Influences on fecundity in Australian fur seals (Arctocephalus pusillus doriferus)

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Recovery of the Australian fur seal (*Arctocephalus pusillus doriferus*) population has been slower than that of other fur seals, perhaps due to nutritional constraints on fecundity. However, the population doubled in recent decades, suggesting that reproductive rates may have changed. Pregnancy rates and birthrates were estimated and the influences of maternal age, size, condition, and lactation status were investigated over 3 consecutive breeding seasons (2003–2005). Mid-gestation pregnancy rate, estimated from plasma progesterone concentrations, was $84\% \pm 3\%$ (mean $\pm$ *SE*) and was negatively influenced only by age ($P < 0.001$). Birthrate, estimated from observations of females with newborn offspring during the breeding season, was $53\% \pm 3\%$ (mean $\pm$ *SE*) and was influenced negatively by lactation status ($P = 0.035$). The difference between pregnancy rates and birthrates suggests that a high degree of late-gestation abortion occurs, especially in younger females. Lactation status was not influenced by any variables, and the high rate ($86\% \pm 2\%$; mean $\pm$ *SE*) suggests that many offspring are suckled beyond the typical weaning period. Although relationships between reproductive rates and body condition were not found, the results are consistent with a nutritional stress hypothesis. The recent increase in population growth is not due to increased fecundity, which remains low compared to other otariids. Paradoxically, high pregnancy rates were observed in young females (3 years), suggesting that rapid maturity is adaptive for benthic foragers. DOI: 10.1644/08-MAMM-A-377.1.

Key words: Australian fur seal, birth, fecundity, influences, otariid, pinniped, pregnancy, progesterone, rates, reproduction

Fecundity and survival control the dynamics of populations (Caughley 1980) and, in most mammals, these parameters are influenced by the balance between energy intake and expenditure (Bronson 1985). Survival requires individuals to gather sufficient energy to support growth and metabolism, whereas fecundity requires females to gather additional resources for the support of gestation and lactation (Widdowson 1981). Accordingly, large mothers, or those with substantial energy reserves, can more readily devote energy toward reproduction than can small mothers or those in poor condition (Bronson 1985). Because females require a period of growth to reach reproductive size and then eventually senesce, fecundity is also age-dependent (Clutton-Brock 1988). Reproducing when nutritionally stressed poses risks to the survival of a female and, therefore, is usually avoided by mechanisms of infertility, abortion of gestation, or abandonment of suckling offspring (Bronson 1989). These mechanisms, operating within environmental and life-history constraints, form adaptive reproductive strategies (Clutton-Brock 1988).

In the family Otariidae (fur seals and sea lions) reproduction is characterized by the production of a single offspring during a synchronized annual breeding season (Atkinson 1997). Reproductive synchrony is maintained by postpartum mating and a period of embryonic diapause between fertilization and active gestation (Boyd 1991b). In high-latitude species offspring are suckled for the duration of embryonic diapause and are weaned as active gestation begins (Boyd 1991b). In contrast, temperate-latitude species suckle offspring for most of the year, and weaning occurs <2 months before the birth of the next offspring (Boyd 1991b). Thus, lactation and gestation occur concurrently, and the energetic demands of the 2 processes are additive. Furthermore, females continually return to a central place (the breeding colony) to suckle their offspring, which limits their foraging range. Reproduction in temperate-latitude otariid is therefore more energetically

expensive than that of other pinnipeds (Costa 1993). A consequence of the annual breeding cycle is that resource availability during the most energetically expensive phase of reproduction, the 3rd trimester of gestation (Trites 1991), is impossible to predict at fertilization, some 10–12 months earlier. To maximize fitness within an unpredictable environment, otariid fertility rates are initially close to 100% and reproductive failures may occur later in the cycle as energy demands mount (Guinet et al. 1998; McKenzie et al. 2005; Pitcher et al. 1998).

The Australian fur seal (*Arctocephalus pusillus doriferus*) is a temperate-latitude species breeding in Bass Strait (Kirkwood et al. 2005), a continental shelf area of low primary productivity between the Australian mainland and Tasmania (Gibbs 1992). Both the Australian fur seal and the conspecific Cape fur seal (*A. p. pusillus*) were overexploited severely during the commercial sealing era (Bonner 1994) but have since been largely protected (Warneke 1975; Wickens and York 1997). The Cape fur seal population forages in the nutrient-rich upwellings of the Benguela Current and recovered rapidly to a size of approximately 2 million individuals (Wickens and York 1997). In contrast, recovery of the Australian fur seal population has been slower and now numbers approximately 90,000 individuals (Kirkwood et al. 2005). The divergent recovery rates and population sizes may be influenced by differing levels of energy availability and subsequent rates of fecundity (Warneke and Shaughnessy 1985). Australian fur seals produce fewer offspring in years when the mean body condition of adult females is low (Gibbens and Arnould 2009) and have the lowest mass-specific rate of growth among offspring of any otariid (Arnould and Hindell 2002). Hence, although some evidence of nutritional constraint on fecundity exists, actual reproductive rates and the maternal characteristics that influence them are unknown. Therefore, this study aimed to determine pregnancy rates and birthrates in Australian fur seals and investigated the influences of maternal age, body size, body condition, and lactation status on these rates.

