FECUNDITY, POUCH YOUNG SURVIVORSHIP AND BREEDING SEASON OF THE NORTHERN BETTONG (BETTONGIA TROPICA) IN THE WILD.

KARI VERNES AND LISA C. POPE


Reproduction in a wild population of northern bettongs (Bettongia tropica) was studied at Davies Creek in northeastern Queensland between November 1994 and February 1997. Using mark-recapture, we recorded 88 individual pouch young (PY) during the study (34 male, 45 female, 9 unknown sex). Using captive-derived growth equations we estimated that 90% of PY survived to permanent emergence from the pouch (PEP). Birth of a new PY coincided with PEP of the previous young 78% of the time; 12% of births occurred within 2-8 weeks of PEP while the remaining 10% probably died before PEP. 96% of adult females carried PY at the time of capture. *B. tropica* bred continuously, with no significant differences in numbers of births recorded in different months. Few young that were marked in the pouch were captured as sub-adults, and none were captured as adults. Limited data on longevity indicated that *B. tropica* can live to at least 5 years. Our data suggest that *B. tropica* has a high reproductive potential; however, the fate of PY after PEP remains poorly known; and this may represent the period of greatest bettong mortality.

Key words: northern bettong, *Bettongia tropica*, reproduction, pouch young survivorship, breeding seasonality, adult lifespan

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THE northern bettong (*Bettongia tropica*) is a small (1.2 kg) potoroid marsupial currently listed as ‘Endangered’ (Davidson 1991; Van Dyck 1991) as a consequence of its highly restricted geographical distribution (Carpenter *et al.* 1993) and a decline in range since the early 1900s (Winter and Johnson 1995). In response to the conservation status of *B. tropica*, a captive colony was established in South Australia in the 1980s (Smith 1998) and in north Queensland in the mid 1990s to study breeding biology and to provide captive stock for potential reintroduction (Johnson and Delean 2001). Work on *B. tropica* in captivity has since yielded information on oestrous and gestation lengths, development of pouch young (PY), age at permanent emergence from the pouch (PEP) and age at sexual maturity. Smith (1998) also demonstrated the utility of cross-fostering with the brush-tailed bettong (*B. penicillata*) to improve the captive rate of increase. Such work has proved valuable because it allowed observations of events that are rarely recorded in the field, such as date of birth and date of PEP. Furthermore, based upon growth equations derived from captive work by Johnson and Delean (2001), birth dates, date of PEP, breeding season, survivorship of pouch young and fecundity of adults can now be accurately estimated for wild populations.

Here we apply growth equations derived by Johnson and Delean (2001) from a captive population of *B. tropica* to a wild population studied in northeastern Queensland between November 1994 and February 1997. In doing so, we present the first detailed estimates of fecundity, breeding season, pouch young survivorship and adult lifespan of *B. tropica* in the wild. Because most of the population under study experienced a prescribed fire, we are also able to make inferences about effects of fire on *B. tropica* reproduction.

STUDY AREA AND METHODS

Our study area was Davies Creek (17°01'S, 145°35'E, altitude 550 m asl) located on the Lamb Range at the western boundary of the Wet Tropics.
world Heritage Area, northeastern Queensland. Collapsible platform cat traps (Mascot Wire Works Pty. Ltd.) baited with a mixture of rolled oats, peanut butter, honey and vanilla essence were used to capture B. tropica. Nine trapping grids were used; the primary site was an 8 x 6-trap grid (48 traps in total) where eight traps were spaced at 30 m intervals along each line, with the six lines spaced at 100 m intervals. Eight smaller ‘satellite’ grids, each consisting of 12 traps (three lines of four traps) were located at various distances (300 – 3500 m) from this main site. During six field trips between November 1994 and May 1996 we trapped all nine sites each for 3 – 4 consecutive nights. During the last four field trips between August 1996 and February 1997 we trapped only the eight smaller satellite grids, again for 3 – 4 nights each.

On November 14, 1995 (approximate mid-point of the primary trapping grid that burned the entire grid and four of the eight satellite grids. The fire was of low-moderate intensity (200 – 3000 kW m$^{-1}$) and burned mainly the grassy ground-layer, destroying the nesting sites of most B. tropica.

