INDIVIDUAL VARIATION IN THE DURATION OF PREGNANCY AND BIRTH DATE IN ANTARCTIC FUR SEALS: THE ROLE OF ENVIRONMENT, AGE, AND SEX OF FETUS

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The duration of 506 pregnancies in Antarctic fur seals (*Arctocephalus gazella*) was measured 1983–1993. On average, pregnancy lasted 359 days, with a range of 340-390 days, representing 20% of the period of post-implantation fetal growth. Pregnancy was longest and birth dates latest in years associated with reduced availability of food. Sex of fetus and birth mass had no effect on the duration of pregnancy or date of birth. However, dates of parturition tended to be consistent within individuals.

Key words: Pinnipedia, pregnancy, birth date, Antarctica

The duration of pregnancy in mammals is remakably consistent within species (Frazer and Huggett, 1974) and would appear to have been highly conserved through natural selection. In cross-species comparisons, there is a strong allometric relationship between maternal body mass and duration of pregnancy, the exponents of which differ between mammals having altricial and those having precocial young (Martin and MacLarnon, 1985). Within species, the fetal growth rate and the duration of pregnancy appear to be resistant to adjustments resulting from environmental fluctuations, although minor effects of maternal nutrition, temperature, litter size, and photoperiod have been found in several species (Racey, 1981). Heterothermic bats show particularly large variation in the duration of pregnancy in relation to temperature (Racey and Swift, 1981). Delayed implantation, rather than varying the rate of fetal growth or the duration of the active growth phase of pregnancy, has been adopted by a wide range of mammals (Renfree and Calaby, 1981), including many carnivores (Martinet et al., 1981; Mead, 1981), as a means of altering the duration of pregnancy. Among the pinnipeds, delayed implantation is probably the means by which the

duration of pregnancy is adjusted to allow mating to occur at a postpartum estrus while maintaining annual reproduction (Boyd, 1991a).

Although most pinnipeds have highly synchronized annual reproduction (Bigg, 1984; Trites, 1992), detailed examination shows that there is interannual variation in the mean date of parturition, which could be attributed to variations in environmental conditions and, to a lesser extent, to ages of adult females in the population (Duck, 1990; Lunn and Boyd, 1993a). Photoperiod at the time of implantation is probably the major factor timing reproductive cycles of pinnipeds (Temte, 1985, 1991, 1994; Temte and Temte, 1993), but interannual changes in the timing of births may also result from variations in environmental conditions that affect body condition at the time of implantation (Boyd, 1984). In some species, nutritional conditions may be more important in determining the timing of breeding cycles than is photoperiod (Stewart et al., 1989).

Among wild mammals, it often is difficult to measure the duration of pregnancy in individuals, either because individuals cannot be followed over protracted periods, or because it is difficult to obtain accurate

measurements of the dates of fertilization or parturition. Moreover, among pinnipeds, studies of pregnancy mainly have involved analyses of cross-sectional data from population samples taken at different times of the year (Boyd, 1984; Stewart et al., 1989; Trites, 1991). There are no previous longitudinal studies of pregnancy in wild pinnipeds. During a 10-year demographic study of Antarctic fur seals (*Arctocephalus gazella*), it has been possible to measure the duration of pregnancy in individuals. This made it possible to test the hypothesis that variation in the duration of pregnancy and the timing of parturition could be attributed to the effects of environmental conditions, age, the timing of fertilization, or individual identity.

MATERIALS AND METHODS

The study was conducted at Bird Island, (54°00′S, 38°02′W), which has been a main focal point for the expanding population of fur seals at South Georgia. Adult female fur seals, which had been tagged (Dalton Jumbo Rototags, Dalton Supplies Limited, Henley-on-Thames, UK) in previous years either as breeding adults or as young within 6 weeks of birth, were observed as present or absent from a specific study beach during each Antarctic summer from 1983–1984 to 1993–1994. Females returned to this beach during November and December to give birth and to mate, on average, 6 days after parturition (Boyd, 1991*b*; Lunn and Boyd, 1993*b*). The date of parturition was recorded for each marked female (*n* of 50–250, depending on the year). Each pup was captured 2–12 h after birth and the mass (± 0.05 kg) was measured and sex of the pup determined. Ages of adult females captured on the study beach were determined from postcanine teeth taken from the seals, usually at the time of first capture, but occasionally several years after first capture (Arnbom et al., 1992; Boyd et al., 1990). Calendar year was defined as the year in which the active fetal growth-phase of gestation occurred.

