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# Reproduction in female swamp wallabies, *Wallabia bicolor*

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**Abstract.** The swamp wallaby (*Wallabia bicolor*) is a common, medium-sized, browsing macropodid marsupial that is unique in many ways. Relatively little is known about the reproductive biology of this species. Previous studies have proposed that the swamp wallaby has a pre-partum oestrus because the gestation period ($\bar{x} = 35.5$ days, $n = 4$) is on average longer than the oestrus period ($\bar{x} = 31.0$ days, $n = 5$) and the period from the removal of pouch young (RPY) to mating ($\bar{x} = 26.0$ days, $n = 3$). In the current study, the period from RPY to birth was confirmed at $\bar{x} = 31.25$ days ($n = 4$) in captive animals, consistent with a pre-partum oestrus. A growth curve for swamp wallaby pouch young was constructed from the progeny of captive animals to estimate the age and date of birth of young in a wild, culled population in South Gippsland, Victoria, and the reproduction of females in the wild throughout the year was examined. Young were born in every month of the year, with no statistically significant variation in the number of young born in each month. Females did not have a period of seasonal anoestrus and conceived throughout the year. Female swamp wallabies in South Gippsland bred continuously throughout the period of this study.

*Extra keywords*: macropodid, marsupial, pre-partum oestrus, seasonal breeding.

## Introduction

Seasonal breeding is a reproductive strategy adopted by most mammals. It is controlled by several factors, the most important of which are food availability, rainfall, ambient temperature and photoperiod and the latter three all influence food availability (Baker 1938 in Sadleir 1972). Macropodid marsupials show a range of breeding strategies. Some are continuous breeders (Merchant and Calaby 1981; Strahan 1991), some are opportunistic breeders, for which seasonal food shortages or drought cause a period of anoestrus (Shield and Woolley 1963; Frith and Sharman 1964; Shield 1968; Tyndale-Biscoe *et al*. 1974; Bolton *et al*. 1982) and others are strictly seasonal breeders with a photoperiodically controlled seasonal quiescence (Berger 1966; Renfree and Tyndale-Biscoe 1973; Catt 1977; Merchant and Calaby 1981; Loudon *et al*. 1985).

The swamp wallaby (*Wallabia bicolor*) is a common, medium-sized, browsing macropodid marsupial that ranges along the east coast of Australia from western Victoria to Cape York Peninsula (Strahan 1991). Because it is unique in its behaviour, dentition, karyotype and reproduction, it is classified as the sole extant member of the genus *Wallabia* (Strahan 1991). It has a reproductive strategy similar to most macropodids with a period of lactationally controlled embryonic diapause. However, in the swamp wallaby, oestrus occurs some days before birth rather than post partum, as is typical of most macropodids (Sharman *et al*. 1966). The only studies on seasonality of births in swamp wallabies show that the degree of seasonality varies from site to site. In north-eastern New South Wales, births were found to be seasonal at one site, which was fenced to exclude dingoes, but not at another site where dingoes were not excluded (Robertshaw and Harden 1986). At the seasonal site, births peaked in March and no young were born between August and September, whereas at the aseasonal site, no clear peak of births was apparent and young were born in every month of the year except August. The continuous pattern of breeding was attributed to females being chased by dingoes, leading to a loss of their pouch young and a subsequent loss of the synchrony of breeding. In Queensland, the swamp wallaby has been described as a continuous breeder but no supporting data were presented (Kirkpatrick 1970*b*).

The aims of the present study were to provide additional reproductive data on the pre-partum oestrus in swamp wallabies and to develop a swamp-wallaby-specific growth curve using a captive colony of swamp wallabies and to use this growth curve to examine the seasonal distribution of swamp wallaby births in a wild population in South Gippsland. Pouch young head length was also analysed to examine seasonality of breeding without the errors associated with estimating pouch young age. The condition of the ovary was used to determine if there was a period of anoestrus and the estimated age of conception of fetuses, embryos and blastocysts in diapause was used to determine if conceptions occurred throughout the year and to extend the knowledge of reproduction in the species.

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## Materials and methods

### *Captive animals*

A captive colony of 56 swamp wallabies from South Gippsland and Coranderrk in south-eastern Victoria established at The Melbourne University Marsupial Colony in Wantirna South was used in the present study. Animals were housed in grassed outdoor enclosures with trees and artificial huts for shelter. In addition to the available pasture, animals were provided with lucerne cubes and water *ad libitum*, fed oats approximately twice a week and given fresh browse every 3–4 days. Experimental animals were caught in long-handled nets and placed in large hessian sacks for all procedures. All procedures were approved by the Animal Experimentation Ethics Committee of the University of Melbourne and the Zoological Parks and Gardens Board Ethics Committee.

