Milk composition and growth in wild and captive Tasmanian pademelons, *Thylogale billardierii* (Marsupialia)

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Abstract. Changes in milk composition (total solids, carbohydrate, protein, lipid and calculated gross energy content) during lactation in three groups of wild (recently culled) and one captive group (fed \emph{ad libitum}) of Tasmanian pademelon (*Thylogale billardierii*) were related to growth rates and body condition. The habitats of the three wild groups differed. Total milk solids were generally greater in the captive group but this difference disappeared in late lactation. Milk carbohydrates showed a general increase to mid-lactation in all groups, decreasing subsequently, but were always greater in the captive group. The captive group's milk protein was always greater than those of wild Groups 1 and 2 but differed from wild Group 3 only in mid-lactation. Milk lipid concentrations started low in all groups; thereafter, the captive group had higher concentrations of lipid in mid-lactation but there were considerable differences between the groups in late lactation with Group 2 having the highest concentrations. Other than in the captive group there was little difference in energy content between early and mid-lactation. Growth rates of young differed between all wild groups, with the captive population exhibiting more rapid growth than all others. Thus, differences in milk composition resulting from different planes of nutrition can lead to differences in growth rates of marsupial young.

Introduction
Studies of milk composition have now been conducted on many marsupial species; however, most of these have been on captive populations, which can differ from their wild counterparts, particularly with respect to nutrition.

Maternal diet influences the composition of the milk produced by lactating mothers and this, in turn, may affect the growth of their young. Reduced food intake or deficiencies in nutrient levels of a lactating female will generally result in a reduced ability to rear young (Sadleir 1969) and many authors have noted that suboptimal nutrient intake in a eutherian mother leads to some alterations in composition of the milk (e.g. Prentice and Whitehead 1987; Verkerk et al. 1999).

In a detailed comparison of the milk of wild and captive common ringtail possums (*Pseudocheirus peregrinus*), Munks (1990) found that the changing levels of total milk solids in samples from wild animals during lactation were similar to those found in milk samples from captive animals. Levels of milk carbohydrate and the percentage contribution made by carbohydrate to the milk solids fraction in wild and captive ringtail possums were also similar. However, protein concentrations in milk samples from wild animals were lower and lipid concentrations were higher than in captive animals.

Muths (1996) measured the composition of wild-caught or shot red kangaroos (*Macropus rufus*) and found several significant differences between her data and those found by others on captive red kangaroos. Her data are particularly relevant for the present study, as she found no significant differences in the milk of wild-caught and recently killed red kangaroos.

Rose (1985) and Taylor and Rose (1987) showed that adult Tasmanian bettongs in the wild weigh less than captive adults and that the condition of wild pouch young is significantly poorer than that of captive pouch young. In addition, bettongs in the wild produce young when smaller/lighter than in captivity, suggesting that they are on a lower plane of nutrition (Rose 1985). Rose \textit{et al.} (2003) showed that variations in the diet in captivity led to compositional differences in the mother's milk. Although they found no differences in total solids, there was more lipid and energy in the milk of wild animals than in those of the captive groups.

*Thylogale billardierii*, also known as the red-bellied pademelon, rufous wallaby or Tasmanian pademelon, is a medium-sized macropodid marsupial that has become extinct on the southern mainland since European settlement and is now found only in Tasmania and on some Bass Strait islands (Calaby 1971). Within Tasmania it is widely distributed and highly abundant, occurring in both highland and lowland areas. It is commonly found in a variety of habitats including rainforest, wet sclerophyll forest and damp areas of dry sclerophyll forest, among dense shrubs or on pasture lands. Pademelons favour thickly forested areas or moist gullies neighbouring open pastures, as they are able to seek shelter in the forested areas during the day and emerge at dusk to browse on the open pastures (Driessen 1992).
The diet of the Tasmania pademelon consists of short green grasses and herbs, occasionally supplemented by browse from taller woody plants (Driessen 1992). The Tasmanian pademelon is most abundant where grassy clearings adjoin sheltering vegetation.