It was not possible to observe the timing of estrus in all the study animals, but estrus usually occurs 5–7 days postpartum (Boyd, 1991*b*; Lunn and Boyd, 1993*b*) and a second estrus has never been observed in Antarctic fur seals, so the time of fertilization was set in all individuals as 6 days postpartum. Multiple linear regression was used to investigate the effects of age, year, date of conception, sex of young, and birth mass on the duration of pregnancy and birth date, using the methods described by Brown and Rothery (1993). Student's *t*-test was used to compare sample means, and differences were considered significant when $P \leq 0.05$.

When considering the influence of environmental variation on duration of pregnancy, two types of years were identified; those apparently having normal availability of prey, and those with reduced availability of prey, based upon data from multispecies monitoring studies carried out in parallel with the current study at Bird Island (Croxall et al., 1988). These studies, together with information about distribution and abundance of krill (Heywood et al., 1985; Priddle et al., 1988), and from fisheries (Kock et al., 1994), showed that 1983–1984 and 1990–1991 were unusual because, among several species of seabirds that relied upon krill for food, there was low hatching and fledging success and abundance of food was reduced. Among the fur seals, the time spent foraging by mothers between returning ashore to suckle their young unusually was long (Lunn and Boyd 1993*a*), growth rates of young were reduced (Lunn et al., 1993), and there also was evidence from records of diving behavior in lactating females that fur seals increased their foraging effort in these years, probably in response to a change in distribution or abundance of prey (Boyd et al., 1994).

RESULTS

The duration, and associated birth dates, of 506 pregnancies were observed involving 248 female and 256 male fetuses, with two in which the sex of the fetus was not recorded. There was no significant difference between the duration of pregnancy or birth date in relation to sex of offspring, although females were significantly lighter than males at birth (Table 1). The standard deviation of the duration of pregnancy was significantly less for male than female fetuses ($\chi^2 = 5.126$, $P < 0.05$) and significantly less for birth mass in males than females ($\chi^2 = 14.5$, $P < 0.001$). Combining data on the duration of pregnancy for the two sexes showed that, on average, the du-

TABLE 1.—*Comparison between the duration of pregnancy, date of birth, and birth mass for male and female fetuses. Birth date is expressed as days after 31 October.*

	Male fetuses			Female fetuses				
	n	Mean	*SD*	*n*	Mean	*SD*	*t*	*P*
Duration (days)	326	358.04	6.38	316	358.21	7.10	0.319	>0.05
Birth date	326	35.94	8.56	316	37.06	8.19	1.693	>0.05
Birth mass (kg)	326	5.64	0.75	316	4.90	0.94	10.746	<0.001

