Reproductive biology of the Tasmanian Bettong (Bettongia gaimardi: Macropodidae)

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(With 1 figure in the text)

The reproductive biology of the Tasmanian Bettong (Bettongia gaimardi) conforms in many respects to that found in related kangaroos. Gestation and the oestrous cycle are of similar duration (21-22 days), and a postpartum oestrus may result in the formation of a blastocyst that remains quiescent (embryonic diapause) throughout most of pouch life. Oestrous cycles including a gestation are shorter (by 1-5 days) than those cycles without a pregnancy. This ‘maternal recognition of pregnancy’ is extended into pouch life as the furred young always vacates the pouch when a new young is born. Pouch life is relatively short (106 days) and, as the Bettong breeds throughout the year, several young may be reared/year. Both males and females become mature before one year.

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Introduction

The Tasmanian Bettong, Bettongia gaimardi has the most secure status of any member of the seriously depleted genus Bettongia (Johnson & Rose, 1983), though little is known of the biology of this small (max. 1.8 kg) rat-kangaroo. The Australian mainland form of this species is believed to be extinct (Poole, 1979), having suffered a dramatic decline in range and numbers since the advent of European man and his introduced eutherian mammals. Only on the island of Tasmania are there sufficient animals for detailed studies, but even here their status is classed as ‘vulnerable’ (Rose, 1986a). Unlike the related and more common Tasmanian species, the Potoroo, Potorous tridactylus, the Bettong lives in the drier, warmer regions of the state, where the vegetation is open and the soils are of low fertility.
Flynn (1930) studied aspects of the reproduction of this species but was unable to breed them in captivity. On the basis of his studies, he suggested that the Tasmanian Bettong had a gestation length of six weeks, longer than any marsupial for which we have information. Sharman (1965) commented that Flynn’s (1930) estimate of six weeks for the duration of pouch life was ‘most unlikely’ and Tyndale-Biscoe (1968), in his study of the reproduction of the related species *Bettongia lesueur*, observed that there is a need for the re-examination of the duration of gestation in the Tasmanian species.

In the Tasmanian Bettong, as in the majority of macropodid marsupials, there is a postpartum oestrus shortly after birth. This usually results in the formation of a fertilized egg that develops to the unilaminar blastocyst stage before entering embryonic diapause (Rose, 1985). This quiescent blastocyst resumes development near the end of pouch life while the furred young still resides within the pouch. On the night of ‘final pouch vacation’, a precise series of events occurs (Rose, 1986b) which is initiated when the pouch of the mother tightens as if drawn by purse strings; this prevents the re-entry of the large young which, however, is still able to suck milk from its mother’s teat which protrudes through the tight pouch entrance. Birth and postpartum oestrus occur on the same night as final pouch vacation, and Rose (1986b) has shown experimentally that, in the Bettong, physiological changes in the mother are responsible, in part, for determining the duration of pouch life.

This paper summarizes the reproductive biology of the Tasmanian Bettong and includes details on the duration of the oestrous cycle, gestation and pouch life.

**Methods and materials**

**Animals**

Details of maintenance and handling in captivity are provided in Rose (1982).

The majority of the data reported here were obtained from 10 initial female Bettongs kept between 1977-1980. Six were caught in the wild and 4 were bred in captivity. Additional data were gained from other captive bred females and animals trapped in the wild as the initial Bettongs died. Usually, 2 females were housed with 1 male. As juvenile males matured, they were separated from their fathers.

**Oestrous cycles and vaginal smears**

The method for obtaining a vaginal smear was the same as that used previously by Peters & Rose (1979). This involved the insertion of a small glass tube into the urogenital sinus up to the posterior vaginal sinus. A thin polyethylene tube with a cotton wool ‘brush’ on the proximal end was pushed through the glass tube and rotated several times. After withdrawal, the ‘brush’ was smeared on to the surface of a clean glass slide and fixed with absolute alcohol and ether (50:50). The smears were stained with modified Shorr’s (1941) stain.