The reproduction of *Thylogale billardierii* is similar to that of most macropodid marsupials (Rose and McCartney 1982a, 1982b; Rose et al. 1999). Rose (1997) demonstrated that hormonal secretions induced by the suckling young pademelon inhibited reproductive cycles in its lactating mother.

Driessen (1992) noted that body condition and growth of this species in the wild was positively correlated with rainfall. He also noted that its dietary protein was higher when the pademelon inhabited areas of pasture rather than native vegetation.

This study aimed to measure and compare milk composition and growth in captive and wild Tasmanian pademelon young, in order to further understand the influence of diet on milk composition and growth. In addition, this is the first attempt to correlate various habitats in the wild with milk composition in a marsupial herbivore.

**Methods**

Samples from wild individuals were collected from culled (shot by professional shooters) animals at nine field locations in Tasmania: Bagdad, Bridgenorth, Bridport, Camden, Golden Valley, Meander, Oldina, Parkham, and Ross (Table 1). Culling (by shooting) was conducted from the beginning of May through to the end of August.

Prior to the commencement of this study a population of captive pademelons was well established at the University of Tasmania. These animals were sampled regularly from the end of June to the beginning of September, a period similar to that of the culling operations. These captive animals were maintained on a diet of pasture-replacement pellets (Pivot Nutrition, Launceston, Tasmania), lucerne chaff (Robert, Hobart, Tasmania) and various food scraps including apple, carrot and silver beet leaves in a semi-natural environment. The habitat they occupied could not be grazed or browsed due to lack of grasses and browsing vegetation so the diet available to captive population differed markedly from the diets of the field populations where browsing vegetation and grasses were the principal food sources consumed (Table 2). Information was not collected on nutritive value or size of plant biomass in the various habitats.

**Growth measurements**

Adult female pademelons from the captive population at the University of Tasmania were caught and placed in individual hessian bags and a 0.1 mL kg⁻¹ injection of Pamlin (diazepam, 5 mg mL⁻¹; Parnell Laboratories, NSW) administered to reduce their stress. The captured pademelons were then taken to the laboratory where their pouch young were removed and placed in a humidicrib at 35°C. The age of any young was determined using the growth equations of Rose and McCartney (1982b) and Driessen and Hocking (1996). In the wild, once an animal was shot its sex was determined and, if female, the pouch was inspected and the adult tagged with a number. Any pouch young were removed and euthanased with a 0.1–1.0 mL injection of Nembutal (pentobarbitone sodium, 60 mg mL⁻¹; Bomac Laboratories, NSW). If present, young at foot were also culled and both young tagged with numbers corresponding to that of the mother. As above, the head length (from snout to the back of the head) and pes length (from the heel to the end of the longest toe pad) of both the adult