ration of pregnancy plus a 6-day postpartum estrous cycle was not significantly different from 365 days, but the range of durations was 340–390 days (Fig. 1). There was a significant positive correlation between duration of pregnancy and birth date ($r = 0.384$, $P < 0.001$). There was no significant difference between the birth date of females that had been pregnant in the previous year and those that had missed a
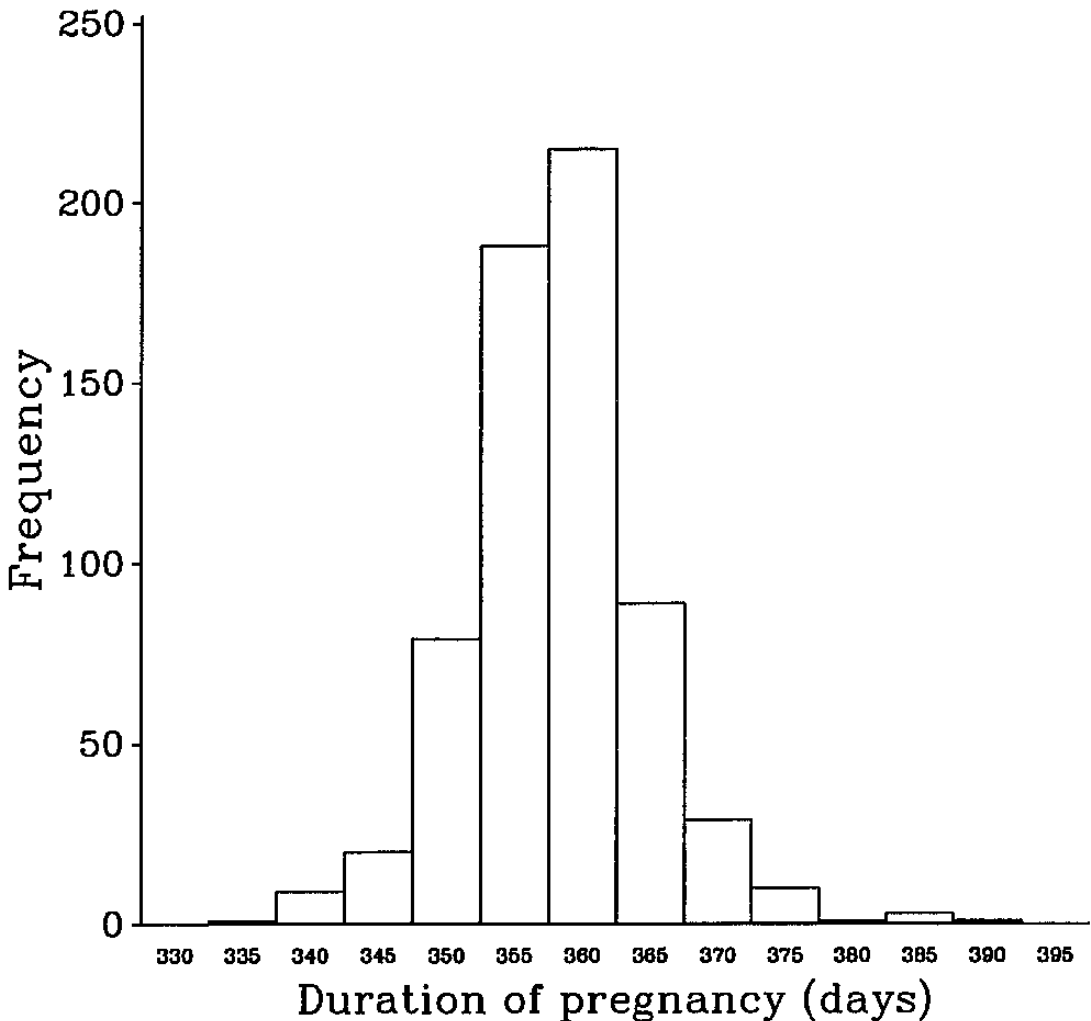

FIG. 1.—Duration of pregnancy in Antarctic fur seals.

pregnancy in the previous year (paired *t*-test within individuals, $t = 0.84$, $P > 0.4$).

The variability in the birth dates of male fetuses was significantly greater than the variability of the duration of pregnancy ($\chi^2 = 19.7$, $P < 0.001$), but this was not the case for females ($\chi^2 = 3.8$, $P > 0.05$). Even after accounting for differences in the birth mass of young due to sex, there was significant variation in birth mass between calendar years ($F_{9,635} = 9.03$, $P < 0.001$), although there was no evidence of a trend in birth mass through time.

Multiple-regression analysis showed that duration of pregnancy was not affected significantly by the age of the mother, sex of the young, or the birth mass of the young, but there was a significant effect of calendar year, which accounted for 19% of the variation in duration of pregnancy, and date of conception, which accounted for 16% of variation in duration of pregnancy (Table 2). Date of conception was negatively related to duration of pregnancy (Table 2). When combined, calendar year and date of conception accounted for 32% of variation in duration of pregnancy. Years in which pregnancy was longest corresponded with those in which food reductions had been observed (Fig. 2). Pregnancy also was longer than average in 1987, when unusually cold water dominated the shelf zone at South Georgia up to the time of breeding (Duck, 1990).

To examine the possibility that duration of pregnancy in young and old females was different from the duration in middle-aged females, age was entered into the model as a quadratic term. However, this made no significant difference to the fit obtained, and, therefore, age was discounted as a variable influencing duration of pregnancy. In addition, there was no significant difference in the fit of the model when interaction terms were used, except for the interaction between the effects of birth mass and date of conception on duration of pregnancy. In this instance, the variance in duration of pregnancy explained by these two variables

declined from 16 (Table 2) to 11% as a result of entering them as interacting terms instead of independently. This suggests that a small negative interaction existed between these two variables in terms of their effect on duration of pregnancy.