MATERIALS AND METHODS

Field procedures.—The study was conducted between 2003 and 2005 at Kanowna Island (39°10′S, 146°18′E), northern Bass Strait, the site of an Australian fur seal colony producing approximately 3,550 offspring annually (Gibbens and Arnould 2009). The colony is dispersed around the island but is concentrated in 2 elevated main breeding areas comprising >75% of the population. Captures were conducted in the main breeding areas from winter to mid-spring (23 June–7 October). All methods pertaining to live animal use were in accordance with guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by ethics committees at the University of Melbourne and Deakin University.

Adult females were selected at random and captured using a modified hoop net (Fuhrman Diversified, Seabrook, Texas). An intramuscular dose of Midazolam (0.15 mg/kg, Hypnovel;

Roche Products Pty. Ltd., Dee Why, New South Wales, Australia) was administered to reduce handling stress and as induction to gas anesthesia (isoflurane—Gales and Mattlin 1998). Seals were transferred to a flat platform, placed on their ventral surface, weighed using a spring scale (200 ± 0.5 kg; Salter, Peterborough, United Kingdom), and measured (± 0.5 cm) for standard length and axillary girth using a metal tape measure (Bonner and Laws 1993). Individually numbered plastic tags (Super Tags; Dalton I.D. Systems Ltd., Henley-on-Thames, United Kingdom) were placed in the trailing edge of each foreflipper, and large numbers were bleached into the dorsal fur using commercial hair bleach. The presence of offspring was noted before capture, and females not observed with offspring were checked for lactation status by manual expression of the teats after injection of oxytocin (0.5–1.0 ml, 10 IU/ml; Heriot Agvet, Rowville, Victoria, Australia) to stimulate milk release. A blood sample was drawn into a heparinized syringe from a small vein in the rear flipper, centrifuged, and the plasma fraction separated and stored at −20°C until analysis in the laboratory for pregnancy determination. After injection of local anesthetic in the gum (10 mg lignocaine hydrochloride, Xylocaine; AustraZeneca Pty. Ltd., North Ryde, New South Wales, Australia), dental elevators were used to extract a 1st postcanine tooth from the lower jaw. The tooth was stored in 70% ethanol until analysis for aging.

During the breeding seasons marked seals in the main breeding areas of the island were observed on 4 occasions each day between the hours of 0800 and 1800 h (EDT) and on other areas of the island once daily between 1000 and 1400 h (EDT). Observations were conducted between 15 November and 15 December in each year, a period approximately 1 week later than that within which 90% of offspring are born (9 November–7 December—Gibbens and Arnould 2009). This period was optimal for resighting marked females with their newborn or yearling offspring suckling or resting alongside. Although offspring born before 15 November could have died before observation, these would have been few in number and unlikely to be a major source of bias. Only observations of females at rest were recorded because females moving through the colony often do not have their young with them (J. Gibbens, pers. obs.). However, it was possible that the offspring of some of the females were obscured or absent during observation. Therefore, to reduce error and bias, birth status was estimated only for those females for which ≥2 consistent resights were recorded (i.e., observed ≥2 times with young or ≥2 times alone). Additionally, resights were required to occur ≥2 days apart so that they were likely to have been separated by a maternal foraging trip and, therefore, represent discrete attendance events (Arnould and Hindell 2001). Females not meeting these criteria were assigned unknown birth status.