During trapping, if a B. tropica had not been captured previously it was injected with a Passive Integrated Transponder (PIT) tag beneath skin at the back of the neck. Pouch young (PY) estimated to be greater than about 70 days old were also PIT-tagged, as we felt they were large enough at this age to be handled and tagged safely. All animals were processed and released at point of capture to minimise trap-related stress. Pouches of females were checked at each capture to note changes in pouch status (PY present or absent) or growth of PY. At first capture of a PY in any one trip, we measured head length, pes length and tail length. Weight was also recorded if the PY was old enough to handle safely. We also recorded which teat the young was attached to, and whether any other teats were being used. The former assisted identification of untagged young on subsequent field trips, while the latter indicated the presence of a young-at-foot (YAF).

An equation developed by Johnson and Delean (2001) to predict age based upon the knowledge of head length (Johnson and Delean 2001; Equation 1) was used to estimate age of wild caught pouch young. We used head rather than pes as we believed our measurements of head to be more accurate than pes, especially on small PY. Error associated with the estimate was calculated by using a second equation (Johnson and Delean 2001; Equation 3). Mean pouch life of 106 days (range 102 - 112; Johnson and Delean 2001) was used to estimate date of permanent emergence from the pouch (PEP). To test the suitability of using captive growth equations for estimating the age of wild animals, we compared the developmental features of wild PY of known age (measured in weeks 1 – 3 of life, and subsequently captured some time later) with the predicted developmental features elucidated by Johnson and Delean (2001). At the second capture, each of these PY ($n = 5$; age range: 7 – 14 weeks) exhibited the predicted features.

**RESULTS**

**Sex ratio of pouch young**

A total of 88 individual PY were recorded (34 male, 45 female, 9 unknown sex) at Davies Creek between December 1994 and February 1997. These data do not indicate a significant departure from a 1:1 sex ratio ($\chi^2 = 1.53, df = 1, p = 0.22$).

**Estimation of age and survivorship of pouch young**

By predicting the birth date of a PY based on head length (with associated error) and then assuming it had a pouch life of 106 days, we could estimate whether the birth of a subsequent young occurred following its emergence, or whether birth occurred following premature PY loss. Using this procedure, we calculated that 90 % of PY whose fate was known ($n = 51$) survived to PEP (Table 1). Birth of a new PY was calculated to have coincided with PEP of the previous young 78 % of the time (Table 1). A further 12 % of births were estimated to have occurred within 2 - 8 weeks of PEP of the previous young (Table 1). We estimated that the remaining 10 % of young were lost at between 22 - 83 days of development (Table 1). The fate of 38 PY was unknown; these young were first recorded in the pouch of females that were not subsequently recaptured during the study.

**Seasonality of births**

Of 120 captures made of adult female B. tropica during the study, 115 (96 %) had PY. According to predicted birth date of PY, births occurred in all months (Fig. 1) and there was no significant seasonal effect on the number of births recorded throughout the year ($\chi^2 = 10.73, df = 11, p = 0.47$).

**Growth of pouch young and sub-adults**

Weighing of PY was not attempted until the approximate mid-point of pouch life, as young are permanently attached to the teat prior to about week 6 - 8 of development (see Johnson and Delean 2001). In the second half of pouch life, growth appeared to be exponential, with young increasing from about 40 g at 60 days development, to between 250 - 300 g by PEP (Fig. 2). The smallest male and female B. tropica captured independent of their mothers...
Table 1. Estimated days elapsed between birth dates of successive *B. tropica* pouch young (PY) born to the same mother, based upon head length of PY. Error is the sum of errors (in days) calculated for successive young. Because post-partum birth usually follows permanent emergence from the pouch (PEP) within 24 hr, these estimates can be considered as estimated length of pouch life, except where indicated with a subscript. a Birth of subsequent PY predicted to have not followed PEP of previous PY with 24 hr. b PY predicted to have died prior to reaching PEP. c PY died in trap (thrown from pouch).