Also in a multiple-regression analysis, birth date ($n = 645$) was negatively related to age, showing that old female fur seals tended to give birth earlier than young females (Table 3), although this effect disappeared when date of conception was included as a variable in the model. However, the effect of age remained when variation due to calendar year, which accounted for 14% of variation in birth date, was taken into consideration (Table 3). Date of conception and birth date were strongly correlated (Table 3), with date of conception explaining 46% of the variation in birth date. There was no additional effect of age entered as a quadratic term in the model, suggesting that birth date was related linearly to age. There was a significant negative interaction between age and date of conception, which meant that, in models in which these terms were entered with interactions, the variance explained by the model declined to 2% from 47% (Table 3) when the terms were entered without interaction. A similar, although less profound, negative interaction occurred between birth mass and date of conception, causing the variance explained by the model to decline from 46%, when the terms were entered without interaction, to 30% when the terms were entered with interaction.

Variation in birth date was examined at the level of individuals for which there were more than four records of birth date and duration of pregnancy and showed that, whereas, there was no variation among individuals in the duration of pregnancy (analysis of variance, $F_{21,102} = 0.28$, $P > 0.05$), there was a tendency for individuals to give birth at particular times (analysis of variance, $F_{21,102} = 11.20$, $P < 0.001$; Fig. 3). In the reduced model involving only individuals with more than four annual cycles

TABLE 2.—*Multiple-regression analysis relating duration of pregnancy to maternal age, calendar year, date of conception, sex of fetus, and birth mass. Calendar year and sex of pup were entered into the models as factors and maternal age, date of conception, and birth mass were entered into the models as variables. Degrees of freedom are shown in parentheses;* *** = *factor significant at* P < 0.001, −(***) = *variable significant at* P < 0.001 *and negatively related to pregnancy duration,* + = *variable significant at* P < 0.05 *and positively related to pregnancy duration, and ns* = *not significant. Also given is the deviance explained by the model. Sample size is 504.*

| | | Factors or variables in model | | | | | | |
Model	n	Age (1)	Year (10)	Sex of pup (1)	Date of conception (10)	Birth mass (1)	R^2 (%)	Deviance
1	1	ns					0.3	46.7
2	1		***				18.8	37.2
3	1			ns			0.0	45.3
4	1				−(***)		16.2	45.4
5	1					ns	0.1	37.9
6	2	+	***				20.0	38.1
7	2	ns		ns			0.4	46.8
8	2	ns				ns	0.5	46.9
9	2	ns			−(***)		15.4	39.7
10	2		***	ns			18.8	37.3
11	2		***			ns	19.4	37.2
12	2		***		−(***)		31.9	31.3
13	2			ns		ns	0.1	45.5
14	2			ns	−(***)		16.4	38.0
15	2				−(***)	ns	16.0	38.2
16	3	+	***	ns			20.1	38.2
17	3	ns	***			ns	20.7	38.0
18	3	ns	***		−(***)		31.7	32.6
19	3	ns		ns		ns	0.5	47.0
20	3	ns		ns	−(***)		15.5	39.8
21	3	ns			−(***)	ns	15.3	40.0
22	3		***	ns		ns	19.5	37.2
23	3		***	ns	−(***)		31.9	31.4
24	3		***		−(***)	ns	32.1	31.3
25	3			ns	−(***)	ns	16.1	38.3
26	4	ns	***	ns		ns	20.8	38.1
27	4	ns	***	ns	−(***)		31.7	32.7
28	4	ns	***		−(***)	ns	32.2	32.6
29	4	ns		ns	−(***)	ns	15.4	40.1
30	4		***	ns	−(***)	ns	32.4	31.3
31	5	ns	***	ns	−(***)	ns	32.4	32.5

recorded, 80% of variation in birth date was explained by individual identity, calendar year, and date of conception. There was no tendency for parturition to occur earlier as individuals aged.