Pregnancy estimation.—Pregnancy status was determined by measuring the concentration of progesterone in plasma. High progesterone concentrations occur in pregnant females, and at around the time of implantation, also occur in
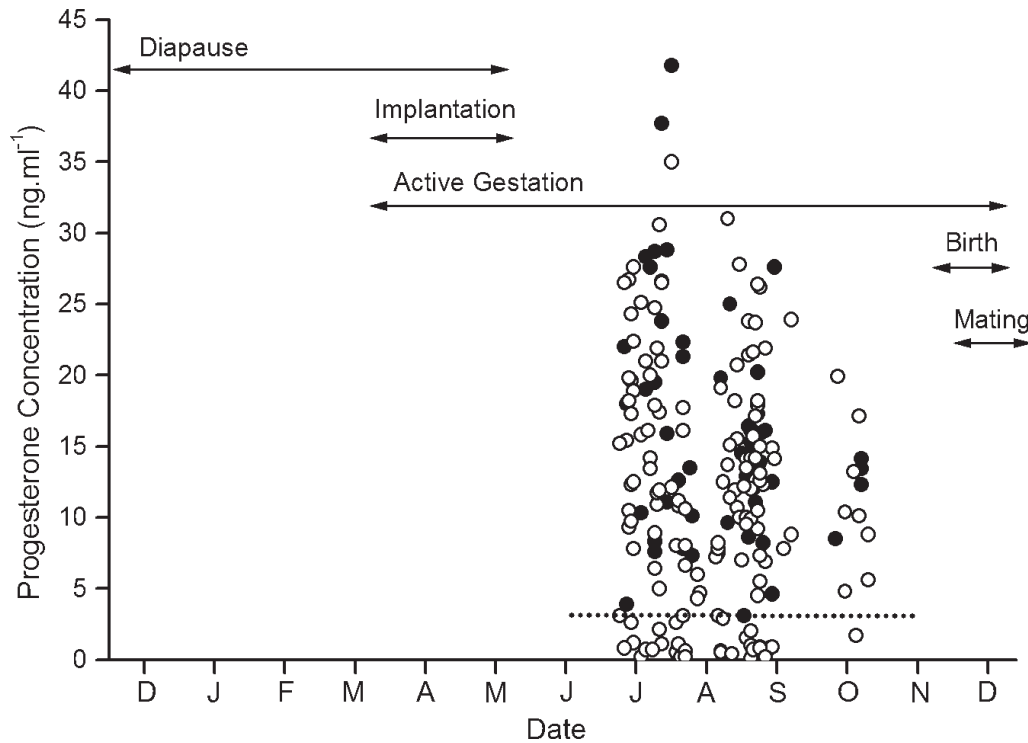
FIG. 1.—Plasma progesterone concentration (ng/ml) at sampling date for female Australian fur seals later observed with newborn offspring (closed circles) and of uncertain pregnancy status (open circles). The pregnancy classification threshold is indicated by the dotted line. Approximate phases of the reproductive cycle are indicated by arrows.

nonpregnant females, a condition termed ''pseudopregnancy'' (Boyd 1991a, 1991b; Guinet et al. 1998; McKenzie et al. 2005). Therefore, pregnancy status cannot be determined until progesterone concentrations diverge, which occurs 1.5 months postimplantation in New Zealand fur seals (*A. forsteri*—McKenzie et al. 2005). The timing of implantation has not been determined in Australian fur seals, but in Cape fur seals and other congenerics it occurs 3–5 months postfertilization (Atkinson 1997; Boyd 1991b). Fertilization occurs approximately 7 days postpartum (Arnould and Hindell 2001; Boyd 1991b), and, therefore, implantation should take place between mid-February and mid-May. In the present study sampling began 1.3 months after the end of this period (Fig. 1), so only a very small proportion of samples may have come from pseudopregnant females. Because no information exists on plasma progesterone concentrations in pregnant and nonpregnant Australian fur seals, pregnancy status was estimated based on individuals having a ''high'' or ''low'' concentration. The threshold between these states was chosen based on the distribution of progesterone concentrations in conjunction with breeding-season observations of marked females with newborn offspring (*n* = 55) that were assumed to have been pregnant when captured.

Progesterone concentrations were measured using coated-tube radioimmunoassay kits (Spectria, Progesterone RIA; Orion Diagnostica, Espoo, Finland) as described by McKenzie et al. (2005) for New Zealand fur seals. The organic component of each sample of plasma was extracted with ethyl acetate, then resuspended in water to achieve a 1:4 dilution. A 50-µl aliquot of diluted extract was added to duplicate polyclonal (rabbit) progesterone antibody-coated assay kit tubes with 500 µl of ^{125}I-progesterone and incubated for 2 h at room temperature before measurement. To provide samples of known high and low progesterone concentrations for each assay run (quality control high and low), samples were used from a female known to have given birth, and a juvenile male, respectively. The interassay coefficient of variation was 10.2% (*n* = 7 assays), and the intra-assay coefficient of variation was 7.5%.