### *Reactivation of blastocysts and pouch young growth curves*

Pregnancy was initiated in captive females by the removal of pouch young (RPY) to reactivate blastocysts in diapause (Tyndale-Biscoe and Renfree 1987). The day of RPY was designated Day 0. On three separate occasions, an attempt was made to witness mating and birth in a group of females after RPY. Throughout early pregnancy (Day 0 to Day 22), females were caught weekly to check for births. During later pregnancy (Day 22 onwards), females were either caught daily to check for births and observed from a stationary vehicle nightly or were observed nightly and caught if they were seen in the typical macropodid birth position (Renfree *et al*. 1989). A total of four females gave birth following RPY and their young (two male and three female) were measured at the intervals shown in Fig. 1. Eight young of unknown age at the start of measurements were also measured and their ages estimated from tammar wallaby (*Macropus eugenii*) growth curves (Poole *et al*. 1991). These ages and head-length measurements were used to construct growth curves.

The oldest pouch young measured survived until it was 177 days old. However, pouch life in the swamp wallaby lasts ∼256 days (Tyndale-Biscoe and Renfree 1987). In the absence of head-length measurements for a similar-sized species of macropodid, head lengths and ages of the smaller tammar wallaby (Poole *et al*. 1991) were used to complete the graph. MATLAB (The MathWork Inc., Natick, MA, USA) was used to derive a line of best fit for the data. A fifth-order polynomial was chosen and used to calculate the ages of wild pouch young based on head length. The accuracy of the growth curve was assessed by comparing the actual age of pouch young used to construct the polynomial with the age calculated using the polynomial.

Because the growth curves and their functions were designed to not just describe growth but to predict age based on head length or bodyweight, they were plotted according to mathematical convention with the variable being measured (head length) on the $x$-axis and the variable to be predicted (age) on the $y$-axis. Although the inverse function provides the same descriptive information about growth, it ceases to predict age.

### *Field animals*

A total of 14 2–3-day trips to a culling site within a paper plantation were undertaken between November 2000 and April 2003. The Grand Ridge Plantation (Maryvale) is located in South Gippsland, Australia, ∼170 km south-east of Melbourne (38°11′S, 146°26′E).

Animals were culled by two shooters under contract to Grand Ridge Plantations. The shooters typically began culling at dusk and animals were shot throughout the plantation under an Authority to Control Wildlife issued to Grand Ridge Plantations. Carcasses were then transported to a mobile laboratory parked in the plantation for processing. Samples were collected in every month of the year except January, when shooting was not carried out.

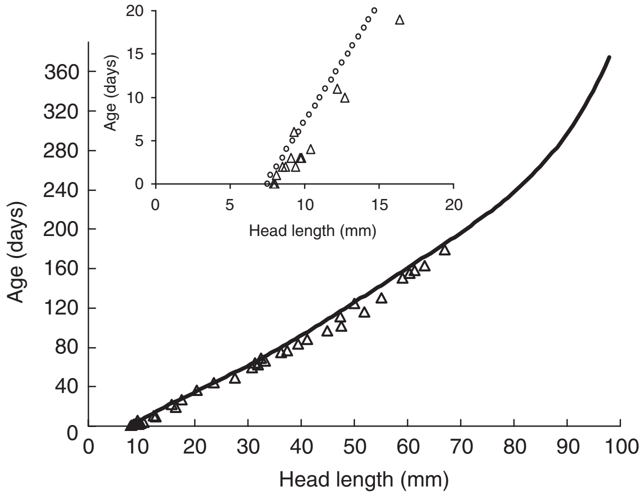


**Fig. 1.** Growth curve based on head length measurements of captive swamp wallaby pouch young and captive tammar wallaby pouch young (Poole *et al.* 1991). The inset shows the scatter of measurements in young less than 20 days old. The equation of the line of best fit is $y = 2.8 \times 10^{-7}x^5 - 6.4 \times 10^{-5}x^4 + 5.4 \times 10^{-3}x^3 - 0.2x^2 + 5.8x - 37.0$. The difference between actual ages of known age pouch young and the ages calculated using this equation ranges between −7.7 days and 7.7 days. △ *Wallabia bicolor*, ○ *Macropus eugenii*, —— polynomial.

### *Female reproduction in the wild*

All wild-shot females were weighed using a 50-kg (±100 g) dial-suspended balance (Salter, Kent, UK) and their pouches were examined. Females with fully everted teats were classed as adults. Sub-adult females were excluded from all subsequent analyses. Adult females were checked for the presence of pouch young.