<table>
<thead>
<tr>
<th>Location</th>
<th>Annual rainfall (mm)</th>
<th>Annual minimum temperature (°C)</th>
<th>Annual maximum temperature (°C)</th>
<th>Elevation (m)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bagdad</td>
<td>600–900</td>
<td>6–9</td>
<td>15–18</td>
<td>220</td>
<td>Improved pasture flats, surrounded by dry sclerophyll forest.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Soil: dry, coarse with outcrops of ironstone.</td>
</tr>
<tr>
<td>Bridgenorth</td>
<td>600–900</td>
<td>6–9</td>
<td>15–18</td>
<td>220</td>
<td>Logging coup, young blue-gum plantation surrounded by dry sclerophyll</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>and isolated tea-tree populations, ex-improved pasture, Sedge banks</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>present. Soil: rich basalt soils.</td>
</tr>
<tr>
<td>Bridport</td>
<td>600–900</td>
<td>6–9</td>
<td>15–18</td>
<td>60</td>
<td>Improved pasture flats, surrounded by tea trees.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Soil: dry loam soils.</td>
</tr>
<tr>
<td>Camden</td>
<td>1200–1800</td>
<td>0–3</td>
<td>9–12</td>
<td>680</td>
<td>Extensive native grasses surrounded by <em>E. delegatensis</em> and <em>E. nitens</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Soils: basalt soils.</td>
</tr>
<tr>
<td>Golden Valley</td>
<td>1200–1800</td>
<td>0–3</td>
<td>9–12</td>
<td>380</td>
<td>Ex-native forest and second-rotation <em>E. delegatensis</em> and <em>E. nitens</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Extensive native grasses surrounded by <em>E. nitens</em>. Soils: high-quality</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>basalt and loam banks.</td>
</tr>
<tr>
<td>Meander</td>
<td>900–1200</td>
<td>0–3</td>
<td>9–12</td>
<td>300</td>
<td>Improved pasture surrounded by plantation of <em>E. nitens</em> and native</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>forest of both wet and dry sclerophyll with minor species. Soil: rich</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>quality basalt and loam banks.</td>
</tr>
<tr>
<td>Oldina</td>
<td>900–1200</td>
<td>6–9</td>
<td>15–18</td>
<td>40</td>
<td>Forest reserve of improved grasses alongside logging coup containing</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>radiata pine. Soil: basalt soil.</td>
</tr>
<tr>
<td>Parkham</td>
<td>900–1200</td>
<td>6–9</td>
<td>15–18</td>
<td>220</td>
<td>Ex-improved pasture with plantation of <em>Eucalyptus nitens</em> ~8 years old</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>grown over the top. Native forest surrounds dry and wet sclerophyll with</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>minor native species. Soil: poorly drained basalt soils.</td>
</tr>
<tr>
<td>Ross</td>
<td>400–600</td>
<td>3–6</td>
<td>15–18</td>
<td>240</td>
<td>Improved pasture flats, extensive native grass areas, fine wool-growing</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>property. Surrounding forest: dry sclerophyll and some minor species.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Soil: dry, claylike soil.</td>
</tr>
<tr>
<td>University</td>
<td>600–900</td>
<td>6–9</td>
<td>15–18</td>
<td>120</td>
<td>No grasses, introduced diet, including lucerne, pasture-replacement</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>pellets, carrot, apple and leaves of silver beet.</td>
</tr>
</tbody>
</table>
and the young were measured to the nearest 0.1 mm using vernier callipers. The weight of the adult and the young was also recorded using balances appropriate for each individual animal.

**Milk collection**

To assist in the milking process of pademelons from the University of Tasmania population, each individual was injected intramuscularly with 0.1 mL kg⁻¹ of the lactation hormone oxytocin (oxytocin synthetic, 10 i.u. mL⁻¹; Heriot Agvet, Victoria) immediately before milking took place. Milk was collected as in Rose et al. (2003, 2005). All samples were labelled and stored at −20°C until analysed. Once milking was completed young were replaced and the adult released into the captive population. Milk collection in the field was performed similarly to the above. Due to the lack of circulation, an injection of oxytocin (0.1 mL kg⁻¹) directly into the mammary gland was used to assist in milk letdown. For easier access to the mammary gland and teat an incision was made down the centre of the length of the pouch. This allowed manual milking to be performed directly into an Eppendorf® tube.

**Milk analyses**

These were carried out as in our recent work (Ikonomopoulou et al. 2005; Rose et al. 2005). Total solids content of milk was determined by the ratio of dry mass to wet mass. Carbohydrate content was determined using the phenol-sulfuric acid method (Dubois et al. 1956) as modified by Messer and Green (1979). Protein content was calculated using the protein dye-binding method of Bradford (1976). The lipid fraction was determined using the creamatocrit method (Lucas et al. 1978) standardised by the Roese–Gottlieb ether extraction technique (cited in Horwitz 1980). Data are presented as g (100 mL)⁻¹ to allow direct comparison with data in Rose et al. (2005). The gross energy content of the milk was derived from the concentration of milk constituents (assuming the gross energy values of 16.1 kJ g⁻¹ (carbohydrate), 24.6 kJ g⁻¹ (protein) and 38.1 kJ g⁻¹ (lipid): Oftedal 1984).