DISCUSSION

This study has shown that the duration of pregnancy and date of parturition in Antarctic fur seals varies among years, and that this is probably a response to changing environmental conditions. Neither the duration of pregnancy nor date of parturition were influenced by sex of fetus or the age of the mother, at least where sequential observations of individuals were concerned. Moreover, birth date, but not the duration of pregnancy, tended to be consistent for individual females.
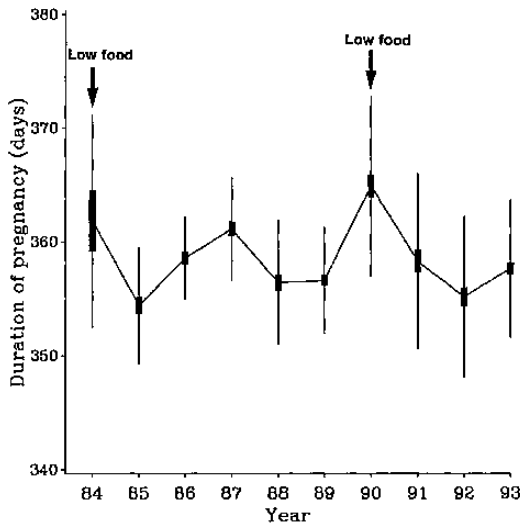
The multiple-linear regressions used in

FIG. 2.—Mean duration of pregnancy in relation to year. Bars show $\bar{X} \pm 1$ *SE*, vertical lines show ± 1 *SD* in relation to year. Arrows show years of low availability of food.

this study assumed that observations were independent. Although this assumption was violated in some analyses because there were repeated observations of the same individuals, the potential effects will have been to produce conservative results. For example, the effect of age on date of parturition may be greater than observed in a comparison using a true cross-section of the population. This is because the effect of individuals giving birth during a narrow range of dates will have artificially reduced the variability. However, because identity of individuals had no effect on duration of pregnancy, the assumption of independence is more easily justified in models where duration of pregnancy was the dependent variable.

How mammals maintain a consistent annual cycle of reproduction has been the subject of intensive study (Bronson, 1988; Lincoln and Short, 1980; Nicholls et al., 1988). Although photoperiod is the common factor controlling the timing of reproduction in many higher vertebrates (Follett, 1982), including seals (Temte, 1994), variability in the timing of births can occur because of

less predictable environmental factors, such as availability of food, and, as suggested by the results of this study, by individual variation in the response to environmental cues. Although the mean duration of pregnancy, together with the 6 days of the postpartum estrous cycle, was not significantly different from 1 year in length, there was a range of 50 days in the potential duration of pregnancy. This represents 13% of the total duration of pregnancy, but is 20% of the duration of the post-implantation phase of pregnancy.

Duration of pregnancy increased in years associated with low availability of food, and this corresponded with later births. The lack of any trend in birth date or duration of pregnancy with time showed that years in which pregnancy was long and, by implication, births were delayed, were followed by years in which pregnancy was short, thus preserving the average birth interval as 365 days. The timing of the postpartum estrus is fixed by parturition (Boyd, 1991*b*), and observations suggest that nonpregnant females also mate close to the peak time for postpartum matings; this suggests that either growth rates of fetuses are being adjusted, or the timing of implantation is varying to preserve the 365-day reproductive cycle. This is supported by the result showing that date of conception was negatively related to duration of pregnancy (Table 2).

The most probable explanation for these observations is that photoperiod is responsible for inducing implantation and, in the Antarctic fur seal, this is likely to occur close to the autumnal equinox (Boyd, 1991*a*, 1991*b*). This appears to be true in several other pinnipeds (Temte, 1991, 1994), including the closely related northern fur seal (*Callorhinus ursinus*—Temte, 1985). During periods of low abundance of food, it appears either that implantation is delayed beyond the normal time, or there is a reduction in the growth rate of fetuses. It is possible that adjustments of both the timing of implantation and growth rate of fe-

TABLE 3.—*Multiple-regression analysis relating birth date to maternal age, calendar year, sex of fetus, date of conception, and birth mass. Calendar year and sex of pup were entered into the models as factors and maternal age, date of conception, and birth mass were entered into the models as variables. Degrees of freedom are shown in parentheses; *** = factor significant at* $P < 0.001$, * *= factor significant at* $P < 0.05$, −(***) *= variable significant at* $P < 0.001$ *and negatively related to date of birth;* −(*) *= variable significant at* $P < 0.05$ *and negatively related to date of birth,* +++ *= variable significant at* $P < 0.001$ *and positively related to date of birth,* + *= variable significant at* $P < 0.05$ *and positively related to date of birth, and ns = not significant. Also given is the deviance explained by the model. Sample size is 504.*