<table>
<thead>
<tr>
<th>PY</th>
<th>Sex</th>
<th>Estimated PEP</th>
<th>Final capture</th>
<th>Days since PEP</th>
<th>Age (months)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>63</td>
<td>F</td>
<td>26/5/95</td>
<td>14/8/95</td>
<td>80</td>
<td>6.6</td>
<td>805</td>
</tr>
<tr>
<td>24</td>
<td>M</td>
<td>30/6/95</td>
<td>19/9/95</td>
<td>81</td>
<td>6.7</td>
<td>850</td>
</tr>
<tr>
<td>73</td>
<td>F</td>
<td>24/6/95</td>
<td>10/9/95</td>
<td>108</td>
<td>7.6</td>
<td>950</td>
</tr>
<tr>
<td>67</td>
<td>F</td>
<td>7/1/95</td>
<td>10/9/95</td>
<td>95</td>
<td>7.2</td>
<td>–</td>
</tr>
<tr>
<td>18</td>
<td>F</td>
<td>5/3/95</td>
<td>23/9/95</td>
<td>79</td>
<td>6.6</td>
<td>895</td>
</tr>
<tr>
<td>79</td>
<td>M</td>
<td>5/3/95</td>
<td>23/9/95</td>
<td>79</td>
<td>6.6</td>
<td>850</td>
</tr>
</tbody>
</table>

Table 2. Re-capture histories of six PIT-tagged sub-adult *B. tropica* that were first recorded as PY. All animals were assumed to be immature at final capture based upon pouch condition (females) or testes size (males).

<table>
<thead>
<tr>
<th>Experimental fire treatment</th>
<th>Born pre-fire &amp; PEP pre-fire</th>
<th>Born pre-fire &amp; PEP post-fire</th>
<th>Born post-fire &amp; PEP post-fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unburnt Sites</td>
<td>10 (90%)</td>
<td>3 (100%)</td>
<td>4 (100%)</td>
</tr>
<tr>
<td>Burnt Sites</td>
<td>37 (89%)</td>
<td>9 (100%)</td>
<td>16 (100%)</td>
</tr>
</tbody>
</table>

Table 3. Number of *B. tropica* PY born on unburnt and burnt sites pre- and post-fire, and number of corresponding PEP events expected on unburnt and burnt sites pre- and post-fire. Numbers in parentheses indicate percentage that actually survived to PEP for each combination.

Of 88 individual PY recorded, 29 were large enough at the time of capture to inject with a PIT-tag. Six of these tagged PY were later recaptured independent of their mothers as sub-adults (Table 2), however, no *B. tropica* tagged as PY were recaptured as mature adults during the study. Twenty-one *B. tropica* were captured as sub-adults that had not been previously tagged (nine female, 12 male). Six of these females were later recaptured as mature adults (i.e., with a PY), and three of the males were subsequently recaptured having attained a weight greater than 1000 g (i.e., adult weight).
Fig. 1. Number of B. tropica births estimated to have occurred in each month from December 1994 to January 1997 at Davies Creek, according to a predictive equation based upon PY head length at time of capture, derived by Johnson and Delean (2001).

Fig. 2. Change in weight of B. tropica PY measured between December 1994 and January 1997 at Davies Creek, against estimated age according to a predictive equation derived by Johnson and Delean (2001) based upon PY head length at time of capture.

Sexual maturity and lifespan

The two smallest mature females (i.e., with a PY) captured during this study weighed 875 g and 950 g, and were likely 9 – 12 months of age (Johnson and Delean 2001). We captured a further eight B. tropica weighing between 750 and 950 g that we deemed to have not yet reproduced, based upon female pouch condition (teats were small buds) or small testes size in males. Mean adult weights (± S.E.) of B. tropica at Davies Creek were 1268 ± 26 g (females; n = 23) and 1220 ± 22 g (males; n = 29; Vernes 1999).

Data collected during our study and by McIlwee (1994) at Davies Creek provided some insights into lifespan of wild adult B. tropica. In addition, the minimum age of reproduction reported by Johnson and Delean (2001) of 10 months was added to the known minimum age of individuals that had achieved adult weight at first capture. By the end of the study, six adult animals (4 male, 2 female) had a known minimum age of > 4 years (4.3 – 4.9 years) and all were still alive.

Effect of fire

Fire did not affect either the likelihood of a female having a PY, or the likelihood of a PY dying before PEP. All five females that were captured without a PY were caught prior to the experimental fire, and all young that died prior to PEP did so before ignition of the experimental fire (Table 3).

