay, Cean Ear and the Farne Islands, where the breeding circumstances are more comparable to Sable Island than Ramsey Island, the pupping period is also more akin to Sable Island with a clear peak and a tail, as described above (Hewer 1957; Coulson and Hickling 1964; Anderson et al. 1975; Coulson 1981). Consistent with our hypothesis of male

Table 4 The relationship between the spread of births (99% of births) and mean adult sex ratio (number of females to males) during the breeding season at several grey seal colonies

Colony	Spread of births (weeks)	Sex ratio	Sources ^a
Sable Island	4-5	1.7	7
Shillay Island	5-7	2.3	1
Cean Ear Island	6-7	5.0	5, 6
Farne Islands	6-7	5.4	2, 4
North Rona Island	8-9	7.5	3, 4

^aSources for these data include: (1) Hewer 1957, (2) Coulson and Hickling 1964, (3) Anderson et al. 1975, (4) Coulson 1981, (5) Anderson and Harwood 1985, Anderson and Curry, unpublished work, and (7) this study

harassment, there is a negative correlation between the degree of synchrony and the sex ratio of adult females to males (Table 4), presumably because there is likely to be a greater level of male harassment associated with lower sex ratios (this study; Anderson and Harwood 1985). As the quality of data are somewhat variable in Table 4, more direct investigation of this relationship should be made.

There are other pinnipeds in which there is a narrow peak in the distribution of births (e.g. harp seal, *Phoca groenlandica*, Myers and Bowen 1989; South American fur seal, Majluf 1992; and northern fur seal, Trites 1992). The extent to which male harassment plays a role in synchrony in these species is unclear. However, there are other factors that may be important in some of these species. For example, predation by sea lion males may in part be responsible for the pattern of births in the South American fur seal (Harcourt 1992; Majluf 1992). In harp seals, synchrony is more likely explained by the instability of ice than by male harassment because males only infrequently interact with females on the ice where suckling occurs.

The Hawaiian monk seal, *Monachus schauinslandi*, has an extended pupping period without a peak (Deutsch 1985; Boness 1990), similar to that of the grey seal on Ramsey Island. Interestingly, like the grey seals on Ramsey Island, monk seal males spend little time on the beaches where females suckle their pups (Deutsch 1985).

Mechanisms by which male harassment might sharpen birth synchrony

There are at least two behavioral mechanisms through which females that give birth during the peak might achieve a reduction in male harassment. The first is a "selfish herd" or "swamping" effect which has been suggested to explain how spatial and temporal clustering might reduce predation (Hamilton 1971; Karban 1982; Ims 1990b). As the ratio of females to males is high and decreases throughout the breeding season (Fig. 2), the attention males pay to a given female earlier in the breeding season may be swamped by the availability of other females compared to later in the season when the ratio reversed.

The second possible mechanism is what we call a "free-ride" effect. We suggest that the tendency of established males neither to investigate nor mount females until they near estrus (Boness and James 1979; Boness 1984) sets up a situation whereby females giving birth synchronously at the beginning of the pupping period escape male harassment for most of lactation. The effect of these females becoming receptive over a period of a few days would be intense sexual activity. This may produce an overall enhancement or facilitation effect (Dewsbury 1978), such that males subsequently more readily approach and even investigate females that have recently given birth and are more than a week away from estrus. We currently do not have data to evaluate the relative importance of these two possible mechanisms, which need not be mutually exclusive.

The question of what mechanism might be controlling the timing of pupping and the trait on which selection might be operating to produce synchronous births can only be speculated on. In pinnipeds delayed implantation could serve as a mechanism by which gestation might be controlled to produce synchrony (Boyd 1991), but we do not know how much individual variability there is in the timing of implantation in a given population or to what extent it might be controllable by individuals. However, it is likely that environmental factors play a major role in dictating the timing of implantation (Boyd 1984, 1991). An alternative mechanism might be that the end of gestation is controllable. Recent work on bison, *Bison bison*, suggests that female bison are able to shorten or lengthen gestation in order to give birth synchronously (Berger 1992) and that breeding synchronously has fitness consequences (Green and Rothstein 1993).

Male harassment as a factor shaping female behavior

Male harassment of females has been suggested as a selective force shaping female reproductive behavior in other species (see Table 4 in Mesnick and Le Boeuf 1991). For example, among other seals harassment by peripheral or subadult males, which results in increased energetic costs and perhaps even injury and death to the female or her pup might in part be responsible for a high degree of gregariousness or harem formation

(Trillmich and Trillmich 1984; Campagna et al. 1992). Indeed spatial and temporal clustering are necessarily linked to some extent, and it may be that in those species in which male harassment has been a factor in maintaining or enhancing harem formation also have been a factor in maintaining or enhancing breeding synchrony. There is some evidence for this in the Southern sea lion, *Otaria byronia*. Southern sea lion females that give birth early in the season compared to during the peak suffer greater mortality of their pups due to separations caused by male harassment (Campagna et al. 1992).

Male harassment may also serve as a factor shaping both female and pup behavior in the northern elephant seal, *Mirounga angustirostris*. Departing females may permit copulations by peripheral males, increasing the probability of being fertilized by poorer-quality males, to avoid injury that might result in death (Mesnick and Le Boeuf 1991). Weanling pups in this species are frequently mounted by subordinate males and are occasionally killed by this activity. Formation of pods and movement out of the rookery and into microhabitat refuges may serve to reduce injury and mortality in weanlings by subordinate male sexual harassment (Rose et al. 1991).

Male sexual harassment of females has also been suggested as a possible factor in the evolution of female choice and lekking, particularly in ungulates (Wrangham 1980; Clutton-Brock et al. 1992). In both primates and some bird species females may travel with dominant males to avoid forced copulation by subadults or other adult males (Mitani 1985; Emlen and Wrege 1986). Our data suggest that, in addition to these other effects on maternal behavior, male harassment may be a factor that can contribute to shaping birth synchrony.

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