The reproductive tract was removed from all adult females and the presence of antral follicles (>2.5-mm diameter) in the ovaries was noted. The proportion of females with antral follicles in each season and in each month was calculated and proportions were compared using $\chi^2$ analysis. The diameter of antral follicles was measured. Females without antral follicles were designated as having follicles of 0-mm diameter and a mean follicle-diameter index was calculated by including females without follicles in the calculation of mean follicle size per season. Indices for each season were compared using ANOVA.

Embryos were removed from females with obvious pregnancies and examined to determine the stage of development. Where no pregnancy was obvious, uteri were flushed to recover unfertilised eggs or blastocysts as previously described (Renfree 1973). All embryos and unfertilised eggs were fixed in 10% neutral buffered formalin (NBF). The conceptuses were classed as either blastocysts in diapause, embryos or fetuses. The embryos and fetuses were measured and described and compared with descriptions and measurements of tammar wallaby pregnancy stages to determine their approximate time to birth (Renfree and Tyndale-Biscoe 1973; Tyndale-Biscoe and Renfree 1987). The time to birth was then estimated by multiplying by the ratio of gestation lengths of the tammar wallaby (∼26.5 days) to swamp wallaby (∼30 days, Tyndale-Biscoe and Renfree 1987).

### *Estimation of date of birth and date of conception*

The head of each pouch young collected in the wild was measured using analogue vernier callipers (Kincrome, Scoresby, Vic., Australia). The polynomial derived in the previous section was used to calculate ages based on head length. The month of birth of pouch young was estimated by subtracting the age from the date of collection. The frequency of young born in each month was calculated after the inclusion of the projected month of birth of reactivated pregnancies. The *G*-statistic (Sokal and Rohlf 1987) was calculated to see if the number of young born in each month differed significantly from a model of equal frequencies of births in each month.

In order to examine seasonality of births while eliminating any artefacts caused by possible inaccuracies of the growth curve, the head lengths of pouch young in each month of collection were compared in SYSTAT (Systat Software Inc., Richmond, CA, USA) using a Kruskal–Wallis analysis (Zar 1999). This non-parametric test was used instead of its parametric equivalent because of a large degree of heteroskedasticity in the data.

The month of conception of blastocysts was estimated for all females with young in the pouch and a blastocyst *in utero*. Because swamp wallabies have a pre-partum oestrus, with mating preceding birth by a few hours to a few days (Sharman *et al.* 1966), the date of conception was taken to be the same as the date of birth of the young in the pouch. The *G*-statistic (Sokal and Rohlf 1987) was calculated to see if the number of conceptions in each month differed significantly from a model of equal numbers of conceptions in each month.

## Results

### *Gestation length after removal of pouch young*

Four females gave birth following RPY in the present study. The period from RPY to birth was 35 days for one female and 30 days for three of the females ($\bar{x} = 31.25$ days).

### *Growth curves*

The rate of growth as measured by head length was highest after approximately Day 220 of pouch life (Fig. 1). Head length increased with age according to the equation:

$$y = 2.8 \times 10^{-7}x^5 - 6.4 \times 10^{-5}x^4 + 5.4 \times 10^{-3}x^3 - 0.2x^2 + 5.8x - 37.0$$

where $y$ is age in days and $x$ is head length in millimetres. The difference between the actual age of pouch young and their age calculated using this equation ranged from 7.7 days to $-7.7$ days.

### *Pouch young births in the wild*

Young were born in every month of the year. The number of young born in each month did not differ significantly from a model of equal frequencies ($n = 82$, $G_{10} = 16.48$, $P = 0.12$, Fig. 2). There was no statistically significant monthly variation in the head length of pouch young collected ($n = 82$, $H_{10} = 8.87$, $P = 0.55$, Fig. 3).

### *Female reproduction in the wild*

Eighty-six adult females weighing between 7 kg and 19 kg ($\bar{x} = 13.75$ kg) were collected from Maryvale ($n_{\text{summer}} = 26$, $n_{\text{autumn}} = 16$, $n_{\text{winter}} = 13$, $n_{\text{spring}} = 31$). Of these, 33 had a large antral follicle on the surface of one ovary that ranged in diameter from 2.6 mm to 5.2 mm. The proportions of females with antral follicles in each season were similar ($n = 86$, $\chi^2_3 = 3.35$, $P = 0.34$, Fig. 4) and the mean follicle diameter index did not vary with season ($n = 86$, $F_3 = 1.84$, $P = 0.068$, Fig. 4). The number of conceptions in each month, as evidenced by the estimated age of conception of embryos in diapause, did not differ significantly from a model of equal frequencies ($n = 65$, $G_{10} = 16.1$, $P = 0.14$, Fig. 5).