Vaginal smears were obtained every second day from 3 females for approximately 6 months. Vaginal smears were obtained less regularly from all other females, although near oestrus animals were smeared daily. In the evaluation of these smears, particular notice was taken of the rise in number of cornified cells and the presence or sudden absence of leucocytes. From the detailed study of 3 Bettongs, it was noted that the sudden loss of leucocytes, coupled with a build up of cornified epithelial cells, was able to pinpoint the date of oestrus. This was corroborated with 10 other females.

The length of an oestrous cycle was taken to be the duration between successive periods of oestrus as measured by changes in the cellular constituents of the vaginal smear and/or the presence of sperm in the smear. The presence of a copulatory ‘plug’ in the urogenital sinus was accepted as sufficient evidence of
oestrus, hence the successive appearance of 'plugs' could also be used to determine the length of oestrous cycles.

Gestation

The duration between the presence of a copulatory 'plug' or oestrus-type smear with sperm and the appearance of a new neonate in the pouch was taken as the gestation length. Vaginal smears obtained after birth allowed the detection of postpartum oestrus. Parturition was never observed. Small pouch young were removed from the pouch and the period until the next birth (and/or oestrus) was noted (delayed gestation).

Pouch life

The duration of pouch life was from the first noted presence of a neonate in the pouch until final vacation was recorded. At pouch vacation, the mother was examined for the presence of a new young and for vaginal oestrus. After vacation, mothers were monitored until weaning.

Breeding season

The monthly occurrence of births over 10 years is presented. These data contain both field and captive observations and were obtained either by knowledge of the actual birth or by extrapolation after estimation of the age of pouch young based on growth curves in Rose (1985). The accuracy of this method of age estimation was better than ±3 days (Rose, 1985).

Breeding seasons in the wild were not investigated per se but data were obtained coincidentally with the capture of adult female Bettongs with pouch young. The captive population was sampled weekly for the presence of pouch young throughout most of the study.

Removal of corpora lutea

Quiescent corpora lutea were surgically excised from 4 females after anaesthesia was induced by Ketalar (Ketamine hydrochloride 10 mg/kg), and maintained by a Halothane/O2 mixture. Simultaneously, the small pouch young were removed during the operation.

Sexual maturity

Maturity was judged to have been reached when a female Bettong produced a young or when a male achieved either a fertile mating or had copious motile sperm in the urine.

Results

Vaginal smears

Cyclic changes in the proportions of the cellular constituents of the vaginal smears were observed in almost all non-lactating female Bettongs. The sequence and nature of the smear changes resembled those described by Hughes (1962) and Tyndale-Biscoe (1968) for Potorous tridactylus and B. lesueur, respectively. For much of the cycle, there appears to be an inverse relationship between the presence of cornified cells and leucocytes. The sudden disappearance of leucocytes and mucus prior to oestrus was the most abrupt of the changes observed in the smear cycle and this criterion was subsequently used in conjunction with the onset of cornification to designate Day 0 of the oestrous cycle, i.e. oestrus (Table 1).
Identification of the day of oestrus was corroborated by the presence of sperm in the smear: in addition, very large numbers of cornified cells in the smear indicated that oestrus had passed. There was an irregular pattern in the presence of the strands of mucus but they were consistently absent on the day of oestrus.

Sperm were only found in the smear on one day of the oestrous cycle, the day of sudden absence of leucocytes and build-up of cornified cells, though small round lightly stained bodies (probably prostatic material) were sometimes present on the day after the finding of sperm in a smear. It seems likely, therefore, that the period of female sexual receptivity lasts for less than 24 hours.

A summary of data on reproductive cycles is provided in Table II. The oestrous cycle was taken as the duration in days between successive periods of cornification associated with leucocyte disappearance and/or the presence of sperm in the smear or as a copulatory plug.