**Statistical methods**

Due to the number of wild field sites, cluster analysis was performed based on the data in Tables 1 and 2 using a Bray–Curtis similarity matrix and multidimensional scaling analysis (Carr 1996), producing a stress level of 0.01.

All milk-composition data were statistically analysed using two-way non-linear analysis of variance (ANOVA) (Wilkinson et al. 1992) to test for significance between groups obtained from the cluster model. The 5% level of probability was accepted as indicating statistical significance. Post hoc tests were performed after all ANOVAs had determined significant interactions between and within groups. Growth parameters were first transformed (ln(x+1)) then analysed by least-squares regression. Analysis of covariance (ANCOVA) (Wilkinson et al. 1992) was used to test for differences in slopes and elevations of the regressions. Growth condition was also analysed using an analysis of covariance. The 5% level of probability was accepted as indicating statistical significance.

**Ethics**

The wallabies were culled by professional shooters licenced by the Tasmanian Parks and Wildlife Service. This work was carried out with the permission of the Animal Ethics Committee of the University of Tasmania under permit no. A0005636.

**Results**

After clustering the habitat data using a Bray–Curtis similarity matrix and multidimensional scaling, analysis resulted in the creation of three ‘habitats’. It was not considered necessary to include the data for the University captive site in this analysis because it differed so greatly from the wild field sites. Fig. 1 indicates that the grouping generated by the multidimensional scaling analysis reflects the Bray–Curtis similarity matrix. Throughout the remainder of the study these habitats will be referred to as Group 1 (Ross, Bagdad, Bridgenorth and Bridport), Group 2 (Parkham, Meander and Oldina), Group 3 (Camen and Golden Valley) and Group 4 (University of Tasmania, captive population). The characteristics of these habitats are described in Table 1 and their available browsing vegetation in Table 2.

Milk samples were grouped into three periods of lactation – early (Weeks 0–15) (while young are sucking frequently), mid (Weeks 16–25) (while young are sucking intermittently) and late (Week 26–weaning) (when young are leaving the pouch and starting to eat vegetation) (Table 3) – as used by Rose et al. (2005).

**Total solids**

Fig. 2a indicates the pattern and comparison of total solids in the milk of three wild (Groups 1, 2 and 3) and one captive population (Group 4). The horizontal lines indicate significant differences between the groups.