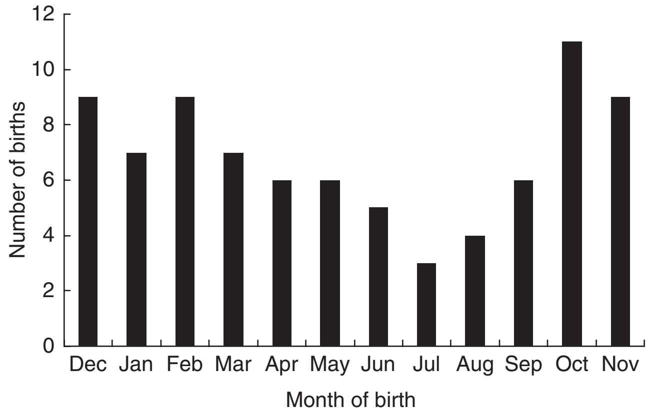


**Fig. 2.** The number of swamp wallaby births in each month of the year at the Maryvale culling site calculated using head length to determine age.

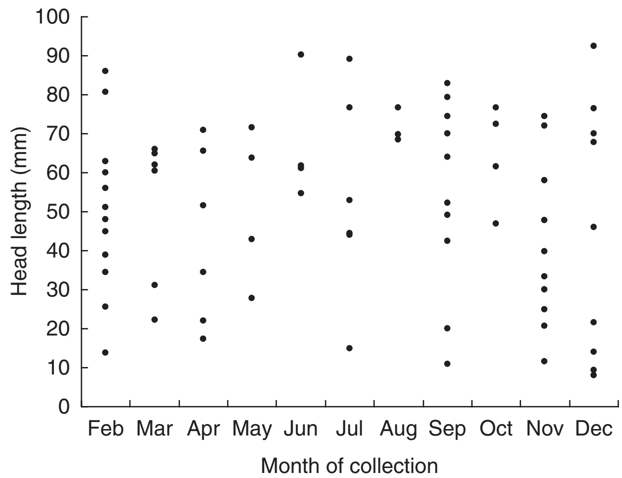


**Fig. 3.** The annual distribution of swamp wallaby pouch young head lengths at the Maryvale culling site.

Most females (77.9%) in the present study were pregnant. Most pregnancies were blastocyst-stage embryos in diapause, but a total of eight reactivated pregnancies were collected ranging from small vesicles to fetal stages (Table 1, Fig. 6). Blastocysts were collected in every season of the year. Five of the females with reactivated pregnancies had no developing follicles on the contralateral ovary (Table 1). The remaining three females had developing follicles ranging from diameter = 3.9 mm to 5.0 mm (Table 1). Two of the females with reactivated pregnancies were collected in summer (December and February), four were collected in spring

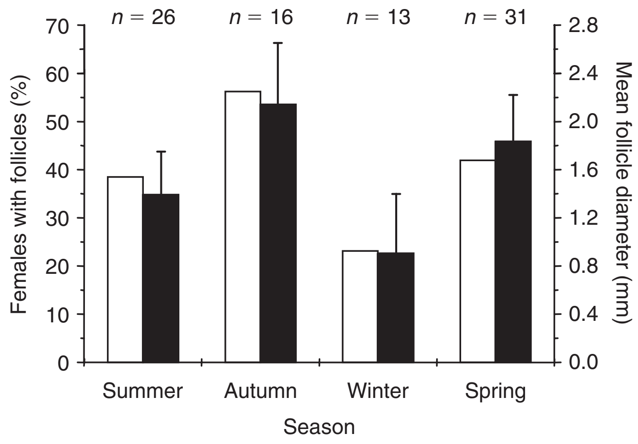


**Fig. 4.** The proportion of swamp wallaby females in each season with developing (>2.5 mm) follicles and the follicle diameter index of females at the Maryvale culling site plotted by season (mean and standard error). Data from December, January and February were assigned to summer, March, April and May to autumn, June, July and August to winter and September, October and November to spring. □, Females with follicles; ■, mean follicle diameter

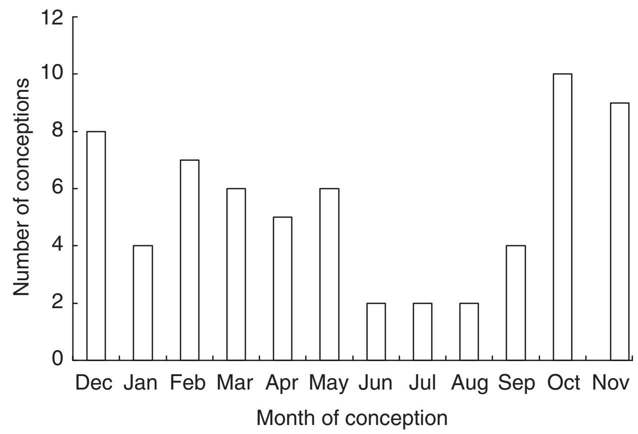


**Fig. 5.** The number of swamp wallaby conceptions occurring in each month of the year at the Maryvale culling site.

(November and October) and one was collected in autumn (March) (Table 1). No reactivated pregnancies were found in the winter months (July to August) (Table 1). No early pregnancies or unfertilised eggs were found in the contralateral uterus of any females with reactivated pregnancies (Table 1).