**Anoestrus**

Anoestrus, as determined by the absence of oestrous cycles and the presence of a dry and scaly pouch, was a rare occurrence because oestrous cycles occurred throughout the year in most females. Anoestrus sometimes occurred immediately after the final vacation of the pouch by a

### Table I

**Variation in vaginal smear over the 22-day oestrous cycle (based on a total of 14 cycles from six Bettongs)**

<table>
<thead>
<tr>
<th>Day of cycle</th>
<th>Cornified cells</th>
<th>Leucocytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>-10</td>
<td>+</td>
<td>±</td>
</tr>
<tr>
<td>-8</td>
<td>±</td>
<td>+±</td>
</tr>
<tr>
<td>-6</td>
<td>±</td>
<td>+</td>
</tr>
<tr>
<td>-4</td>
<td>±</td>
<td>+±</td>
</tr>
<tr>
<td>-2</td>
<td>+</td>
<td>+±</td>
</tr>
<tr>
<td>Oestrus</td>
<td>+±</td>
<td>-</td>
</tr>
<tr>
<td>+2</td>
<td>+++++</td>
<td>-</td>
</tr>
<tr>
<td>+4</td>
<td>++++</td>
<td>-</td>
</tr>
<tr>
<td>+6</td>
<td>+++</td>
<td>±</td>
</tr>
<tr>
<td>+8</td>
<td>+</td>
<td>±</td>
</tr>
<tr>
<td>+10</td>
<td>+</td>
<td>±</td>
</tr>
</tbody>
</table>

### Table II

**Summary of reproductive phenomena in B. guimardi**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Number of observations</th>
<th>Mean ± S.D. (days)</th>
<th>Range (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oestrous cycle</td>
<td>46</td>
<td>22.6 ± 3.5</td>
<td>17-37</td>
</tr>
<tr>
<td>Gestation length</td>
<td>15</td>
<td>21.3 ± 0.8</td>
<td>20-22</td>
</tr>
<tr>
<td>RPY* to birth</td>
<td>13</td>
<td>17.6 ± 0.9</td>
<td>16-19</td>
</tr>
<tr>
<td>RPY to oestrus</td>
<td>16</td>
<td>18.9 ± 1.3</td>
<td>17-22</td>
</tr>
<tr>
<td>Birth to oestrus</td>
<td>35</td>
<td>0.5 ± 0.5</td>
<td>0-2</td>
</tr>
<tr>
<td>Pouch life</td>
<td>17</td>
<td>106.1 ± 2.5</td>
<td>101-111</td>
</tr>
<tr>
<td>Weight at final pouch</td>
<td>17</td>
<td>354.6 ± 50.0 g</td>
<td>291-460 g</td>
</tr>
</tbody>
</table>

*RPY = removal of pouch young*
young Bettong. Other animals also failed to produce young but these animals always displayed a pink, moist pouch.

**Gestation and parturition**

The mean gestation length is 21.3 days ± 0.8 (5 ± S.D.) with little variation in this value (the range being 20–22 days) (Table II). Parturition was never observed nor were there ever any behavioural indications during the day as to the imminence of birth. It seems probable that birth occurs within the confines of the nest.

It is logical to assume that, as birth and postpartum oestrus/mating usually occur on the same night, birth would precede oestrus. Otherwise, the persistent male and/or his ejaculate would be likely to interfere with the birth process.

The sex ratio of neonates is 1:1; of 64 births for which sex was recorded, 32 were male and 32 female.

**Delayed gestation|embryonic diapause**

The mean duration in time from the removal of a pouch young (RPY) to birth of the previously quiescent blastocyst (delayed gestation) is 17.6 ± 0.9 days. This is approximately four days shorter than the normal gestation length.

The fertilized egg produced at postpartum oestrus remains dormant in the uterus for most of the period during which there is a young in the pouch. Towards the end of pouch life, the quiescent blastocyst begins to develop so that a new birth coincides closely with final vacation of the pouch by the larger young. In fact, pouch vacation, birth and postpartum oestrus (based on smears or a copulatory plug), occur on the one night (Rose, 1986b), the large, furred young being excluded by the strong contraction of the pouch to make way for its small sibling.

