Breeding season and embryonic diapause in crabeater seals (Lobodon carcinophagus)

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Direct observation of 387 embryos in the early stages of development was combined with observations on breeding behaviour and reproductive biology obtained from the published literature, to estimate the timing of births, oestrus, ovulation and implantation, and to derive estimates of the duration of pregnancy, embryonic diapause and active gestation for crabeater seals (Lobodon carcinophagus). The total duration of pregnancy (conception to birth) is estimated to be 11.3 months (344 days). It is estimated that the pupping season extends from late September to early November, with peak births in mid-October. The estimated mean duration of lactation is approximately 17 days; the mean date of weaning is 31 October (14 October to 17 November); and the mean date of conception is 4 November (18 October to 21 November). Oestrus, ovulation and conception occur approximately 4 days after weaning. Estimates of times of weaning and conception were made assuming that the preimplantation period is the same in all individuals. The mean date of implantation of the embryo is 24 January ± 17 days; the duration of embryonic diapause is 2.7 months (81 days); and the duration of active gestation (implantation to parturition) is 8.8 months (264 days).

Introduction

None of the Antarctic ice-breeding seals form colonies as dense as those of the land-breeding species. Crabeater seals (Lobodon carcinophagus) are usually spread thinly over a vast area, occupying one of the most remote habitats, and are correspondingly difficult to study. Owing to their inaccessibility, very little was known of their breeding behaviour until a few decades ago, and knowledge is still sparse compared with that on the more accessible seal species. Three scientific expeditions to the Bransfield Strait in October to November, devoted to such investigations (Siniff et al., 1979; Bengtson and Siniff, 1981), indicated that in the breeding season the densities of crabeater seals (0.7–0.8 per km²) on pack ice are much lower than in the summer (several per km²) when the ice extent is less, but there was some evidence of clumped distribution. For the most part, ‘family groups’ or ‘triads’ (each consisting of a breeding female, a newborn pup and a breeding male) form when a pregnant female hauls out to give birth on a suitable ice floe and is joined by a male, before or after parturition. The family group remains within a small area, usually one floe, until the pup is weaned (usually when the male drives it away). The male defends the family group against other adult males, protecting his right to mate when the female comes into oestrus. When the pup is weaned, the adults maintain close contact as a male–female pair, and the male prevents the female from leaving the floe. Most ice-breeding seals mate in the water (Stirling, 1975; Riedmann, 1990; Atkinson, 1997), but the effort expended by the male crabeater seal in remaining close to the female strongly indicates that in this species mating of the parous females, at least, occurs on the ice.

Bengtson and Siniff (1981) found at postmortem examination that almost all female crabeater seals in family groups had not yet ovulated and 60% of those in male–female groups had not ovulated, whereas the majority of lone females had ovulated already and a corpus luteum was forming or formed. This finding indicates that ovulation occurs shortly after the pup is weaned.

Estimates of the lactation period of the crabeater seal are 5 weeks (Laws, 1958), 4 weeks (Siniff et al., 1979) and 17 days (range of 14–21 days) (Shaughnessy and Kerry, 1989). Apart from the last estimate, the durations are largely conjectural.

Embryonic diapause (delayed implantation) occurs in many mammalian species (Enders, 1963), and appears to be the rule in pinnipeds (Scheffer, 1958; Atkinson, 1997). Harrison et al. (1952) reported that embryonic diapause occurs in the crabeater seal. Laws (1984) reviewed delayed implantation in five Antarctic seal species, including the crabeater seal, and concluded...
that the average duration of embryonic diapause varies among species from 48 to 125 days, and active fetal growth varies from 226 to 269 days. In the crabeater seal, the total duration of pregnancy was estimated to be 335 days, the duration of embryonic diapause 80 days and implantation to birth 255 days.

The aim of the present study was to estimate the total duration of gestation, the duration of embryonic diapause and the duration of active gestation (implantation to parturition) in crabeater seals by drawing on published work and our own observations of early embryos. First, quantitative observations of embryos from a large sample of crabeater seals are reported, and from the data the mean date (and confidence limits) at which implantation of the blastocyst occurs, is estimated. Second, published field observations of breeding behaviour during the breeding season are summarized (mainly from Øritsland, 1970; Siniff et al., 1979; Bengtson and Siniff, 1981; Shaughnessy and Kerry, 1989). Finally, taking advantage of the precise quantitative data on the implantation period, and relating these dates to other elements of the annual reproductive cycle, the timing of births, lactation, oestrus and ovulation are discussed, and estimates of the duration of pregnancy, diapause and active gestation are derived for this species.