		Factors or variables in model						
Model	n	Age (1)	Year (10)	Sex of pup (1)	Date of conception (10)	Birth mass (1)	R^2 (%)	Deviance
1	1	−(***)					7.9	69.7
2	1		***				13.7	61.6
3	1			ns			0.8	70.0
4	1				+++		45.6	70.8
5	1					ns	0.0	38.3
6	2	−(***)	***				21.3	60.5
7	2	−(***)		ns			8.6	69.5
8	2	−(***)				ns	7.9	70.2
9	2	−(*)			+++		47.1	40.1
10	2		***	ns			14.2	61.4
11	2		***			ns	13.6	62.0
12	2		***		+++		56.2	31.3
13	2			ns		ns	0.8	70.5
14	2			ns	+++		45.7	38.4
15	2				+++	ns	45.5	38.7
16	3	−(***)	***	ns			21.7	60.5
17	3	−(***)	***			ns	21.5	60.8
18	3	ns	***		+++		57.7	32.6
19	3	−(***)		*		ns	8.7	69.7
20	3	−(*)		ns	+++		47.2	40.2
21	3	−(*)			+++	ns	47.0	40.5
22	3		***	ns		ns	14.3	61.8
23	3		***	ns	+++		56.3	31.4
24	3		***		+++	ns	56.5	31.3
25	3			ns	+++	ns	45.6	38.8
26	4	−(***)	***	*		+	22.3	60.3
27	4	ns	***	ns	+++		57.7	32.7
28	4	ns	***		+++	ns	58.0	32.6
29	4	−(*)		ns	+++	ns	47.0	40.1
30	4		***	ns	+++	ns	56.6	31.3
31	5	ns	***	ns	+++	ns	58.2	32.5

tuses occur, depending upon the stage of the reproductive cycle when nutritional stress occurs. The number of young born is reduced in years following those where births were late on average (Lunn and Boyd, 1993*a*), and this supports the view that nutritional stress both alters the timing of births and reduces the probability of fe-

males conceiving and carrying a fetus to term. Based on evidence from northern fur seals (Trites, 1991), the nutritional condition of mothers can influence growth rate of fetuses. The lower variability in the duration of pregnancy for male than for female fetuses suggests that either the growth rates of female fetuses are more variable
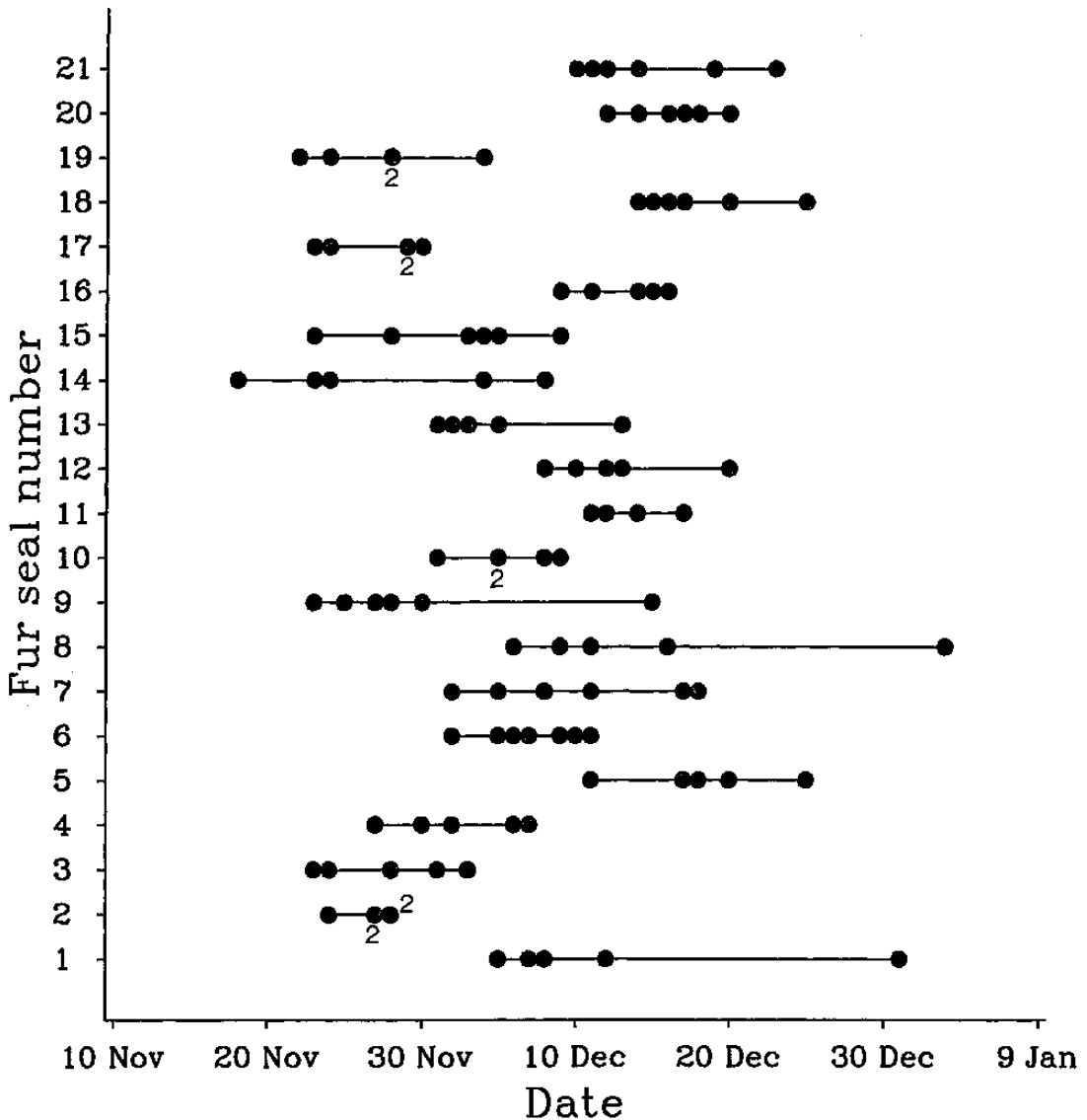
FIG. 3.—The dates of parturition in individual Antarctic fur seals. Only individuals for which more than four pregnancies and births had been recorded were included. Numerals on the graph indicate two births on the same date.

