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REPRODUCTION OF THE ESTUARINE DOLPHIN (*SOTALIA GUIANENSIS*) ON THE COAST OF PARANÁ, SOUTHERN BRAZIL

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The estuarine dolphin (*Sotalia guianensis*) is common along most of the Brazilian coast, but little is known about its reproduction. We analyzed the gonads of 50 individuals incidentally caught in fishing nets on the coast of Paraná, southern Brazil, between 1997 and 1999. Testes of adult males were ≤31.9 cm in length and ≤11.6 cm in width and ≤3.3% of the total body mass. Relative size of testes suggests a multimale mating system with sperm competition. Females ovulate in both ovaries, although the left ovary matures earlier than the right. Males reached sexual maturity at 7 years and at body lengths estimated at 170–175 cm. Females matured at 5–8 years of age and at body lengths of 164–169 cm. The reproductive cycle was estimated at 2 years, with no marked seasonality in ovulation or timing of birth. Gestation was about 12 months, fetal growth rate was 9 cm/month, and length at birth was estimated at 92.2 cm. Females older than 25 years had senescent ovaries.

Key words: Brazil, estuarine dolphin, reproduction, *Sotalia guianensis*

The estuarine dolphin (*Sotalia guianensis*) was recently separated as a distinct species from the freshwater tucuxi (*Sotalia fluviatilis*) based on tridimensional morphometric analysis (Monteiro-Filho et al. 2002). The estuarine dolphin (vernacular name as suggested by Watson 1988) is perhaps the most common of coastal dolphins of the southwest Atlantic Ocean. It occurs from Honduras in Central America (15°58′N, 85°42′W—da Silva and Best 1996) to Santa Catarina in southern Brazil (Simões-Lopes 1988). Incidental catches of the species are reported all along the Brazilian coast (Di Beneditto et al. 1998; Rosas 2000; Siciliano 1994; Simões-Lopes and Ximenez 1990). Although total population size is unknown, the species is of conservation concern (International Union for the Conservation of Nature and Natural Resources 2000; Schouten 1992), and there is need for information on its reproduction (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, in litt.).

Reproduction of the estuarine dolphin has been studied macroscopically by Ramos (1997) and Ramos et al. (2000) on the Rio de Janeiro coast of southeastern Brazil. All other studies on reproduction of dolphins in the genus *Sotalia* have been carried out on the tucuxi (*S. fluviatilis*) in the Amazon basin (Best and da Silva 1984; Harrison and Brownell 1971). The objectives of our study were to determine both macroscopic and histological aspects of reproduction in estuarine dolphins incidentally caught in fishing nets on the coast of Paraná, southern Brazil. We investigated age and length of sexual maturation, polarity of ovulation (left and right ovarian activity), periodicity of ovulation, reproductive cycle, length and

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seasonality of birth, gestation period, and nutritional composition of milk. We compare our findings with the literature on reproduction in the tucuxi and other cetaceans.

MATERIALS AND METHODS

Routine necropsies were performed on all estuarine dolphins incidentally caught or found stranded on the beaches of the coast of Paraná, southern Brazil (25°18′–25°58′S, 48°05′–48°35′W), between 1997 and 1999. Biological and morphological characteristics, including sex, body mass, and total length (measured in a straight line in an axial projection from the tip of the beak to the central notch of the tail) were recorded for each carcass (Norris 1961). The gonads of 50 dolphins (27 males and 23 females) were collected and preserved for 24 h in a solution of 80% ethanol, 40% formalin, and glacial acetic acid in the proportions of 85:10:5. Gonads were then stored in 70% ethanol until histological preparations were made.

The testes were excised and weighed with the epididymides, and linear dimensions were recorded (length and maximum width). Dimensions are given as mean of left and right testes, and the mass is expressed as total mass of both testes with epididymides. The ovaries were excised, weighed, and measured. Lengths and widths were expressed as means of the left and right ovaries and the masses as the combined mass of both ovaries. Tissues were examined as standard histological preparations 6 μm thick, stained with hematoxylin and eosin, and Masson's trichrome. Values are presented as mean ± *SE* unless otherwise stated.