<table>
<thead>
<tr>
<th>Field location</th>
<th>Browsing vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bagdad</td>
<td>Cocksfoot (Dactylis glomerata), browntop bent (Agrostis capillaris), broad leaf weed, perennial ryegrass (Lolium perenne), white clover (Trifolium repens)</td>
</tr>
<tr>
<td>Bridgenorth</td>
<td>Browntop bent (Agrostis capillaris), sweet vernal grass (Anthoxanthum odoratum), Yorkshire fog grass (Holcus ionatus), buzzy (Acaena novae zelandiae)</td>
</tr>
<tr>
<td>Bridport</td>
<td>Cocksfoot (Dactylis glomerata), perennial ryegrass (L. perenne), white clover (T. repens)</td>
</tr>
<tr>
<td>Camden</td>
<td>Sweet vernal grass (Anthoxanthum odoratum), browntop bent (A. capillaries), white clover (T. repens L.), Yorkshire fog grass (H. ionatus)</td>
</tr>
<tr>
<td>Golden Valley</td>
<td>Juncus spp., Carex spp.</td>
</tr>
<tr>
<td>Meander</td>
<td>Perrenial ryegrass (L. perenne), Yorkshire fog grass (Holcus ionatus), white clover (T. repens), cocksfoot (D. glomerata)</td>
</tr>
<tr>
<td>Oldina</td>
<td>Cocksfoot (Dactylis glomerata), browntop bent (Agrostis spp.)</td>
</tr>
<tr>
<td>Parkham</td>
<td>Danthonia decumbens (native), trefoil (Lotus sueveolans), browntop bent (Agrostis spp.), hair grass (Vulpia spp.), buzzy (A. novae zelandiae), Cyperaceae spp. Some native grasses</td>
</tr>
<tr>
<td>Ross</td>
<td>Subterranean clover (Trifolium subterraneum L.), Hair grass (Vulpia spp.)</td>
</tr>
<tr>
<td>University</td>
<td>No browsing vegetation</td>
</tr>
</tbody>
</table>
A significant difference occurred in the interactions between the groups and the periods of lactation ($F_{6,67} = 2.4260, P = 0.035$). During early lactation (0–15 weeks) the total solids fraction in the milk of the wild populations represented 9.0–10.4% of the milk and remained relatively constant throughout mid-lactation (16–25 weeks). No significant differences in total solids were found during early and mid-lactation between the three wild populations. During late lactation, at the time of pouch emergence, the percentage of total solids increased to 20–27%, with a significant difference occurring between wild Groups 1 and 2.

The captive population had a significantly higher value (>17%) than all wild populations for total solids during early lactation; this increased to >22% during mid-lactation and was significantly different from that of all wild populations.

During late lactation, however, the total solids of the captive group remained relatively constant.

**Carbohydrate content**

Fig. 2c indicates that the general trend for carbohydrate concentration for both wild and captive populations throughout lactation was an increase from early lactation to mid-lactation (and a rapid decrease during late lactation). Significant differences between wild populations are apparent as well as significant differences between captive and wild populations ($F_{6,110} = 4.4502, P = 0.0005$).

During early lactation significant differences occurred between wild Groups 1 and 2, as well as between Groups 1 and 3. Early lactation values of carbohydrate concentration for the wild populations were 5.7–7.3 g (100 mL)$^{-1}$, increasing slightly during mid-lactation (6.7–10.2 g (100 mL)$^{-1}$), with Groups 2 and 3 significantly different during this period. Carbohydrate concentration then decreased to values of 0.1–4.7 g (100 mL)$^{-1}$ in late lactation, resulting in a significant difference between Groups 1 and 3. The captive population had significantly higher carbohydrate concentrations throughout all stages of lactation than did the wild populations.

**Protein content**

The protein content of the milk of wild and captive groups increased as lactation progressed. Significant differences were found between wild populations and between captive and wild populations (Fig. 2b) ($F_{6,116} = 2.8745, P = 0.012$).

The protein content of the milk from the wild populations was 6.3–8.7 g (100 mL)$^{-1}$ during early lactation. The protein content of wild groups increased slightly during mid-lactation, with protein content ranging from 7.6 to 8.8 g (100 mL)$^{-1}$. Significant differences occurred between Groups 1 and 3 as well as between Groups 2 and 3 during early lactation; however, no significant differences were found between wild populations during mid-lactation. Protein content increased during late lactation and a significant difference occurred between Groups 1 and 2, between Groups 1 and 3 and between Groups 1 and 4.

The milk of the captive population contained 10.1 g (100 mL)$^{-1}$ of protein during early lactation, with an increase occurring during mid-lactation that changed little in late lactation (14.4 g (100 mL)$^{-1}$), unlike the wild groups. Group 4 differed significantly from Groups 1 and 2 during