Four females with young less than ~10 days of age were collected (Table 2). Three females with young aged ~2, 7 and 9 days had a blastocyst in one uterus (Table 2). One female with a young collected on the day of birth had no blastocyst *in utero* and no enlarging follicle on either ovary (Table 2).

## Discussion

Female swamp wallabies in the South Gippsland population bred year-round throughout the period of the present study. A growth curve to estimate the age of pouch young from their head length was constructed. Young were born and conceived in every month of the year and the proportion of females with antral follicles and the mean follicle size did not change with season. The interval from RPY to oestrus was confirmed at 31.25 days, consistent with a pre-partum oestrus and one female had a blastocyst *in utero* likely to have been conceived pre-partum.

A growth curve for the swamp wallaby based on head length was developed for the first time during this project. In the present study, too few animals were measured for calculations of confidence intervals to be meaningful. However, studies in other species of macropodid show that confidence intervals increase from a few days at the start of pouch life to a few months at the end of pouch life (Poole *et al*. 1982*a*, 1982*b*, 1991; Delaney and De'ath 1990; Jones *et al*. 2004). Therefore, measurements of smaller swamp wallaby pouch young should yield more accurate estimates of age.

Growth data could only be collected until Day 177 of pouch life, so tammar wallaby data (Poole *et al*. 1991) were used to complete the curve. Head length is the most accurate predictor of age for all species of macropodid studied (Delaney and De'ath 1990; Poole *et al*. 1991; Jones *et al*. 2004). There are several papers that model age and the growth of bodyweight, pes length, manus length, tail length, arm length, ear length and head length in various species of non-macropodid (Lyne and Verhagen 1957; Taylor and Rose 1987; Serena and Soderquist 1988; Rose 1989) and macropodid marsupials (Sharman *et al*. 1964; Kirkpatrick 1965, 1970*a*; Ealey 1967; Kirkpatrick and Johnson 1969; Murphy and Smith 1970; Poole *et al*. 1982*a*, 1982*b*, 1991; Rose and McCartney 1982; Delaney and De'ath 1990; Jones *et al*. 2004) but only five studies model age and head length growth in species of *Macropus* (Sharman *et al*. 1964; Murphy and Smith 1970; Poole *et al*. 1982*a*, 1982*b*, 1991). In order to eliminate error in the swamp wallaby growth curve associated with both phylogenetic effects and growth-rate differences, head-length measurements of similar-sized members of the *Macropus* genus, which is most closely related to *Wallabia* (Kirsch *et al*. 1997), should have been used. Although the agile wallaby (*M. agilis*), red-necked wallaby (*M. rufogriseus*) and the whiptail wallaby (*M. parryi*) are closest in size to the swamp wallaby (Strahan 1991), no growth curves based on head length are available for these species. Therefore, the extensive tammar wallaby dataset of Poole *et al*. (1991) was used. Tammar wallaby adults are considerably smaller than swamp wallaby adults, and pouch young of the tammar wallaby are presumably smaller than young of the swamp wallaby for any given age. Using the distal part of the curve developed in the current study is, therefore, likely to overestimate age. However, the proximal portion of the head-length growth curve derived in the current study only overestimated and underestimated age by up to 7.7 days. In the absence of other growth curves based on

**Table 1. Month of collection, description and reproductive status of female swamp wallabies (*Wallabia bicolor*) with embryos collected at the Maryvale culling site**
The letters a–f correspond to the images in Fig. 6. CA, corpus albicans; CL, corpus luteum; LHS, left-hand side; PY, pouch young; RHS, right-hand side