The diameters of ≥15 circular seminiferous tubules were measured on each slide at a magnification of 100× using an ocular reticle. Males were considered sexually immature if only spermatogonia and Sertoli cells were observed inside the seminiferous tubules; pubescent dolphins were those that also had primary spermatocytes and spermatids; and mature dolphins were those that had spermatozoa present inside the seminiferous tubules.

The number and dimensions (length and width) of corpora albicantia in each ovary and the presence and dimensions of any corpus luteum were recorded. Mammary glands were pressed manually to assess the presence of milk. The ovarian follicles were categorized as primordial follicle, unilaminar primary follicle, multilaminar primary follicle, secondary follicle, and Graafian follicle (Gartner and Hiatt 1994). At least 10 of each type of follicle, when present, were measured at magnifications of 40× and 100× using an ocular reticle. Females were considered sexually mature if they had ≥1 corpus albicans or corpus luteum in the ovaries. We considered females with nonatretic Graafian follicles ≥760 μm but with no signs of ovulation in the ovaries as pubescent because the mean diameter of nonatretic Graafian follicles of pubescent females was 759.9 μm.

Ages were estimated by counting the number of growth-layer groups observed in the dentine (Hohn et al. 1989). Ages of individuals <1 year old were estimated in months, using as a base the percent proportion of the mean distance between neonatal line and end of the growth-layer group of the 1st year (Rosas 2000).

The reproductive cycle was estimated by subtracting age of sexual maturation from age of the animal, and the value obtained divided by total number of ovarian scars observed in the 2 ovaries. Neonatal length was estimated by mean length of newborn individuals in the sample (Perrin and Reilly 1984).

Gestation period was estimated using 2 different methods. The Hugget and Widdas-Laws method (Perrin and Reilly 1984) assumes that fetal growth is directly related to time and occurs in 2 phases: a linear phase ($t_g - t_0$), which occurs for most of the period, and a nonlinear phase (t_0). The linear and nonlinear phases were estimated by equations presented by Kasuya (1977) for delphinids. We also used the comparative method (Perrin and Reilly 1984), which assumes a relationship between duration of gestation and size at birth.

Milk was collected from a nursing female estuarine dolphin. This animal was incidentally caught together with a young suckling female in a gillnet set for flatfish on 9 July 1999. Age of the calf was estimated at 5 months, and it had only milk in its stomach, suggesting that they were a mother-and-calf pair. The milk sample was analyzed for protein, fat, and mineral content. Protein was determined using analytical procedures of the Adolfo Lutz Institute (Instituto Adolfo Lutz 1985), and fat was determined by hydrolysis. Concentrations of most minerals (Na, K, Ca, Mg, Fe, Zn) were determined by

TABLE 1.—Dimensions and mass of testes of *S. guianensis* from the coast of Paraná, Brazil. Ratio of mass of testes to body mass is expressed as percentage of total body weight.

	Immature			Mature		
	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*
Length (cm)	7.4	1.8	12	25.5	3.5	14
Width (cm)	2.3	0.9	12	9.6	1.1	14
Mass, left + right (g)	52.3	33.5	12	2,270.0	0.9	14
Testes mass/body mass (% of body weight)	0.11	0.09	10	2.5	0.7	13

atomic absorption spectrophotometry. Phosphorus concentrations were determined by visible ultraviolet spectrophotometry.

RESULTS

Anatomical aspects of reproduction in males.—Testes of adult males measured up to 31.9 cm in length and 11.6 cm in width, reaching a testes mass–body mass ratio of 3.3%, with a mean ratio of 2.5% (Table 1).