### Table 3. Details of the number of milk samples obtained from the four groups of pademelons

<table>
<thead>
<tr>
<th>Stage of lactation</th>
<th>Group 1</th>
<th>Group 2</th>
<th>Group 3</th>
<th>Group 4</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early (≤15 weeks)</td>
<td>31</td>
<td>22</td>
<td>5</td>
<td>14</td>
<td>72</td>
</tr>
<tr>
<td>Mid (16–25 weeks)</td>
<td>25</td>
<td>28</td>
<td>18</td>
<td>6</td>
<td>77</td>
</tr>
<tr>
<td>Late (≥26 weeks)</td>
<td>11</td>
<td>7</td>
<td>11</td>
<td>5</td>
<td>34</td>
</tr>
<tr>
<td>Total</td>
<td>67</td>
<td>57</td>
<td>34</td>
<td>25</td>
<td>183</td>
</tr>
</tbody>
</table>
early lactation and from Groups 1, 2 and 3 during mid-lactation. However, by the time of late lactation Group 4 was significantly different only from Group 1.

**Lipid content**

In wild populations lipid concentrations remained low throughout early and mid-lactation (<10 g (100 mL)^{-1}) but increased markedly during late lactation. No significant differences were found within the wild groups during early and mid-lactation periods. Significant differences occurred between wild groups only during late lactation (Fig. 2d) \((F_{6,103} = 3.0389, P = 0.0089)\) with Group 2 having the highest concentrations.

The lipid content of the milk of the captive population increased between early and mid-lactation, becoming significantly different to that of the wild groups; however, no significant differences between the captive and wild populations were evident during early lactation. Significant differences did occur, however, between the captive population and Groups 1 and 2 during late lactation, with Group 1 having a lower lipid concentration and Group 2 having a higher lipid concentration than the captive population.

**Energy content**

Using the values of 16.1 kJ g^{-1} (carbohydrate), 24.6 kJ g^{-1} (protein) and 38.1 kJ g^{-1} (fat) (Oftedal 1984), the total energy content of milk at early, mid and late lactation for all four groups was estimated (Fig. 3).

The total milk energy for Groups 2 and 4 increased as lactation progressed. The energy value for the milk of the captive population increased steadily (938 to 1819 kJ mL^{-1}) throughout lactation; however, the energy value of the milk of Group 2 increased rapidly between mid and late lactation, resulting in the highest milk energy value (2610 kJ mL^{-1}) during late lactation. The total milk energy for Groups 1 and 3 changed little or decreased slightly between early and mid-lactation but increased markedly during late lactation, resulting in the milk of Group 2 having higher milk energy content (1980 kJ mL^{-1}) than that of the captive population.

In summary, total solids were greater in the captive group but this difference disappeared by late lactation. Carbohydrates showed a general increase to mid-lactation, decreasing subsequently, but were always greater in the captive group. Protein gradually increased through lactation; the captive group’s milk protein was greater than that of wild Groups 1 and 2 in early lactation but was greater than that of all wild groups during mid-lactation. Group 1 had the lowest protein concentration in late lactation. Lipid concentrations started low in all groups; thereafter the captive group had higher concentrations of lipid in mid-lactation but there were considerable differences between the groups in late lactation, with Group 2 having the highest concentrations. Other than...
in the captive group (the milk of which had the greatest energy content, and the energy content of which increased from early to mid-lactation) there was little difference between early and mid-lactation. However, the energy content increased in all groups in late lactation, with Group 2 again having the highest energy. Not surprisingly, the graphs of lipid and energy content over time appeared very similar.

**Growth**

In all four populations, the weight of the young showed an exponential increase with increasing age. Each curve was logarithmically transformed and a regression equation calculated:

- Group 1  \[ y = 0.224x + 1.070 \quad (r^2 = 0.960) \]
- Group 2  \[ y = 0.213x + 1.177 \quad (r^2 = 0.961) \]
- Group 3  \[ y = 0.200x + 1.385 \quad (r^2 = 0.946) \]
- Group 4  \[ y = 0.229x + 1.068 \quad (r^2 = 0.973) \]

where \( y \) = weight and \( x \) = age (ln(age)).