Age determination.—Extracted teeth were rinsed in flowing water for ≥6 h to remove ethanol, then immersed in a hydrochloric acid decalcifying agent (RDO; Apex Engineering Products Corporation, Aurora, Illinois) until flexible to the touch (8–24 h). Decalcified teeth were rinsed in deionized water for ≥6 h, embedded in a mounting compound, then ≥6 sections were cut on a microtome at −10°C to a thickness of 25 µm. After staining with hemotoxylin and fixing with a solution of 5% ammonia, the 6 sections with best definition were mounted on glass slides using a mounting compound (Distyrene, plasticizer, and xylene [DPX]) and glass coverslip. Sections were viewed with transmitted light on a stereomicroscope (4–10×) with a rotatable polarizing filter. Each pair of alternating dark and light bands in the tooth cementum indicate 1 year of growth in the species (Arnould et al. 2003) and bands were counted to determine age at the previous birthday (median birth date 23 November—Gibbens and Arnould 2009). Five blind readings were made for each tooth and the median value was used as the final age. A single

person performed all readings to reduce interreader variability and because accuracy increases with reader experience (McCann 1993).

Definition of variables and statistical analyses.—Body size was defined as standard length. Body condition was estimated by regressing mass against body size with a power function, and using the residuals as a body condition index. This type of body condition index has been shown to correlate with sternal blubber depth in Australian fur seals (Arnould and Warneke 2002). Measures of body mass for pregnant female seals were corrected by subtracting the estimated mass of the fetus and placenta. Fetal mass was estimated from capture date using fetal growth curves derived from a previous study ($n = 67$—Arnould and Warneke 2002), with placental mass assumed to be 10% of fetal mass (Boyd and McCann 1989).

The likelihoods of being classified as pregnant, lactating, resighted, and (for those that were resighted) having given birth were each modeled using binary logistic regression (Afifi et al. 2004). Capture date, age, standard length, body condition index, pregnancy status, and lactation status were used as explanatory variables, except pregnancy status was not included in the birth status model. Mass was not included in any models because of its strong correlations with age (Pearson $r = 0.71$) and standard length ($r = 0.86$—Afifi et al. 2004), and because exploratory analysis indicated that it was not a significant predictor of any status. A backward stepwise elimination method was used, where all variables were entered in the 1st step of the model and the least significant variable was eliminated from the next step (if $P > 0.1$). Results are presented for each variable included in the final step. Analyses were performed with statistical software SPSS 16.0 (SPSS, Chicago, Illinois).

Means are presented ± 1 *SE* and compared using unequal variance *t*-tests (Ruxton 2006) or, where sample sizes were low, using Mann–Whitney *U*-tests (Walpole and Myers 1985). Statistical tests were considered significant if $P < 0.05$.

RESULTS

The mean age of captured females was 7.9 ± 0.3 years (range: 3–20 years, $n = 207$), and 75% of females were aged ≤ 10 years. Mean female standard length was 153.3 ± 0.6 cm (range: 131.0–174.0 cm) and body mass was 77.5 ± 0.9 kg (range: 45.0–110.5 kg). Growth in length follows a von Bertalanffy function with 95% of asymptotic length attained at 5 years of age (Arnould and Warneke 2002); however, the present study only measured adults of 3+ years. This portion of the age–length relationship could be approximated with linear regression ($F_{1,206} = 168.58$, $P < 0.0001$; $r^2 = 0.43$). Age also was weakly correlated with the body condition index (linear regression: $F_{1,206} = 5.75$, $P = 0.0174$; $r^2 = 0.03$). Hence, body size and condition tended to increase over the lifetime of individual female seals. Most females were lactating (86% $\pm$ 2%), and lactation rates did not vary by year (Table 1). Logistic regression analyses indicated that none of the explanatory variables examined were useful for predicting lactation status (Table 2).

TABLE 1.—Annual reproductive rates with sample sizes in parentheses, and results of chi-square tests for interannual variation ($d.f. = 2$ in all cases).