| Image | Date collected | PY sex | PY age (days) | Gravid uterus | Left ovary | Right ovary | Embryo size and description | Estimated gestation age (days)[A] |
|---|---|---|---|---|---|---|---|---|
| a | December 2002 | No PY | – | LHS | CL diameter = 5.0 mm | Follicle diameter = 5.0 mm | Vesicle diameter = 1 mm | 10–11 |
| b | December 2002 | PY | 351 | LHS | CL diameter = 5.9 mm | CA diameter = 4.0 mm | Vesicle diameter = 2.0 mm | 12–14 |
| Specimen not shown | March 2003 | PY | 64 | LHS | CL diameter = 5.6 mm | No enlarging follicle or CA | Vesicle diameter = 2.0 mm | 12–14 |
| c | November 2000 | No PY | – | RHS | No enlarging follicle or CA | CL diameter = 6.2 mm, CA diameter = 3.3 mm | Vesicle diameter = 2.7 mm | 13–15 |
| d | October 2001 | No PY | – | RHS | Follicle diameter = 3.9 mm | CL diameter = 6.2 mm | Vesicle with embryonic plate and primitive streak diameter = 17.5 mm | 16–17 |
| e | February 2001 | No PY | | RHS | Three follicle diameter = 4.5, 4.2, 4.2 mm, CA diameter = 3.5 mm | CL diameter = 4.9 mm | Fetus, greatest length = 5.6 mm Forelimbs paddles without digits, no hindlimb buds, external heart, three pharyngeal folds | 23–24 |
| Specimen not shown | November 2000 | No PY | – | RHS | CA (not measured) | CL (not measured) | Fetus, greatest length = 10.1 mm Forelimbs paddles with digits forming, hindlimb buds | 24–25 |
| f | October 2001 | No PY | – | LHS | CL diameter = 6.2 mm, CA diameter = 3.9 mm | Two CA diameter = 3.1 mm, 2.9 mm | Fetus, crown–rump length = 10.8 mm Forelimbs with digits, hindlimb buds, internal heart | 25–26 |

[A]Estimated from embryonic descriptions and growth curves in Tyndale-Biscoe and Renfree (1987).