than those of males or that the timing of implantation was more variable. The case for a more variable growth rate for female fetuses was supported by the more variable birth mass for females than males.

In the reduced model, up to 80% of variation in the birth date could be explained by the combination of calendar year, date of conception, and individual indentity. The

dates of parturition for individual mothers covered a significantly narrower range than for the population as a whole. Thus, some females tended to give birth consistently early in the season, while others gave birth consistently later (Fig. 3). Lunn and Boyd (1993*b*) found that young females, especially those breeding for the first time, tended to give birth later in the birth season, and

this result is reflected in the negative relationship between age and date of birth (Table 2). However, this effect was not significant in a multiple-regression analysis when date of conception was included in models, because date of conception was itself influenced by age. Age on its own explained only 8% of the variation in birth date, but was not a significant factor when considered at the level of individuals. This suggests that the apparent effect of age on birth date may result from females that tend to breed late in the breeding season having lower survival. This would have resulted in the tendency for them to be excluded from the reduced multiple-regression model, because individuals that bred fewer than five times were excluded.

In conclusion, this study has shown that variation in the duration of pregnancy is both a response to environmental variations, where pregnancy is extended in years of low availability of food, and a mechanism regulating the reproductive cycle to last 1 year. It also has shown that variation in birth date was caused partly by a tendency for individuals to give birth at specific times of the year, indicating that there was a range of responses to the environmental factor (probably photoperiod), which is responsible for the timing and synchronization of reproductive cycles. Responsiveness to an annual environmental cue may be genetically entrained, as indicated by studies of wild rodents (Desjardins et al., 1986). In this case, a diversity of response within the population, as suggested by the individual variation shown in Fig. 3, would result in rapid adaptation through natural selection of the proximate cue timing reproduction during a systematic temporal shift in environmental conditions. Such a shift in conditions would have an important influence on reproductive success, and could include, e.g., the climate during the period when young are reared (Trites and Antonelis, 1994). This may explain the evolution of some of the observations of clinal variation in the timing of reproduction in several species of pinnipeds (Boyd, 1991a; Temte et al., 1991), because, judging from the individual variation existing within the single population in this study, such clinal trends could develop rapidly through natural selection.

ACKNOWLEDGMENTS

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