The four populations were significantly different \( (F_{3,98} = 17.3, P < 0.001) \). From the above regression equations it is evident that the University population (Group 4) had the greatest slope (i.e. grew more rapidly) compared to all wild populations. Group 1 had a steeper slope than Groups 2 and 3 and Group 2 had a steeper slope than Group 3. Therefore the young pademelons in the captive population grew more rapidly than the wild young, however, differences in growth also occurred among wild populations.

An index of condition (body mass/head length: Rose et al. 2003) was estimated for each young; this relationship varied little during early pouch life for the four populations. During mid and late pouch life, however, captive and wild Group 1 pouch young had an improved body ‘condition’ compared to the other two wild populations, Groups 2 and 3.

After transformation, the regression equations calculated for each population are:

- Group 1  \[ y = 0.091x - 0.153 \quad (r^2 = 0.942) \]
- Group 2  \[ y = 0.071x + 0.004 \quad (r^2 = 0.974) \]
- Group 3  \[ y = 0.071x + 0.014 \quad (r^2 = 0.956) \]
- Group 4  \[ y = 0.097x - 0.089 \quad (r^2 = 0.941) \]

where \( y \) = body mass / head length and \( x \) = ln(age).

All four populations were significantly different \( (F_{3,98} = 9.0143, P < 0.001) \). From the above regression equations it is evident that the captive population has a steeper slope than the wild populations. Wild Group 1 is slightly steeper in slope than the remaining two wild groups and Groups 2 and 3 are similar in slope but slightly different in elevation.

**Discussion**

A cautionary note should be added in that although we have measured milk concentrations we have not measured milk consumption among the four groups. If this differed between groups it would also explain some of the differences in growth. However, this study has found differences in milk composition between captive and wild Tasmanian pademelons and for the first time between populations of wild marsupials from different habitats in the wild.

Rose et al. (2003) have shown that diet can influence the quality of milk produced by the Tasmanian bettong, Bettongia gaimardi, another Tasmanian macropodid marsupial. Green et al. (1988), Merchant et al. (1994) and Trott et al. (2003) pointed out that, from their studies of inter- and intraspecific transfers of marsupial pouch young and milk production in the tammar wallaby, growth may be either enhanced or restricted by the quality or quantity of milk supplied.

The environment has an important effect on lactation of the Tasmanian pademelon, causing significant differences in milk composition and growth of pouch young between captive and wild populations. Although captive and wild populations have been used as a comparison in some previous research, this study is the first to demonstrate differences in milk composition between wild populations of a marsupial.

In captivity, female Tasmanian pademelons produce young throughout the year; however, in the wild a period of peak births occurs during April–June (Rose and McCartney 1982a; Driessen 1992). This may indicate that nutritional and environmental factors are involved with female fertility and subsequent lactation in the wild. The reason for the apparently marked differences in milk composition by the captive and wild populations in this study may reflect the differences in the diets of the three wild and one captive population. The captive population was maintained in a temperate region protected from seasonal variation and where required metabolic activity is reduced by a constant supply of food and an

![Fig. 3. Mean changes (± s.e.) in energy content of the milk from three wild groups (Groups 1–3) and one captive group (Group 4) of Tasmanian pademelons for early, mid and late lactation. Horizontal lines reflect significant differences.](image-url)
absence of predators and competitors. This has enabled a continuous reproductive pattern and high quality of maternal milk, leading to young having high body condition.

In contrast, the habitats of the wild populations could be characterised by climatic variability. Wild Group 1 browsed on high-nutrient-improved pasture grasses and was subject to high temperature and low rainfall. Similar vegetation was available for Group 2; however, higher rainfall and milder temperatures enhanced the quantity of vegetation and the quality of milk produced compared with Group 1. Wild Group 3 experienced high rainfall and lower temperatures. Greater quantities of vegetation for this group were available for browsing; however, the quality of the maternal diet was somewhat reduced due to the lack of improved pasture grasses and abundance of native grasses.