Materials and Methods

Data collection

Crabeater seals were collected from Marguerite Bay, on the west side of the Antarctic Peninsula (approximately 68°S, 68°W). It is a large bay, surrounded by glaciers and mountains up to 1500 m, which freezes over in the autumn but retains variable amounts of pack ice and fast ice in the summer months.

All data were collected between 1967 and 1978 from seals shot at random for dog food from early February to late March (_permitted at the time under the Agreed Measures of the Antarctic Treaty and permits issued by Base Commanders at Stonington, Adelaide and Rothera Stations). The dates of collection were not planned, but were determined by the ship’s itinerary, which in turn was influenced by logistical needs of resupplying the Antarctic stations. Usually within an hour of death, the uterus and embryonic membranes of 387 females, ranging in age from 4 to 21 years, were opened, and the conceptus removed after the umbilicus was cut close to the body. The embryo was blotted to remove surface moisture, weighed to the nearest 0.01 g and the straight-line, nose–tail length recorded to the nearest 1.0 mm. With the exception of the smallest conceptuses that would have been damaged by handling, the embryo was measured by uncurling it and then lying it on its side and tracing the dorsal curvilinear outline. Dividers were then used at 0.3, 0.5 or 1.0 cm spans to measure the straight-line length.

Estimation of implantation date

From our data alone (that is, without reference to average birth weight and duration in the literature) it was possible to establish regression models of growth rate using the cube root of fetal weight \( W^{1/3} \) and fetal length as a function of time in days since 2 November (see below), and to use these models to estimate the mean date of implantation (with 95% confidence intervals) using the inverse prediction method described by Zar (1984). A polynomial model was also fitted to the data to allow for the potential curvilinear growth during the early growth stage and the mean date of implantation was estimated from these models.

Calculations of duration of embryonic diapause and date of implantation were made using two equations:

\[ L = a + bt, \]

where \( L \) = length of embryo, \( a \) = intercept, \( b \) = slope, and \( t \) = time (days) between 2 November (see below) and date of collection. The weight of the embryo was used to make a similar calculation using the following formula:

\[ W^{1/3} = a + bt, \]

where \( W \) = weight of embryo.

The calculations were made for all years, using a ‘common’ sample of 339 animals in which both embryo weight and length were known. All calculations were based on the assumption that all births occurred on 2 November, so that new variable development times could be calculated for each specimen, as the number of days that elapsed between 2 November and the date on which the embryo was collected (thus, 1 February = 92 days, that is, November + December + January + 1; 1 March would be 120 days development time). Note that even a large error in this assumed birth date would not affect the calculation of the mean implantation date from the intercept of the calculated regression, and its confidence limits.

Results

The 358 embryos that could be measured accurately ranged in length from 1.8 cm to 17.8 cm, and in weight from 0.01 g to 31.0 g. That is, the largest embryos were only approximately 13% of the length and 0.15% of body weight at birth (138 cm and 20 kg, respectively, see below). In addition, almost all the data collected in this study were within the earlier, slower period of prenatal development as the placenta is growing, up to about a month after implantation. The sex of embryos was recorded when possible, and was not significantly different from 1:1 at this stage.
Table 1. Summary of observations related to the time of pupping in crabeater seals (Lobodon carcinophagus)