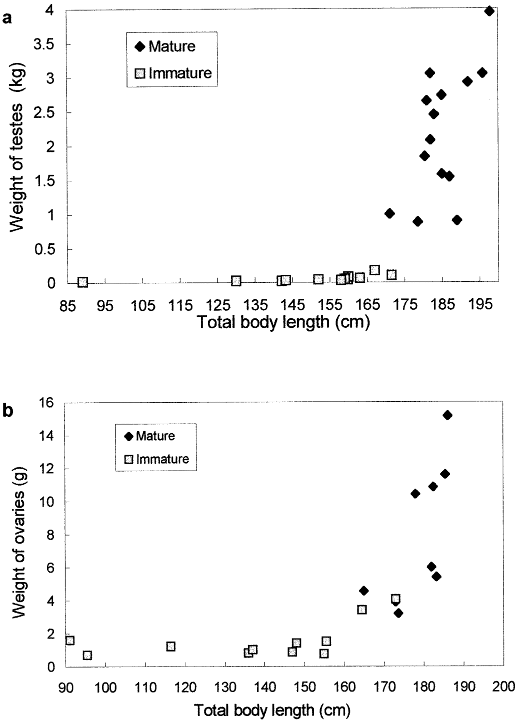

FIG. 1.—Relation between mass of gonads and total body length of estuarine dolphins (*S. guianensis*) from the coast of Paraná, Brazil: a) mature and immature testes (kg) and b) mature and immature ovaries (g).

This ratio did not show any seasonal tendency in the limited sample of mature males, suggesting year-round testicular activity. Additionally, histological analyses of the testes showed that after maturity, spermatogenesis is constant throughout the year. Diameters of seminiferous tubules at different stages of maturity were 51.4 ± 8.0 μm ($n = 233$) for immature males, 75.3 ± 15.1 μm ($n = 50$) for pubescent males, and 196.1 ± 39.3 μm ($n = 491$) for mature males. Diameters of seminiferous tubules showed large variation during maturation of testes. There were some regions of the testes where diameters were 50 μm, which is typical of immature animals, and other regions in the same gonad where they were 190 μm, characteristic of sexually mature males.

Histological analyses of testes showed that males were sexually mature at total lengths between 170.0 and 175.0 cm (Fig. 1a). The smallest mature male was 171.0 cm long and the longest immature male 171.5 cm long (pubescent). Males attained sexual maturity at an estimated age of 7 years.

Anatomical aspects of reproduction in females.—Mean weight of mature active ovaries was >5 times as heavy as that of immature females (Table 2), and the ratio of ovary mass to body mass was as high as 0.02%, with the presence of a corpus luteum of pregnancy in one of the ovaries. The largest corpus luteum had a diameter of 2.8 cm and was associated with pregnancy. Mean diameter of nonatretic Graafian follicles of pubescent females was

TABLE 2.—Dimensions and mass of ovaries of *S. guianensis* from the coast of Paraná, Brazil. Ratio of mass of ovaries to body mass is expressed as percentage of total body weight.

	Immature			Mature active			Senescent		
	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*
Length (cm)	2.3	0.5	11	3.2	0.4	8	2.5	0.19	4
Width (cm)	1.0	0.2	11	1.7	0.3	8	1.3	0.05	4
Mass, left + right (g)	1.6	1.0	11	8.3	4.2	8	3.4	0.34	4
Mass of ovaries/body mass (% of body mass)	0.005	0.002	11	0.010	0.004	8	0.005	0.0007	4

759.9 μm. Ovaries of immature females contained atretic Graafian follicles with a mean diameter of 428.1 μm (Table 3). However, atretic Graafian follicles measuring up to 750 μm were also observed in newborn females.

The maximum number of corpora albicantia or corpora lutea observed macroscopically in ovaries of 1 female was 14, with 10 in the left ovary and 4 in the right. In the sample of 11 mature females, 2 had ovulated exclusively from the left ovary and 1 exclusively from the right. All others had ovulated from both ovaries. Of the 78 ovarian scars counted in mature females, 71.8% were found in left ovaries and 28.2% in the right. Left ovaries typically accumulated 3 scars before the right started its maturation. Corpus accumulation rate was higher in the left (4.7 ± 3.4, $n = 11$) than in the right ovary (1.8 ± 2.1, $n = 11$). Females with corpora lutea in ovaries, and which were not pregnant or lactating, were observed in June ($n = 1$), July ($n = 1$), and October ($n = 2$).

Absence of ovaries from 5- and 7-year-old females in our sample did not allow a reliable estimate of age of sexual maturity in this sex. However, no 4-year-old females were sexually mature, and all 8-year-olds were, suggesting that sexual maturity is attained between 5 and 8 years. On the basis of analyses of ovaries, females were sexually mature at total body lengths of 164.0–169.0 cm (Fig. 1b), with the smallest mature female measuring 165.0 cm (lactating) and the largest immature pubescent female measuring 173.0 cm.