The wild populations had milk with a lower nutrient content and consequently their young had a reduced body condition compared with the captive population. These restrictions on milk composition and growth may allow the mother to cope more successfully with a variable environment, which may be subject to water restrictions and restricted food availability.

Rose et al. (2005) studied the milk composition of six Tasmanian pademelons in captivity, although their diet differed from the captive pademelons in this study in that they ate grass and shrubs supplemented with solid dog food. The results for composition of milk were similar to those from Group 4 in the present study though protein concentrations in late lactation in the earlier study were lower. They found that although milk concentrations changed little during lactation the energy content increased almost four-fold from 540 ± 39 kJ (100 mL)^{-1} (mean ± s.e.) to 1908 ± 102 kJ (100 mL)^{-1}. Carbohydrate concentrations decreased from 13.3 ± 0.1 g (100 mL)^{-1} (early lactation) to 10.9 ± 0.9 g (100 mL)^{-1} in mid-lactation, falling to 4.8 ± 0.9 g (100 mL)^{-1} in late lactation. Lipid increased from 6.3 ± 1.1 g (100 mL)^{-1} to 12.5 ± 4.1 g (100 mL)^{-1}, reaching 31.4 ± 5.0 g (100 mL)^{-1} in late lactation. Protein increased from 3.3 ± 0.1 g (100 mL)^{-1} to 9.7 ± 1.6 g (100 mL)^{-1} in mid-lactation to 14.0 ± 1.5 g (100 mL)^{-1} in late lactation. This relatively high level of lipid and protein in late lactation may be the cause of the more rapid growth and, hence, shorter pouch life of the Tasmanian pademelon than the well-studied tammar wallaby, Macropus eugenii (Green et al. 1988; Dove and Cork 1989).

Although lactation in marsupials appears to be a predetermined process (Trott et al. 2003) in that the suckling of the young has little influence on milk composition, this study has indicated that aspects of milk composition, growth and condition of young are influenced by environmental factors. Sadleir (1969) put forward the view that in marsupials, although reduced food intake or deficiencies in food quality result in detrimental effects on the ability to rear young, up to a certain point females will mobilise their own body reserves to produce milk before the quantity or quality of the milk decreases. It appears that the Tasmanian pademelon may be well able to make use of this phenomenon given that its early lactation takes place in autumn/winter when food is abundant due to higher rainfall, and maternal body condition can be ‘stored’ for the drier period when young are leaving the pouch in early summer. Other species, for example the koala (Logan and Sanson 2003), may increase the efficiency of feeding during lactation, compensating for the higher energetic demands by increasing intake and, to a lesser degree, investing more in each mouthful. Several studies have compared growth/condition of marsupial pouch young in captivity with that in the wild. Some studies reported little, if any, difference between growth of wild and captive pouch young (Shield and Woolley 1961; Sharman et al. 1964; Sadleir 1969; Close and Bell 1990; Delaney and De’ath 1990), while others have found differences (Ealey 1967; Wood et al. 1983; Taylor and Rose 1987; Munks 1990; Rose et al. 2003). These variable findings may be explained by the differences in the mother’s ability to produce milk by metabolising her body fat and/or muscle. This might occur when the diet in the wild is suboptimal; alternatively, there may be substantial differences between the diet in the wild and in captivity.

It should also be considered that adequate water intake and metabolism is important for lactation (Tauson et al. 1998). Although Groups 1 and 2 lived in drier habitats most lactation takes place in the cooler autumn and winter months, hence water restriction is not a likely factor hampering lactation in these groups.

Food availability limits the amount of energy and the levels of specific nutrients that are allocated to the developing young. Variations in the quality and quantity of food can alter the energy costs to the mother of acquiring food, which, in turn, alters the composition and quantity of milk produced and hence the pattern and rate of growth of the young. This and other studies now indicate that there is some plasticity in the concentration of the various components of marsupial milk, which, in turn, can affect growth.

References


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