<table>
<thead>
<tr>
<th>Observation</th>
<th>Location</th>
<th>Date of birth</th>
<th>Length at birth (cm)</th>
<th>Weight at birth (kg)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Several newborn pups, one newly born</td>
<td>Bellingshausen Sea</td>
<td>September</td>
<td>–</td>
<td>–</td>
<td>Racovitza, 1900</td>
</tr>
<tr>
<td>Newborn pup</td>
<td>–</td>
<td>September (possibly late September)</td>
<td>–</td>
<td>–</td>
<td>Lockley, 1945</td>
</tr>
<tr>
<td>Live pups present</td>
<td>Crown Prince Gustav Channel</td>
<td>After mid-October (none before)</td>
<td>–</td>
<td>–</td>
<td>Laws and Taylor, 1957</td>
</tr>
<tr>
<td>Family group with pup, estimated age 1–3 weeks</td>
<td>Argentine Islands</td>
<td>20 October</td>
<td>–</td>
<td>–</td>
<td>O’Gorman, 1963</td>
</tr>
<tr>
<td>Average date of birth estimated</td>
<td>South Orkney Islands</td>
<td>Mid-October</td>
<td>135–140</td>
<td>–</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Single family group</td>
<td>–</td>
<td>About 14 October</td>
<td>–</td>
<td>–</td>
<td>Corner, 1972</td>
</tr>
<tr>
<td>Pup in one of two family groups</td>
<td>–</td>
<td>October</td>
<td>–</td>
<td>–</td>
<td>Corner, 1972</td>
</tr>
<tr>
<td>No newborn pups among 254 adults killed 27 Oct to 15 Nov</td>
<td>Balleny Islands Scott Island</td>
<td>Before 27 October</td>
<td>–</td>
<td>–</td>
<td>Tikhomorov, 1975</td>
</tr>
<tr>
<td>Five family groups, each with a pup</td>
<td>Off Enderby Land</td>
<td>Second half of October</td>
<td>Mean 138</td>
<td>Mean 20</td>
<td>Shaughnessy and Kerry, 1989</td>
</tr>
</tbody>
</table>

*First newborn pup observed 2 October. Of 132 females caught, 42.9% were pregnant or lactating before 11 October, but none were pregnant and only 1.3% lactating after 22 October. No seals were caught between 12 and 22 October.

Implantation and embryonic diapause

By application of equations (1) and (2) to all data, implantation was estimated to occur in the second half of January. There was a significant relationship between time since 2 November and fetal length \( L = -224.66 + 2.76t; F(1,337) = 507.6, P < 0.01 \) and the cube root of fetal weight \( W^{1/3} = 6.646 + 0.077t; F(1,337) = 515.0, P < 0.01 \). The mean date of implantation estimated using fetal length was 21 January (95% confidence interval (CI) 19–22 January), and when the cube root of fetal weight was used, the estimated mean date of implantation was 28 January (95% CI 19 January to 2 February). In the case of both fetal length and cube root of fetal weight models, the insertion of an additional term to account for non-linear growth did not have a significant influence on the model (fetal length, \( F(1,337) = 0.493, P < 0.483 \); cube root of fetal length, \( F(1,337) = 0.93, P < 0.336 \)). When embryonic length was used in the calculation to estimate the variation about the mean date of implantation, the estimated 95% confidence limits were 3 January to 8 February. When the cube root of embryonic weight was used, estimated 95% confidence limits were 10 January to 12 February.

Analysis of error

The smallest embryo recorded was 18 mm in length and weighed 0.01 g. The ovaries of an additional 71 females examined in February and March showed an apparently functional corpus luteum and small Graafian follicles, but no embryo or fetus was found. It was hypothesized that either these seals were still in diapause or that the embryo was too small to be observed by either unskilled observers or biologists (the gross appearance of the uterus shows little or no enlargement at this stage). In a small number of seals, very recent early embryonic loss is possible. Comparison of five samples from week 1 to week 4 of February and early March showed seals in this category, as a percentage of all females examined were: 19.4, 20.9, 6.4, 11.4 and 8%, respectively, but were not significantly different. Comparing the first and second halves of February showed a significant decline from 20.2 to 10.3% \( (P < 0.05) \); between the first half of February to early March the decline from 20.2 to 8% was highly significant \( (P < 0.01) \). These results indicate a significant decline in blastocysts and smaller embryos missed by collectors from February to March, as embryos implant, grow, enter the ‘collectable’ population and become less likely to be missed.

Birth, lactation, weaning and ovulation

The sparse information in the literature pertaining to the time of pupping, peak birth date, the duration of lactation and time of weaning, and the timing of ovulation and conception are summarized (Tables 1–3). Despite the geographical spread, the observations all fit a pupping season with peak numbers of births in
Table 2. Summary of information related to the duration of lactation and time of weaning in crabeater seals (Lobodon carcinophagus)

<table>
<thead>
<tr>
<th>Observation</th>
<th>Date</th>
<th>Lactation</th>
<th>Length at weaning (cm)</th>
<th>Weight at weaning (kg)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weaned pup observed</td>
<td>24 Oct</td>
<td>10–14 days</td>
<td>–</td>
<td>–</td>
<td>Corner, 1972</td>
</tr>
<tr>
<td>Pup just before weaning</td>
<td>–</td>
<td>–</td>
<td>168</td>
<td>113</td>
<td>Siniff et al., 1979</td>
</tr>
</tbody>
</table>

On the basis of an assumed weight at birth of 20 kg, weaning weight 80–110 kg, and their data on measured daily weight gains of two pups (mean 4.2 kg), Shaughnessy and Kerry (1989) concluded that the lactation period was 14–21 days, mean 17 days.