Should pouch young be lost or experimentally removed, the quiescent blastocyst is reactivated and a new young may be born in the absence of a male.

**Postpartum oestrus**

Oestrus usually occurs (n = 19) on the night of birth; it occurred one day later on 15 occasions and on one occasion two days after the birth.

There is a significant difference in time, when one compares the period between a mating and a postpartum mating (i.e. a fertile cycle) of 21.9 ± 0.9 days with a mating to mating without an intervening gestation (i.e. an infertile mating) of 23.4 ± 1.3; P < 0.01 (t-test, d.f. = 33). The fertile cycle is about one-and-a-half days shorter than the infertile cycle.

**Monthly distribution of births**

Bettongs appear to be continuous breeders, both in captivity and in the wild, as births occur in all months of the year. Figure 1 presents monthly distribution of a combination of the actual births in captivity (i.e. where birth dates were known) and the crude birth data from the wild (i.e. birth dates extrapolated from the estimated age of the pouch young). Although there appears to be a trend for more births to occur in the winter, this was not significant (χ² = 12.6, d.f. = 11, P > 0.3). With one exception, all wild-caught adult females (n = 44) either had a pouch young or showed evidence of recently having had one (e.g. an enlarged teat). The one wild-caught adult
female that had neither a young nor an enlarged teat showed an oestrus-type smear on the day after capture. Either this animal was undergoing her very first oestrus or she had recently lost a small young.

Pouch life

The average duration of pouch life, i.e. the period from birth until permanent vacuation of the pouch, is 106.1 days, and young weigh an average of 354.6 g at that time. There are no differences in the length of pouch life between male and female young (Rose, 1986b). The 'interim' pouch life, or period when the young is able to leave the pouch and return into it, is short, lasting for less than two weeks. After final pouch vacation, the young continue to suck milk for 6-9 weeks until weaned.

Removal of the corpus luteum

Removal of the corpus luteum (CLX) from four quiescent females was followed by oestrus-type smears on day 6 after CLX, day 7 (twice) and day 18. In no case did parturition occur.

The corpus luteum from the single animal that came into oestrus 18 days after the operation did not have the histological appearance of a quiescent corpus luteum as described by Rose (1985) but rather that of an atretic corpus luteum. Using the assumptions of Tyndale-Biscoe, Hearn & Renfree (1974), the length of the follicular phase of the oestrous cycle in B. gaimardi can be estimated as approximately seven days. As the total length of an oestrous cycle is 22 days, then the 'luteal' phase will be about 15 days in duration (i.e. 22 - 7 days); this has been confirmed histologically (Rose, 1985). Gestation (21 days) continues for a further six days (21 - 15 days) over the length of the luteal phase.

Sexual maturity

The mean age of maturity was 272 ± 53 days or approximately 40 weeks (nine months), there being little difference between the two sexes. All animals were mature by age 52 weeks. The two deciduous premolar teeth were replaced by the single sectorial premolar by this age (Rose, 1985) and this event may also serve as an indicator of maturity.
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Discussion

Reproduction in the Tasmanian Bettong conforms to the predominant macropodid pattern (Sharman, Calaby & Poole, 1966; Tyndale-Biscoe et al., 1974; Renfree, 1981; Tyndale-Biscoe & Hinds, 1981). The lengths of the oestrous cycle and gestation are similar and a postpartum oestrus occurs shortly after birth. The single blastocyst formed after this postpartum mating remains dormant (‘embryonic diapause’) until near the end of pouch life when suckling becomes intermittent. Final emergence from the pouch is closely followed by birth and oestrus, with the result that both young (one in and one out of the pouch) suck concurrently from separate teats.