A reproductive cycle of 2 years was estimated. However, females can ovulate at shorter intervals of 1.5 and 1.8 years. Females older than 25 years typically possessed senescent ovaries, which were smaller in size (Table 2), deformed in shape, with no or very little activity, and with a severely depleted number of primordial follicles. The mean combined weight of ovaries of females ≤24 years old (excluding those with corpora lutea) was significantly greater ($t = 2.7$, $d.f. = 10$, $P < 0.05$) than the av-

TABLE 3.—Diameters of follicles in immature, pubescent, and mature ovaries of *S. guianensis* from the coast of Paraná, Brazil.

	Mean diameter of follicles (μm)								
	Immature			Pubescent			Mature		
	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*n*
Primordial follicles	37.1	5.6	66	40.4	5.6	30	40.7	6.1	62
Unilaminar primary follicles	58.1	11.1	71	62.4	7.5	29	62.7	11.3	74
Multilaminar primary follicles	108.7	30.2	48	107.6	29.8	20	119.4	27.3	20
Secondary follicles	186.7	46.0	47	182.9	47.3	14	236.2	64.2	12
Graafian follicles	428.1	185.7	50	759.9	513.6	32	1,073.8	586.1	53

erage mass of ovaries of females >25 years old.

Gestation, birth, and lactation.—The gestation period estimated by the Hugget and Widdas-Laws method was 11.6 months, whereas the estimate derived by the comparative method was 11.7 months. Fetal growth rate was estimated at 8.9 cm/month. Newborn individuals (total lengths 89.1–95.0 cm) were recorded in May, July, August, and December (autumn, winter, and summer) and had a mean length of 92.2 ± 2.7 cm. Four large fetuses (78.5–88.0 cm) were found in the months of December, February, March, and April. One female estuarine dolphin that died from unknown causes was found floating in the Paranaguá Bay in March 1998. This animal died with a calf of 88.0 cm in length, whose tail and posterior end of the body protruded from the mother's genital canal. The size of the fetus and the position of birth suggest that it was a gestation taken to term.

Lactation period was estimated as ≥8.7 months, corresponding to the age of the oldest animal that still had milk in its stomach. The nutritional composition of milk was, for protein, 9.5 g/100 g; for fat, 17.1 g/100 g; for Na, 148.3 mg/100 g; for K, 129.1 mg/100 g; for Ca, 48.8 mg/100 g; for Mg, 8.1 mg/100 g; for Zn, 1.03 mg/100 g; and for P, 98.0 mg/100 g. The Fe concentration was lower than resolution of the method (<0.5 mg/100 g).

DISCUSSION

Kenagy and Trombulak (1986) pointed out that among the larger mammals, the testes of odontocete cetaceans are the largest in relation to their body mass. They further noted that species of mammals with high frequencies of copulation have large testes in relation to body mass, whereas testes are small in species in which copulation is infrequent. According to Gomendio et al. (1998), the relationship between relative testes size and mating system is so strong in mammals that relative testes size can be used as a good indicator of mating systems. The power function used to assess the allometric relationship between testes mass and body mass (Kenagy and Trombulak 1986) shows that testes of *S. guianensis* are approximately 13 times larger than was predicted for their body mass, suggesting a multimale mating system.

Although dimensions of testes of dolphins of the genus *Sotalia* have not been previously described, Best and da Silva (1984) presented the ratio of testes mass to body mass for *S. fluviatilis* in the central Amazon. This ratio is <1% in immature individuals. However, in mature *S. fluviatilis* males the ratio varies from 2.5% to 5% (Best and da Silva 1984), suggesting that tucuxi have testes that are proportionally even larger than those of *S. guianensis* (0.9–3.3%). The disproportionately large testes of adult male *S. fluviatilis* led Best and da Silva (1984) to suggest a polyandrous mating system. However, polyandry is a very rare mating system among mammals (Flowerdew 1987), and there is as yet no evidence that it occurs in any cetacean (Connor and Peterson 1996). A promiscuous mating system with sperm competition may be more likely for dolphins of the genus *Sotalia*, in which both sexes copulate with more than 1 individual. Seasonality in testicular activity was not detected in the estuarine dolphin, unlike the seasonality suggested for mature male *S. fluviatilis* in central Amazonia by Best and da Silva (1984).