Table 3. Summary of information related to ovulation and mating (conception?) in crabeater seals (Lobodon carcinophagus)

<table>
<thead>
<tr>
<th>Observation</th>
<th>Date</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spermatozoa present in testis sections</td>
<td>22 October</td>
<td>Bertram, 1940</td>
</tr>
<tr>
<td>Three male–female pairs</td>
<td>September</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Six male–female pairs</td>
<td>1–21 October</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Ten male–female pairs</td>
<td>22–31 October</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Males without epididymal spermatozoa</td>
<td>Before 10 October</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Males with free epididymal spermatozoa</td>
<td>From 6 October onwards</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Ovaries with mature follicles, but had not ovulated</td>
<td>24, 28, 29 October</td>
<td>Øritsland, 1970</td>
</tr>
<tr>
<td>Recent ovulation</td>
<td>28, 29, 31 October</td>
<td>Øritsland, 1970</td>
</tr>
</tbody>
</table>

mid-October, extending from late September to early November, that is, similar in duration to the implantation period. The results indicate an individual lactation period of approximately 17 days (Shaughnessy and Kerry, 1989), with pups being weaned in a similar pattern to births. Weaning is probably followed some 4 days later by ovulation and in most instances, conception.

Discussion

Apart from early embryonic development, prenatal growth in length is assumed to be linear for crabeater seals, as shown in many species of mammals by Huggett and Widdas (1951). Provided that appropriate data are available, prenatal growth can be described by linear regression relating fetal length or cube root of weight, and time, which intersects the baseline at time $t_0$ and adjustment is made for the period of non-linear growth in the early part of pregnancy (Huggett and Widdas, 1951). No attempt was made to draw a fetal growth curve in this way, because the sample in the present study included only the early part of the post-implantation gestation period.

Accurate estimation of the timing of implantation of the embryo, which is not open to field observation, would be expected to be very difficult in an Antarctic pack-ice-breeding seal. However, in the sample of Marguerite Bay crabeater seals used in the present study the estimation of implantation timing is firmly based upon chronological data on embryo length and weight, which were available as a result of the fortuitous timing of the collection periods. Paradoxically, it is much more difficult to arrive at firm estimates of average and range of dates of birth, lactation and weaning, and conception, which are needed to ascertain the annual reproductive cycle, due to the difficulty of direct observation. The species is largely inaccessible in the breeding season, and apart from a few directed research expeditions mentioned earlier, much of the evidence is from isolated observations from ships. In this regard, the timing of formation and break-up of family groups, and the presence or absence of pups reported in the present study, is instructive. Further to those observations, and important to reaching conclusions about the reproductive biology of this species, Siniff et al. (1979) reported 89 family groups sighted in the 1976 and 1977 seasons, between 7 October and 16 November, with peak numbers in early to mid-October. Price (1980) observed two family groups. The pups when first seen at 16:00 h on 29 October were ‘bright golden yellow’, indicating amniotic fluid still staining the usual pale coffee-coloured lanugo. The younger, the pelage of which was wet, might have been born that day, the other pup a few days earlier. The younger pup was chased off by the male on 14 November, indicating that weaning occurs at about 17 days of age. The older pup and its mother had disappeared by 14 November. The previous sighting was on 8 November, when the cow was still repelling the male, so weaning occurred between 8 and 14 November, at age $> 11–17$ days, consistent with weaning at about 17 days. Price (1980) also observed one male–female pair between 14 and 18 November, consistent with oestrus occurring 4–5 days after weaning. R. M. Laws (unpublished) counted 98 crabeater seals from 6 to 8 November 2000 in heavy pack ice in Norway Bight, South Orkney Islands. The seals included four females with pups, which appeared not
to be associated with males, which is unusual. Other pups, family groups or male–female pairs might have been present, but in the prevailing conditions were not recognizable. Siniff et al. (1979) reported 95 male–female pairs sighted in the 1976 and 1977 seasons, between 7 October and 16 November, with peak numbers just after the break-up of family groups. These authors reported that females come into oestrus after weaning. Re-examining the data, the family group distribution is skewed to the left and the male–female pair distribution is skewed to the right. Smoothed cumulative curves (as simple running averages by threes, converted to percentages for direct comparison) indicated that the male–female pair distribution is about 4 days later than the family groups. It was considered that oestrus occurs within 4 days after weaning (when the male drives the pup away). Bengtson and Siniff (1981) obtained ovaries from 94 female crabeater seals over a 2 week period, 1–14 November, 1977. All post-ovulation females were in male–female pairs (nine) or alone (14). With one exception, all females collected in family groups had not yet ovulated, and no females had ovulated before weaning their pups. Of those in male–female pairs, 60% had not yet ovulated; ovulation occurred when still paired, but mostly at or just after dissolution of the pair bond.