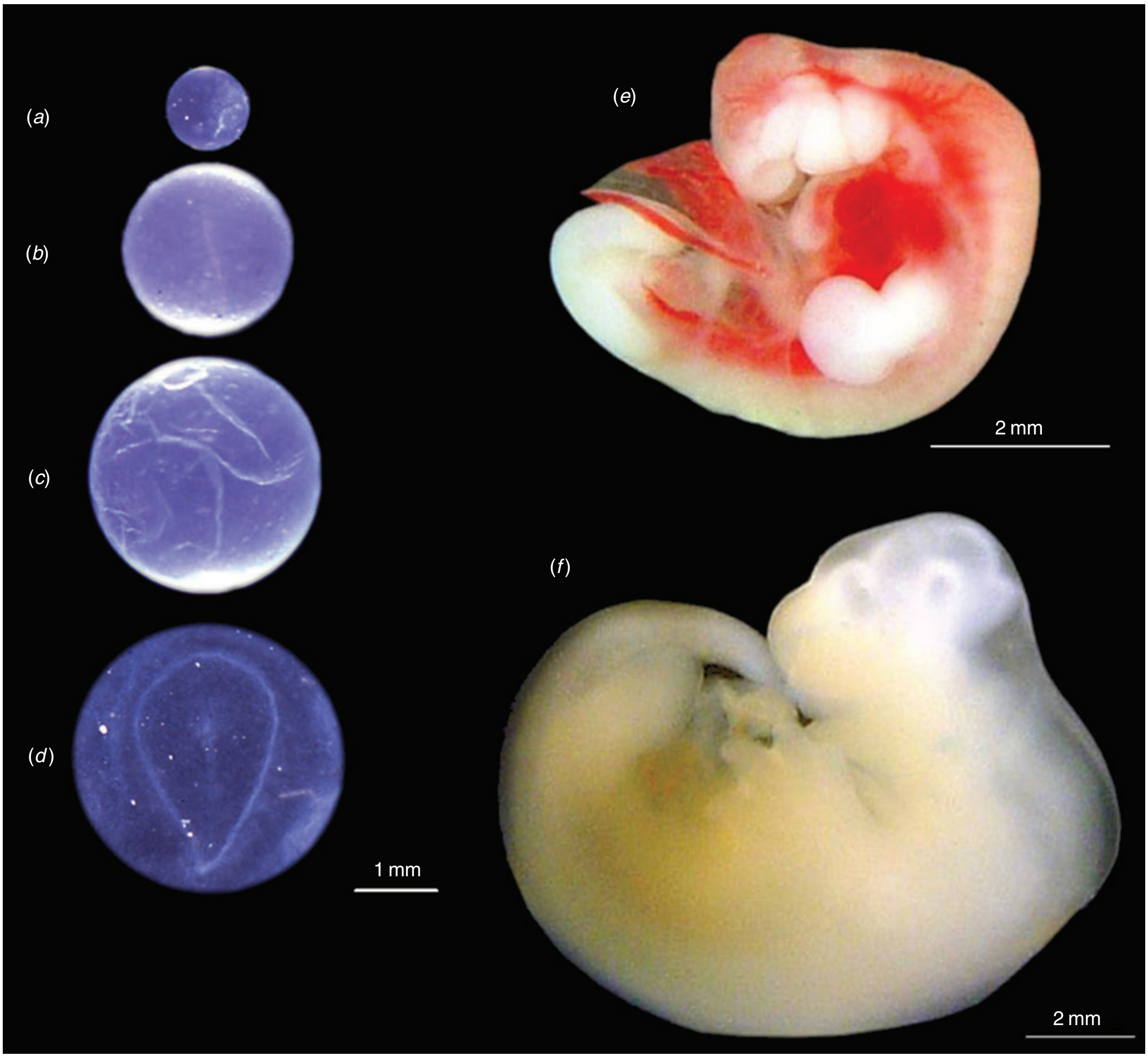


**Fig. 6.** Vesicles and fetuses collected from swamp wallaby females at the Maryvale culling site. Full descriptions of embryos and the reproductive state of mothers are given in Table 1. (*a*) Vesicle (diameter = 1 mm) ~11 days post reactivation (~19 days before birth). (*b*) Vesicle (diameter = 2 mm) ~14 days post reactivation (~16 days before birth). (*c*) Vesicle (diameter = 2.7 mm) ~15 days post reactivation (~15 days before birth). (*d*) Detail of the embryonic plate and primitive streak of vesicle (diameter = 17.5 mm) ~17 days post reactivation (~13 days before birth). (*e*) Fetus (greatest length = 5.6 mm) ~23 days post reactivation (~7 days before birth). (*f*) Fetus (crown–rump length = 10.8 mm) ~26 days post reactivation (~4 days before birth).

head length, despite the problems mentioned above, the head-length growth curve developed in this study was deemed of sufficient accuracy to predict pouch young age to the nearest month.

In the current study, pouch young were born in every month of the year and the calculated *G*-value (Sokal and Rohlf 1987) was not significant, indicating that swamp wallabies at Maryvale breed continuously. In addition, there was no statistically significant monthly variation in the average head length of pouch young collected, as is expected from a continuously breeding population. Seasonality of births in swamp wallaby populations varies from site to site. In their 1986 study, Robertshaw and Harden (1986) found a seasonal pattern of births in a population where dingoes had been excluded and a continuous pattern where they were not excluded. They attributed the lack of seasonality to harassment of females by dingoes, which caused a loss of pouch young and a subsequent loss in the synchrony of births. Although there are no dingoes in the South Gippsland paper plantations (Menkhorst 1995), a similar loss of synchrony could be explained by harassment of females by foxes and feral dogs at the site. Alternatively, because shooting at

**Table 2. Month of collection and reproductive status of female swamp wallabies (*Wallabia bicolor*) with young less than 10 days old collected at the Maryvale site**

CA, corpus albicans; CL, corpus luteum; LHS, left-hand side; PY, pouch young; RHS, right-hand side

| PY sex | PY age (days) | LHS uterus | LHS ovary | RHS uterus | RHS ovary |
|---|---|---|---|---|---|
| PY | 0 | Nothing | CA diameter = 5.4 mm | Nothing | CA diameter = 3.5 mm |
| PY | 2 | Blastocyst[A] | Follicle diameter = 3.8 mm, CL diameter = 5.1 mm | Nothing | CA diameter = 4.5 mm |
| PY | 7 | Blastocyst | CL not measured | Nothing | CA diameter = 4.6 mm |
| PY | 9 | Nothing | CA diameter = 4.3 mm | Blastocyst | CL diameter = 4 mm, 2 old CA |

[A]Blastocyst likely to have been conceived pre-partum. See text for details.

regular intervals and intensively over consecutive nights is the main method of population control at the Maryvale site, it is possible that the shooters are fulfilling the same function as the dingoes in the Robertshaw and Harden (1986) study.

The continuous pattern of births found at Maryvale may not be due to females losing pouch young. In most species of macropodid marsupials, seasonal patterns of births are due to a photoperiodically controlled embryonic diapause (seasonal quiescence) or to a period of seasonal anoestrus. Photoperiodically controlled diapause is found in strictly seasonal breeders and results in a restricted pattern of births that is constant from year to year and site to site (Berger 1966; Renfree and Tyndale-Biscoe 1973; Catt 1977; Merchant and Calaby 1981; Loudon *et al.* 1985). Seasonal anoestrus is caused by seasonal food shortages and does not persist when sufficient food is available, resulting in a pattern of births that varies from site to site and year to year (Shield and Woolley 1963; Frith and Sharman 1964; Sharman and Pilton 1964; Shield 1968). The swamp wallaby is not a strictly seasonal breeder and it is likely that the seasonal pattern of births in the absence of dingoes (Robertshaw and Harden 1986) was caused by seasonal anoestrus. Because the population in the current study lives within a timber plantation, enough high-quality browse may be available year-round to maintain female body condition and oestrus in every season. In addition, because the population is culled, there may be lower densities of swamp wallabies in this population than in the one studied by Robertshaw and Harden (1986), reducing competition for resources and allowing animals to achieve better body condition.