DISCUSSION

As noted by Johnson and Delean (2001), B. tropica appear to have a similar reproductive strategy to other bettongs studied. Basic information on oestrous cycle length, gestation length and pouch life are now known for most Bettongia species, and for each of these parameters there is minimal interspecific variation (Seebeck and Rose 1989; Johnson and Delean 2001). In captive B. tropica and Tasmanian bettongs (B. gaimardi), birth and post-partum oestrus usually follow pouch vacation, and all three events usually occur within a 24-hr period (Rose 1986; Johnson and Delean 2001). Our wild population appeared to follow this same pattern; when consecutive young were recorded from a single female in this study, birth of a new young was typically estimated to have occurred within a few days of the predicted pouch emergence of the previous young. Breeding in our wild population was continuous, with births recorded in all months. Our data support earlier field observations by Johnson and McIlwee (1997) who suggested a continuous breeding season in B. tropica at Davies Creek; and captive work by Johnson and Delean (2001) who recorded continuous breeding in their captive population. Continuous breeding appears to be typical of other potoroids also (Seebeck and Rose 1989). Thus, given a pouch life of 106 days, a female B. tropica can theoretically rear three successive pouch young to permanent pouch emergence annually. This theoretical possibility is probably realised in most instances, given that 90 % of PY whose fate was known were predicted to have survived to permanent pouch emergence, and only 4 % of adult females captured did not have a PY.

Potoroids are relatively long lived, with a lifespan in the wild of more than seven years (Seebeck and Rose 1989). Although our time-series was insufficient to derive equivalent maximum ages for B. tropica, our data indicate that they are capable of living at least 4 - 5 years. Sexual maturity and first reproduction occur within the first year of life for most potoroids.
(Seebeck and Rose 1989), including B. tropica (Smith 1998; Johnson and Delean 2001). This is further supported in the field by our observation that the two smallest females recorded with PY in this study had achieved only approximately 75% of mean adult body weight. Thus, each female B. tropica probably achieves several years of reproductive activity.

Adult survivorship probability estimates during this study were in the order of 80% or above (Vernes 1999), suggesting that marked individuals left the population at a relatively low rate. Since longevity and fecundity in B. tropica are both relatively high and that population size at Davies Creek appears to be stable, it would follow that either juvenile mortality within or emigration from the population must also be high. Only six of 29 PIT-tagged PY were subsequently captured as sub-adults, and none were captured as adults. Our results thus suggest either high mortality of young following permanent emergence from the pouch, or high emigration of sub-adults from the study area. Both Rose (1987) and Johnson and Delean (2001) also note that the relatively short pouch life, early maturity, continuous breeding and long life-span of Bettongia indicate a theoretically high breeding potential.

Rose (1986) proposed that predation and environmental disturbance might limit B. gaimardi from reproducing themselves more than twice in a lifetime. Johnson and Delean (2001) also speculated that environmental factors and predation might have similarly suppressed the breeding potential of B. tropica. Our study of a wild population of B. tropica suggests that the theoretical breeding potential is realised in most instances, at least during the period that young are in the pouch. Furthermore, we could determine no effect of fire on any of the reproductive parameters we measured (since fecundity and PY survivorship were consistently high), suggesting that reproductive success is high regardless of fire-related disturbance. This is not surprising; Vernes (2000) did not detect any immediate effect of fire on adult survivorship, nor were there any negative effects of fire on home range (Vernes and Pope 2001), foraging success (Vernes and Haydon 2001) or dietary ecology, including body condition (Vernes et al. 2001). We acknowledge, however, that our conclusions regarding fire may be species and location-specific. Following relatively more intense fires in Western Australia, Christensen (1980) noted higher rates of mortality among adult B. penicillata than Vernes (2000) recorded for B. tropica.

We have very limited data on the fate of sub-adult animals in the population and so can only speculate on survivorship among this age class. More than likely, the period of highest mortality risk for B. tropica would be from the time of PEP, when the young at foot weighs about 300 g, to attainment of adult weight (1200 g), and this is certainly the cohort from which we recorded the lowest re-capture rates of tagged individuals. Nonetheless, the potential exists for the study area at Davies Creek to be a source population for adjacent Lamb Range locations to the north (Bridle Creek) and west (Emu Creek), both of which appear to have substantially lower B. tropica densities than Davies Creek (McIlwee 1994; Laurance 1997; L. Pope, pers. obs.). Pope et al. (2000) provide genetic evidence to indicate that Bridle Creek, the northernmost population in the Lamb Range, is likely sourced from Davies Creek. However, genetic results also indicate limited dispersal throughout the Lamb Range, perhaps further supporting a hypothesis of high sub-adult mortality (Pope et al. 2000). We conclude, therefore, that future research on B. tropica should include detailed examination of the fate of sub-adult animals after they leave the pouch, as sub-adult survival may be a factor limiting population growth in B. tropica in some parts of its range.

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REFERENCES


estimation and development of pouch young.