Both Riedmann (1990) and Atkinson (1997) reviewed the reported information about reproduction in phocid seals and showed that all seals enter oestrus and mate either during late lactation or soon after the pup is weaned. Six land-breeding phocids had an average lactation period of 31 days and twelve ice breeders had an average lactation period of 29 days. However, of the ice-breeding phocids, four species that breed on land-fast ice (Caspian, Baikal, ringed and Weddell) weaned on average at 48 days; the data for the Baikal seal indicated 68 days. Pack-ice species weaned on average at 20 days, but if the hooded seal, which weaned at 4 days (Bowen et al., 1985), is excluded the average for pack-ice seals is 22 days. Shaughnessy and Kerry (1989) estimated that weaning occurred at 17 days of age for the crabeater seal.

The accurate timing of the implantation period, presented earlier, provided the opportunity to attempt to fit a chronology to the other related events in the development of the embryo and fetus. Taking the duration of the implantation period as a ‘template’ for the average and range of the other main events in the annual cycle of the female, it was now possible to fit averages and ranges of dates defining births, weaning and conception, using observations reported in the literature supplemented with information summarized in the present study.

In conclusion, the pupping season for crabeater seals is estimated to be from late September to early November, with a mean date of birth of 15 October. Referring to the implantation period, and averaging dates from length and weight, gives a mean date of implantation of 24 January, with 95% confidence limits from 7 January to 10 February, or ± 17 days. If the preimplantation period is the same in all individuals, 95% of births are expected to occur between 28 September and 1 November, and assuming a lactation period of 17 days, the mean date of weaning is expected to be 31 October ± about 17 days. The mean date of ovulation and conception (weaning date plus 4 days) is expected to be 4 November ± about 17 days. Taking this argument further, the period when observers might expect to see family groups on the floes is from late September to mid-November, and male–female groups should be seen from about the beginning of October to approximately 20 November.

When actual observations of births, lactation, weaning and conception are compared with the predicted periods for the presence of seals in these stages, the predicted periods are in quite close agreement with observation. This analysis also indicates that the chronology of the breeding season does not vary greatly over the (circumpolar) geographical range of the species, except for a few anomalous records (Racovitza, 1900; Wilson, 1907). This finding is in contrast to phocid seal species that are tied to land or fast ice, such as elephant and Weddell seals, where there is a latitudinal spread in pupping seasons (Laws, 1960; Kooyman, 1981).

Finally, for the crabeater seal the following were estimated (i) the total duration of pregnancy, from conception to birth, is 344 days (11.3 months); (ii) the duration of embryonic diapause is 81 days (2.7 months); and (iii) the duration of active gestation (implantation to birth) is 264 days (8.7 months).

The embryo collection field-work depended greatly on the collaboration of the ship’s masters, Captains J. M. Cole, E. M. S. Phelps (also as Chief Officer) and T. Woodfield; and on Chief Officers M. L. Shakesby and A. Baker, who conducted the sealing operations and helped with the biological sampling. The authors would also like to thank many members of the British Antarctic Survey who took part in the field operations. It is not possible to mention all of them by name, but special thanks are expressed to B. Bostelman, I. Everson, G. Maxwell and the late M. G. White. The authors are grateful to C. Ricketts and K. Reid for advice on statistical procedures.

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