Year	Lactation rate (n)	Pregnancy rate (n)	Birthrate (n)
2003	88% (58)	85% (58)	48% (23)
2004	82% (67)	85% (67)	64% (36)
2005	85% (82)	81% (82)	46% (35)
χ^2	1.393	0.712	2.706
P	0.498	0.700	0.258

The distribution of progesterone concentrations (Fig. 1) was analyzed by allocating each value to a 1 ng/ml class and analyzing class frequencies. The highest frequencies of occurrence were in the 0–1 ng/ml and 12–13 ng/ml classes, suggesting that these represented nonpregnant and pregnant females, respectively. The lowest frequency of occurrence was in the 5–6 ng/ml class, and the lowest progesterone concentration for a female observed with an offspring in a subsequent breeding season (and, therefore, pregnant when sampled) was 3.1 ng/ml. The threshold value used to classify females as either pregnant or nonpregnant was therefore set at 3.1 ng/ml. Females classified as nonpregnant (≤ 3.0 ng/ml) had a mean progesterone concentration of 0.99 ± 0.1 ng/ml ($n = 34$), and females classified as pregnant (≥ 3.1 ng/ml) had a mean of 15.15 ± 0.6 ng/ml ($n = 173$). Some of the variation in concentration of progesterone among pregnant females could be explained by negative relationships with age (linear regression: $F_{1,172} = 11.31$, $P = 0.0009$; $r^2 = 0.06$) and sampling date (linear regression: $F_{1,172} = 8.12$, $P = 0.0049$; $r^2 = 0.05$). Overall, 84% $\pm$ 3% of females were estimated to be pregnant, with no interannual variation in pregnancy rate (Table 1). Age was the only variable that predicted pregnancy, and younger females were more likely to be pregnant than older ones (Table 2). Age-specific pregnancy rates (Fig. 2) were higher for females between 3 and 10 years of age than for females that were 11 to 16+ years old ($U = 48$, $n_1 = 8$, $n_2 = 6$, $P = 0.0007$).

Of the 207 adult females that were captured, 68 were not resighted during the following breeding season, 45 were resighted once, and 94 were resighted ≥ 2 times (Table 3). The likelihood of being resighted ≥ 2 times was influenced by age, pregnancy status, and capture date (Table 2). Females resighted ≥ 2 times were younger by a mean of 1.6 years ($t_{204} = 3.33$, $P = 0.0005$), had a 17% higher pregnancy rate ($t_{190} = 3.38$, $P = 0.0004$), and tended to have later capture dates than other females ($t_{167} = 2.60$, $P = 0.0051$; Table 3). Age distributions of resighted females were similar between years (age $\bar{X}$, 2003: 6.7 ± 1.4 years; 2004: 7.1 ± 1.2 years; 2005: 7.2 ± 1.2 years; *t*-tests: $P > 0.05$ in all cases). Fifty-three percent (± 3%) of the females that were resighted ≥ 2 times were determined to have given birth that year. Twenty-seven adult females (29%) were observed with yearling offspring, and of these, 11 attended to both a yearling and a newborn. Adult female seals resighted with newborn offspring were less likely to have been lactating the previous winter than females without newborns (Table 2). Although age was

TABLE 2.—Binary logistic regression models of the likelihoods of lactation, pregnancy, resighting, and birth.

Model	Explanatory variables	n	χ^2	$d.f.$	P	Exp(B) (95% confidence interval)[a]
Lactation	None	207	—	—	—	—
Pregnancy	Age	207	33.074	1	<0.001	0.729 (0.646–0.823)
Resighting	Overall model	207	22.281	3	<0.001	
	Date		6.488	1	0.011	1.015 (1.003–1.026)
	Pregnancy		4.719	1	0.030	2.859 (1.108–7.375)
	Age		4.305	1	0.038	0.907 (0.828–0.995)
Birth	Lactation	94	4.447	1	0.035	0.217 (0.044–1.065)

[a] Odds ratio corresponding to 1 unit of change in the explanatory variable. Values < 1 indicate the variable has a negative influence.