The presence of Graafian follicles in newborn females was unexpected because these are the most mature form of ovarian follicles (Banks 1992). However, in some mammals (lagomorphs and carnivores) differentiation of the oogonia into primary oocytes occurs immediately after birth, whereas in other groups (ruminants, swine, and humans) it occurs in the fetus (Banks 1992). It is possible that in species in which differentiation of oogonia occurs during the fetal phase, follicles start their development because of the influence of maternal hormones and can reach Graafian follicle stage.

These follicles will then become atretic after birth as tissue exchanges between mother and fetus cease. We therefore assume that differentiation of oogonia into primary oocytes in the estuarine dolphin occurs during the fetal phase. According to Harrison and Brownell (1971) and Best and da Silva (1984), ovulation in *S. fluviatilis* occurs exclusively in the left ovary. However, this type of corpus accumulation does not occur in *S. guianensis*. Both ovaries are functional, and this dolphin can be classified as type II of Ohsumi (1964), in which the right ovary matures later than the left.

Body length at sexual maturation estimated for females in this study was similar to that estimated by Schmiegelow (1990) and Ramos (1997), who based their studies only on macroscopic analyses. However, body length at sexual maturation in males is slightly less than the 180 cm estimated by Schmiegelow (1990) and Ramos (1997), probably because the earlier studies lacked histological analyses. According to Best and da Silva (1984), sexual maturation of *S. fluviatilis* occurs at body lengths of 139.0 cm in males and 132.0–137.0 cm in females. Differences in length at sexual maturity compared with *S. guianensis* may be related to different body sizes of the 2 species. Maximum total body length and body mass recorded for *S. fluviatilis* were 152.0 cm and 53 kg (Best and da Silva 1984), whereas maxima were 206.0 cm (Barros 1991) and 121 kg for *S. guianensis* (Rosas 2000). Ramos et al. (2000) estimated attainment of sexual maturity at 6 years for both sexes of estuarine dolphins, on the basis of macroscopic analyses of the gonads. This is younger than age of sexual maturity estimated for males in our study and could be an artifact of the lack of histological analyses in the earlier work carried out by Ramos et al. (2000). Although it was not possible to accurately establish the age of sexual maturation in female estuarine dolphins in our study, the range of 5–8 years is similar to that estimated by Ramos et al. (2000).

Although the mean reproductive cycle was estimated at 2 years in females up to 24 years of age, we detected more frequent ovulations in some females, ranging from 1.5 to 1.8 years. This may be because of the loss of a calf during gestation or lactation, with a subsequent reestablishment of the estrous cycle. In females older than 25 years the mean ovulation time increased to 1 ovulation every 2.5 years, which is probably because of senescence, as observed in ovaries of some females >25 years old. The smaller ovarian mass of females above this age seems to corroborate the hypothesis that some females start a postreproductive phase. Reproductive senescence has also been reported in other cetaceans, such as *Globicephala macrorhynchus* and *Stenella attenuata* (Marsh and Kasuya 1984; Perrin et al. 1976), although this is the 1st report for the genus *Sotalia*.

The estimated length at birth (92.2 cm) corroborates some of the previous estimates (Ramos 1997; Schmiegelow 1990) but is not in agreement with those presented by Borobia (1989) and Ramos et al. (2000) for estuarine dolphins. An estimated neonatal length of 105.0 cm derived by Borobia (1989) was based on dolphins collected from different populations and not on direct inspection for the presence of fetal folds and umbilical cords. The estimated length at birth of 106.0 cm (Ramos et al. 2000) was based on the Gompertz growth model using only 1 newborn individual and very few ($n = 3$) animals older than 12 years, which can result in a growth curve that overestimates lengths at birth. According to Best and da Silva (1984), the length at birth of *S. fluviatilis* is about 75.0 cm, which is considerably smaller than any estimates for *S. guianensis*.