Sixty-seven of the 86 females collected were pregnant (77.9%). Of these, 59 females were pregnant with blastocysts in diapause, with the remainder being pregnant with various stages of reactivated pregnancy, all but one of these being collected in spring or summer. The length of diapause is ~10 times that of pregnancy after reactivation, which means that females are 10 times more likely to be found with a blastocyst in diapause than with a reactivated pregnancy. Because half as many females were collected in winter as in spring or summer, the failure to find any reactivated pregnancies in winter may not be due to the absence of these pregnancies in the population at this time but due to an insufficient sample size. Calculating the age of conception for all females with pouch young and blastocysts showed that females conceived young throughout the year.

None of the females with reactivated pregnancies had a blastocyst in the contralateral uterus, which would have confirmed the presence of a pre-partum oestrus in the wild. Robertshaw and Harden (1986) stated the same in their study and concluded that this was due to an insufficient sample size. Females with embryos conceived at a pre-partum oestrus would show concurrent occupation of uteri for a period of 6 days or less. This is a very short time interval and makes finding females in this state unlikely. Of the eight females collected with reactivated pregnancies, only three (two with small vesicles and one with a near-term fetus) had developing follicles on the contralateral ovary. These enlarging follicles ranged in diameter from 3.9 mm to 5.0 mm. Because folliculogenesis in marsupials takes approximately 2 weeks (Tyndale-Biscoe and Renfree 1987), it is not possible to distinguish between a pre-partum and a post-partum oestrus.

There is a limited body of evidence supporting the occurrence of a pre-partum oestrus. Sharman *et al.* (1966) ‘tentatively assumed’ that the swamp wallaby has a pre-partum oestrus. These researchers noted that the gestation period was, on average, 35.5 days long ($n = 4$, Fig. 7). This is longer than the oestrous cycle in swamp wallabies, which is, on average, 31 days long ($n = 5$, Fig. 7). Nine females mated 1–7 days before birth and three of these matings (4, 6 and 7 days before birth) were viable, resulting in the birth of young following RPY or pouch emergence. These are small sample sizes and the data come from captive animals, not wild. In the current study, four females gave birth after the removal of their pouch young (RPY). The average time from RPY to birth was 31.25 days, which fits with the relative timing of birth and mating previously described (Sharman *et al.* 1966) (Fig. 7). Unfortunately, we never observed mating before (or after) birth in the captive animals that gave birth after RPY. However, three of the four wild females collected with a neonatal young in the pouch had a blastocyst in diapause *in utero*. Of these, one female had a young approximately 2 days old. Because it takes 5–7 days for a tammar wallaby blastocyst to enter diapause

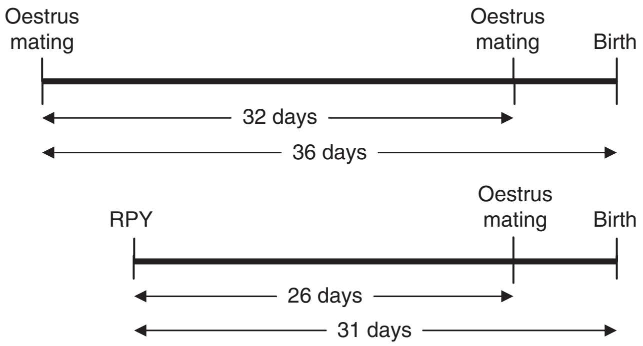


**Fig. 7.** Diagram showing the length of time between successive oestrus cycles ($n = 4$, Sharman *et al.* 1966), the time from mating to birth ($n = 4$, Sharman *et al.* 1966), time from removal of pouch young (RPY) to mating ($n = 3$, Sharman *et al.* 1966) and the time from RPY to birth ($n = 4$, current study).

(Tyndale-Biscoe 1984; Tyndale-Biscoe and Renfree 1987) it is likely that a similar amount of time is required for swamp wallaby blastocysts to enter diapause. Thus, this blastocyst was most likely conceived at a pre-partum oestrus. The presence of a pre-partum oestrus, especially in the wild, remains enigmatic and requires further study for confirmation.

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