The results from the present study show that reproduction in *B. gaimardi* is very similar to that of *B. lesueur*. Tyndale-Biscoe (1968) commented on the unique position that *B. lesueur* and *B. penicillata* hold in having the shortest gestation period of any species of macropodid yet examined. He further commented that the six-week gestation period proposed by Flynn (1930) for *B. gaimardi* ‘remains in doubt’. The present data justify this suspicion and further show that the gestation period in *B. gaimardi* (21 days) is similar to that of *B. lesueur* and *B. penicillata*. Flynn (1930) suggested that, on the basis of his limited observations, pouch life of the Tasmanian Bettong would be very short; he concluded that pouch life must approximate six weeks. Sharman (1965) pointed out that six weeks would be a very short pouch life and would conflict with observations of other macropodids. The duration of pouch life in *B. gaimardi* (106 days) is in fact similar to that in *B. lesueur* (116 days; Tyndale-Biscoe, 1968) and *B. penicillata* (100 days; Sampson, 1971).

In most marsupials studied, parturition coincides with the end of the luteal phase in the uterus. However, in many macropodids, gestation is extended past the luteal phase into the follicular phase by what has been termed a foeto-placental influence (Tyndale-Biscoe et al., 1974). This lasts for approximately six days in the Tasmanian Bettong.

That the presence of the foetus/placenta might affect the length of the macropodid oestrous cycle has been demonstrated by Merchant (1976, 1979) and Merchant & Calaby (1981). In each case, the period from oestrus to postpartum oestrus was significantly shorter than the period from oestrus to oestrus (i.e. without an intervening gestation) as found in this study.

The foeto-placental unit can have an additional effect upon the marsupial mother as this study and Rose (1986b) have recently shown that birth and/or the occurrence of oestrus can affect the length of pouch life in the Bettong by precipitating pouch contraction, thus preventing re-entry by the large young.

External factors often influence the reproduction of mammals. It is logical to assume that mammals will tend to produce their young at a period of the year when environmental conditions are optimal for the survival of both mother and young (Sadleir, 1969). Applying this logic, Sharman et al. (1966) and Tyndale-Biscoe (1973) have suggested that those marsupials living in regions where spring is a time of abundant food (e.g. south-eastern Australia including Tasmania) will breed so that young leave the pouch during the spring, when there is an increase in the growth of vegetation. This ‘rule’ generally holds true, though factors other than purely environmental ones can affect the onset and duration of the breeding season, e.g. interspecific competition (Dickman, 1982). However, *B. gaimardi*, unlike most larger macropodids, but like other rat-kangaroos, is a continuous breeder, able to breed throughout the year in captivity and in the wild. Both Flynn (1930) and Zuckerman (1953) suggested that the Tasmanian Bettong probably bred for most of the year. There are important dietary variations between the rat-kangaroos, many of which are mainly fungivorous (Lee & Cockburn, 1985), and the larger herbivorous
kangaroos. Possibly, there is less seasonal variation in the food eaten by the potoroines or perhaps, and more probable, they are able to vary their diet opportunisically throughout the year.

The relatively short pouch life and early maturity (within a year) of the Bettong, coupled with continuous breeding and a five-year life span (Rose, 1982), suggest that it could have a relatively high breeding potential. However, factors including predation and environmental disturbance would lower this potential so that it seems unlikely that Bettongs would reproduce themselves more than twice during a life-time (Rose 1986a). This could account in part for an inability to replenish animal numbers in the wild after the heavy predation and environmental change that has occurred on mainland Australia (King, Oliver & Mead, 1981), and may partly explain the endangered status of all mainland Bettongs.

Summary

The Tasmanian Bettong has a reproductive biology that is similar to other kangaroos but most events occur over a shorter period. The short gestation (21 days) is closely followed by a postpartum oestrus which results in the formation of a blastocyst, which remains quiescent for most of the period that the pouch is occupied. Towards the end of pouch life, the blastocyst is reactivated such that its birth coincides precisely with vacation of the pouch by its sibling. The above events, the short pouch life (106 days) and continuous breeding see that the Bettong is able to produce several young/year.

I wish to thank the Tasmanian National Parks Wildlife Service for allowing the capture of Bettongs and Prof. D. M. Stoddart and Dr R. Swain for commenting on the manuscript.

REFERENCES


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