significantly associated with pregnancy status, age did not influence the likelihood of birth. In addition, age-specific birthrates (Fig. 2) were not related to age (linear regression, weighted to sample size: $F_{1, 11} = 0.92$, $P = 0.357$; $r^2 = 0.087$). Estimated age-specific abortion rates (pregnancy rate minus birthrate) were significantly higher in females aged 3–10 years than in those aged 11–15 years ($U = 31$, $n_1 = 8$, $n_2 = 5$, $P = 0.008$). Assuming a 1:1 sex ratio at birth (Wickens and York 1997), the estimated fecundity rate (live female offspring per adult female per year—Caughley 1980) is 0.266.
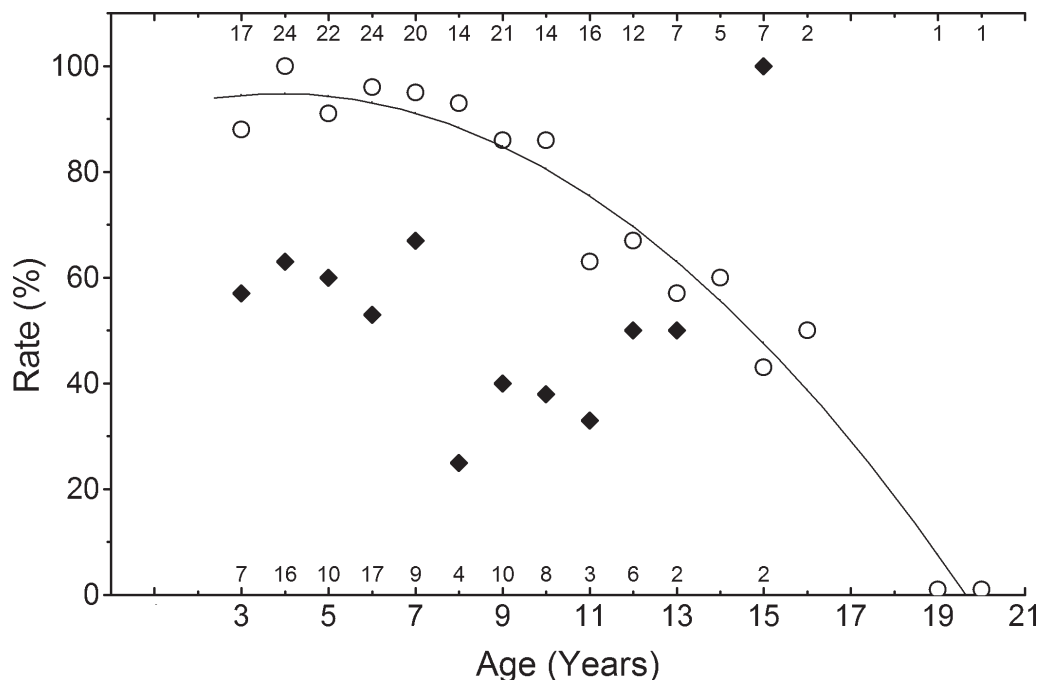
DISCUSSION

In the present study a substantial difference was observed between mid-gestation pregnancy rates and birthrates, suggesting that many pregnant Australian fur seals do not carry their fetus to full term. Mid-gestation pregnancy status was influenced by age but not by the energetic correlates of size, condition, or lactation status. Surprisingly, age had little influence on birth status. However, differences between age-specific pregnancy rates and birthrates indicated that older pregnant females were more likely to complete gestation than younger ones. Furthermore, birth status was influenced by lactation status, suggesting that the cost of provisioning existing offspring reduces the ability of pregnant females to carry their fetus to term.

Likelihood of pregnancy did not decrease with time, suggesting that few abortions occurred during the sampling period. Although some otariid studies have observed declining pregnancy rates between early and late gestation (Arnould et al. 2003; McKenzie et al. 2005; Pitcher et al. 1998), the sampling period of the present study was relatively brief and limited to mid-gestation. The relatively constant likelihood of pregnancy also suggests that the positive bias potentially caused by pseudopregnancy was low, because rates of pseudopregnancy decline rapidly in the postimplantation period (Guinet et al. 1998; McKenzie et al. 2005).

Bias also can exist if the threshold concentration of progesterone in plasma for distinguishing between pregnant and nonpregnant females (set at 3.1 ng/ml, based on our results) was incorrect. Because progesterone concentrations were influenced by age and sampling date, a single threshold

FIG. 2.—Age-specific pregnancy rates (circles) and birthrates (diamonds), with sample sizes shown on the axes. Regression equation ($F_{2,13} = 13.52$, $P < 0.001$; $r^2 = 0.96$): pregnancy rate $= -0.38\text{age}^2 + 2.88\text{age} + 89.3$.

TABLE 3.—Female characteristics according to incidence of resighting during breeding season. An asterisk (*) indicates a significant difference (*t*-tests, $P < 0.05$) between groups.

Resighting status	n	No. pregnant	Pregnancy rate (%)	No. with offspring	Birthrate (%)	Age ($\bar{X} \pm SE$)
≥2 resights	94	87	93*	50	53.2	7.1 ± 0.3*
≤1 resight	113	86	76*	—	—	8.6 ± 0.4*
All females	207	173	84	—	—	7.9 ± 0.3

value may not accurately indicate pregnancy status for all females. Females with progesterone concentrations slightly below the threshold (e.g., 1.0–3.0 ng/ml, $n = 10$, 5% of sample) or slightly above it (e.g., 3.2–5.0 ng/ml, $n = 7$, 3% of sample) could have been classified incorrectly. Nevertheless, the estimated pregnancy rate observed in our study (84%) was comparable to pregnancy rates reported for the conspecific Cape fur seal (78–79%—Butterworth et al. 1995; Guinet et al. 1998) and other fur seals for which data exist (71–86%—McKenzie et al. 2005; Wickens and York 1997).