Schmiegelow (1990) reported births of estuarine dolphins all year round, with a probable peak during spring and summer. However, on the coast of Rio de Janeiro, births appear to occur from spring to autumn, with a peak in the autumn months (Ramos et al. 2000). In contrast, Best and da Silva (1984) suggest a strong seasonality in births of *S. fluviatilis* in the central Amazon, with births occurring when river levels are lowest. This synchronization of births with low water levels should benefit females in late gestation and early lactation because fish prey are more concentrated in lakes during the dry season in the Amazon and are thus more accessible to the dolphins. The absence of such a marked hydrological cycle in the habitat of the estuarine dolphin probably allows it to reproduce throughout the year.

The gestation period estimated in our study (11.6–11.7 months) was similar to other estimates (11.3–12.0 months—Ramos 1997; Schmiegelow 1990) and probably reflects a consistency of this reproductive parameter throughout the distribution of the estuarine dolphin. The gestation period estimated for *S. fluviatilis* in the central Amazon, however, was between 10.0 and 10.3 months (Best and da Silva 1984), which is approximately 10% shorter than for *S. guianensis*. The fetal growth rate estimated in our study (8.9 cm/month) was not different from that estimated by Schmiegelow (1990—8.7 to 8.9 cm/month) for estuarine dolphins from the Cananéia-Paranaguá region. The fetal growth rate estimated by Ramos et al. (2000) for estuarine dolphins from the coast of Rio de Janeiro (9.4 cm/month) was about 5.5% greater than our estimate, which may be because of an overestimation of the body length at birth.

Until recently, the lactation period of the estuarine dolphin was completely unknown. However, Ramos (1997), studying estuarine dolphins incidentally caught in fishing nets on the coast of Rio de Janeiro, concluded that lactation lasts 9.4 months. This estimate was based on the assumption that the proportion of mature females in the sample, which are in a particular reproductive condition, is directly proportional to the relative length of time spent in that condition (Perrin and Reilly 1984). This method, however, assumes that there is no sampling bias caused by selectivity, which is not always true when the animals come from incidental captures. The method employed to estimate a lactation period of at least 8.7 months in our study also has limitations. The presence of milk in the stomach cannot be detected in small quantities, especially when mixed with solid food (Perrin and Reilly 1984). The fat and protein content of the milk was comparable to that of milk of other delphinids (Eichelberger et al. 1940; Ridgway 1972; Worthy 1990). However, Mg and Ca were lower than in other dolphins (Eichelberger et al. 1940; Gewalt 1978; Rosas and Lehti 1996). It is known that milk composition undergoes considerable changes during lactation (Worthy 1990), and milk analysis from a greater number of estuarine dolphins should be performed throughout the entire lactation period in order to determine nutritional changes during this time and to improve comparisons with milk of other species.

The coastal distribution of *S. guianensis* makes it very vulnerable to many human activities, and knowledge of its biology is still rudimentary. Our results provide new information about reproduction in this poorly known but vulnerable cetacean. However, continued studies of reproduction in estuarine dolphins are needed to further improve knowledge of its reproductive biology and population dynamics.

RESUMO

O boto cinza (*Sotalia guianensis*) é um dos golfinhos mais comuns ao longo da costa brasileira, no entanto muito pouco é conhecido sobre sua reprodução. Neste trabalho foram analisadas as gônadas de 50 indivíduos acidentalmente capturados em redes de pesca no litoral do Paraná, sul do Brasil, entre 1997 e 1999. Os testículos de machos adultos podem medir até 31.9 cm de comprimento e 11.6 de largura, e alcançar até 3.3% do peso corporal total do animal. O tamanho relativo dos testículos sugere um sistema reprodutivo envolvendo múltiplos machos, com competição de espermatozóides. Fêmeas ovulam em ambos

os ovários, no entanto a maturidade do ovário esquerdo é atingida antes do que a maturidade no direito. Os machos atingem a maturidade sexual aos 7 anos de vida, com comprimentos totais entre 170 e 175 cm. Fêmeas estão sexualmente maduras entre os 5 e 8 anos, com comprimentos totais entre 164 e 169 cm. O ciclo reprodutivo foi estimado em 2 anos, sem uma marcada sazonalidade na ovulação ou na época de nascimento. O tempo de gestação é de cerca de 12 meses, a taxa de crescimento fetal é de 9 cm/mes, e o comprimento de nascimento foi estimado em 92.2 cm. Fêmeas acima de 25 anos de idade podem apresentar ovários senescentes.

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