The logistic regression model of pregnancy likelihood was not influenced by body size, condition, or lactation status, suggesting that energetic factors were not critical to maintaining pregnancy during mid-gestation. This contrasts with Cape fur seals, in which the likelihood of pregnancy during early to mid-gestation was influenced by body condition (Guinet et al. 1998). However, seasonal changes in body condition, presumably related to variation in availability of food, follow different patterns in the 2 subspecies. The body condition of Cape fur seals reaches a minimum during early to mid-gestation and then improves as the breeding season approaches (Guinet et al. 1998). In contrast, the body condition of Australian fur seals is highest during winter (when females in the present study were sampled) but declines as breeding season approaches, reaching a minimum during the 3rd trimester (Arnould and Warneke 2002) when fetal growth is greatest (Trites 1992). Therefore, pregnancy in Australian fur seals may only become condition-dependent during late gestation, as has been reported for Steller sea lions (*Eumetopias jubatus*—Pitcher et al. 1998).

Pregnancy rate was strongly age-dependent and followed the typical mammalian pattern of being higher in younger females than in older ones (Bronson 1989; Wickens and York 1997). Most (88%) 3-year-olds were pregnant, and 59% were lactating, indicating they 1st attained pregnancy at age 2 years. Pregnancy rates of younger females could have been positively biased because only those of adult appearance were selected for capture. Hence, smaller females, which are less likely to be sexually mature (Laws 1956), might have been avoided. Nevertheless, the rate of pregnancy among 3-year-olds in this study was similar to values previously reported for the species by a study not subject to this type of capture bias (Arnould et al. 2003). The high rate of pregnancy observed in 3-year-olds suggests that Australian fur seals attain sexual maturity earlier than Cape and most other fur seals, which attain it between 4 and 6 years (Butterworth et al. 1995; Dabin et al. 2004; McKenzie et al. 2007; Wickens and York 1997). Similarly divergent rates of body growth have been reported in

the fur seals, indicating that Australian fur seals grow and reach maturity relatively rapidly (Arnould and Warneke 2002). Although rapid maturity can indicate that resources are plentiful (Bengtson and Laws 1985; Pistorius et al. 2001), the low birthrate observed in the present study and the nutrient-poor nature of the environment (Gibbs 1992) suggests that this was unlikely.

Rapid maturity instead could be adaptive. In benthic foraging otariids (those that spend most foraging effort near the substrate of continental shelves) the benthos can be inaccessible to juveniles whose small bodies lack sufficient oxygen storage capability for sustained diving (Costa and Gales 2003; Fowler et al. 2006; Pitcher et al. 2005). The Australian fur seal is the only predominantly benthic foraging fur seal, and juveniles are unable to match the dive durations of adults (Arnould and Costa 2006; Arnould and Hindell 2001; Spence-Bailey et al. 2007). Consequently, juvenile Australian fur seals cannot gain nutritional independence until attaining a relatively large size. Rapid growth in a nutrient-poor environment can be achieved by a relatively high degree of maternal investment provided by extended lactation. Adult female Australian fur seals often provision offspring beyond the 10-month period typical of temperate-latitude otariids (Boyd 1991b; Hume et al. 2001), and in the present study 29% were resighted with yearling offspring (i.e., approximately 1 year old). Furthermore, their mid-gestation lactation rate was 33% higher than the birthrate, suggesting that provisioning may continue well into a 2nd year. Other otariids foraging on the benthos of nutrient-poor continental shelves, such as the Steller sea lion (Pitcher et al. 1998) and Australian sea lion (*Neophoca cinerea*—Higgins and Gass 1993), display similarly extended periods of lactation.

In the present study 53% of adult females resighted ≥2 times were observed with newborn offspring during the breeding season. However, these females had a 17% higher mid-gestation pregnancy rate than those observed once or not at all, suggesting that the actual birthrate may be lower. Conversely, offspring that die or are abandoned soon after birth may not be observed with their mothers, negatively biasing the birthrate. These 2 potential sources of bias would be conflicting and, therefore, unlikely to influence the results greatly.

Despite a low birthrate, a common indication of nutritional stress in many mammal populations (Bronson 1985), the likelihood of birth was not influenced by body condition. However, body mass was measured during mid-gestation, and mid-gestation body mass may not reflect late-gestation body mass when energetic demand is greatest and body condition is minimal (Arnould and Warneke 2002). Spontaneous abortions

can occur in females unable to maintain sufficient body condition during late gestation, and, hence, energy income (foraging) at that time could be more important than energy capital (lipid reserves) accumulated previously (Boyd 2000). In a concurrent study performed from 2003 to 2007 the mean body condition of adult females during winter was correlated with numbers of newborn offspring, earlier breeding, and oceano-graphic variables, indicating that reproductive success was influenced by environmentally mediated body condition (Gibbens and Arnould 2009). Therefore, we suggest that body mass be measured close to parturition, otherwise it may be difficult to determine how body condition influences fecundity.

Lactating females were less likely to produce offspring than were nonlactating adult females, suggesting that the energetic demands of provisioning existing young may limit resources available to the fetus. For example, some lactating otariids produce smaller offspring and have lower late-gestation pregnancy rates than do nonlactating females (Lima and Paez 1995; Pitcher et al. 1998). Because of their relatively rapid rate of growth and early age at maturity (this paper; Arnould and Warneke 2002) and the limited foraging ability of juveniles (Spence-Bailey et al. 2007), Australian fur seals and other benthic foragers may be adapted to provisioning juveniles until they are large enough to forage independently, sometimes at the expense of successful gestation.

The 31% difference we observed between rates of pregnancy and rates of birth suggested that a substantial number of pregnant females aborted their fetuses before parturition. Because the likelihood of pregnancy did not decline with sampling date, failures probably occurred after the sampling period by late-gestation abortion, stillbirths, or abandonment of newborn offspring. Aborted fetuses commonly are observed in the colonies of Australian fur seals, particularly during the 3rd trimester (J. Gibbens, pers. obs.). Similar rates of spontaneous abortion have been reported for New Zealand fur seals (35%—McKenzie et al. 2005) and Steller sea lions (40%—Pitcher et al. 1998), suggesting that pregnancy rates may not be reliable indicators of fecundity in otariid seals, except when sampling occurs very close to parturition.

Abortion was more common among younger-aged adult seals. Although birthrates were similar across all age classes, higher pregnancy rates were observed in younger seals (3–10 years; 92%) than in older seals (11+ years; 57%), suggesting that reproduction in younger seals is regulated by late-term abortion. In contrast, most older seals that were pregnant when they were captured during mid-gestation were resighted later with a newborn offspring. Fertilization rates are typically high in otariids (Guinet et al. 1998; Lunn and Boyd 1993; McKenzie et al. 2005), presumably because the availability of resources at the time of maximum energy demand is largely unpredictable (Boyd 1991b). Boyd (1991b) suggested that nutritionally stressed pinnipeds avoid repro-ductive costs by failing to implant after diapause, thereby completely avoiding gestation. However, late-gestation abor-tion has been proposed as a more common strategy in temperate-latitude otariids (McKenzie et al. 2005; Pitcher et

al. 1998). In our study the latter strategy was evident among younger females, and older ones could be more prone to reproductive failure at the time of fertilization, implantation, or early gestation. The birthrate estimated by the present study was substantially lower than birthrates reported in rapidly increasing populations of New Zealand fur seals (67–70%—Goldsworthy and Shaughnessy 1994; McKenzie 2006), subantarctic fur seals (*A. tropicalis*, 84%—Hes and Roux 1983), and Antarctic fur seals (*A. gazella*, 68%—Lunn et al. 1994; Wickens and York 1997). Instead, the birthrate in the present study was similar to birthrates reported in steady or declining populations of Australian sea lions (birthrate: 71% per 17.6 months = 48% per year—Higgins and Gass 1993) and Steller sea lions (late-gestation pregnancy rate: 55%—Pitcher et al. 1998). Although some species of fur seals have demonstrated very low birthrates during years of anomalously low food availability (e.g., McKenzie et al. 2005), we do not believe this occurred during the present study because offspring production by Australian fur seals during 2003–2005 was close to the long-term mean for censuses conducted from 1997 to 2007 at Kanowna Island (Gibbens and Arnould 2009). Therefore, the fecundity of Australian fur seals may be relatively low in general, which in turn could be the proximate factor that limited recovery of the population following the cessation of commercial sealing in the 1830s (Kirkwood et al. 2005; Ling 1999). However, during the past 2–3 decades, the Australian fur seal population has doubled in size (Kirkwood et al. 2005). Because fecundity has not changed greatly during this period (1971–1972 late-gestation pregnancy rate: 55%—Arnould et al. 2003), it is unlikely that resource availability for pregnant females was altered. Therefore, the population might not have reached density dependence and may continue to grow in the near future.

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