

## Milk Composition in the Northern Brown Bandicoot, *Isodon macrourus* (Peramelidae, Marsupialia)

J. C. Merchant and J. A. Libke

Division of Wildlife and Ecology, CSIRO, P.O. Box 84, Lyneham, A.C.T. 2602.

### Abstract

Milk samples were obtained at regular intervals throughout lactation from northern brown bandicoots, *Isodon macrourus*, in captivity. Total concentration of milk solids was initially 7% (w/w) and increased linearly to 45% (w/w) by 55 days. Carbohydrate, lipid and protein concentrations increased from about 2% (w/w) to about 7-8% (w/w) at 30 days. Thereafter they diverged, with lipid increasing to between 25-30% (w/w) at 56 days, protein reaching maximal values of 10-15% (w/w) at just over 40 days and carbohydrate gradually declining to about 5% (w/w) at 56 days before a rapid fall to 1-2% (w/w) at the completion of lactation. The milk of the bandicoot exhibits a similar pattern of change during the course of lactation to that shown by other marsupials.

### Introduction

Milk composition in the marsupials has been studied in some detail only in recent years. Several authors have reported sequential changes in the milk solids fraction of marsupials, e.g. Gross and Bolliger (1959) for the brush-tailed possum, *Trichosurus vulpecula*, and Lemon and Barker (1967) for the red kangaroo, *Macropus rufus* (= *Megaleia rufa*). However, most work on a single species has been done on the monotocous and seasonally breeding tammar wallaby, *Macropus eugenii* (Green *et al.* 1980). A similar study of the eastern quoll, *Dasyurus viverrinus*, has just been completed (Green *et al.* 1987). The latter species is also a seasonal breeder but one that produces several young (Hill and O'Donoghue 1913). The peramelid marsupial, *I. macrourus*, the subject of the present study, is also polytocous with an average litter size of 3-4; however, it may breed continuously throughout the year in some parts of its range (Gordon 1974). In addition, it has one of the shortest lactational cycles of any marsupial irrespective of size and the young are generally described as having a very fast rate of growth (Mackerras and Smith 1960; Lyne 1964). Young bandicoots are born after a gestation period of about 12 days (Lyne 1974) and lactation continues for about 60 days in *I. macrourus* (Gemmell 1982). At about 43 days into lactation an oestrus occurs (Gordon 1974) at which the female may be fertilized so that weaning of the first litter is followed closely by birth of the next.

The aim of this study was therefore to determine whether lactation in the bandicoot followed a similar pattern to that of the other marsupial groups so far examined. This information would allow a greater appreciation of the generality or otherwise of lactational patterns in marsupials. The present paper deals with milk composition and is part of an overall study aimed at determining the energetic costs to the mother of sequential lactations throughout a breeding season.

## Methods

### *Animal Colony*

The captive colony was established in June 1983 with six females and five males live trapped at Dorrigo, N.S.W. These females did not have young in the pouch but started breeding in August after 2 months in captivity at the Division of Wildlife and Ecology, CSIRO, Canberra, A.C.T. Examination of the females' pouches every 2 days established the approximate birthdates of the first young. In eight cases, birth had only just occurred (between 1017 h and 1215 h) as young found in the pouch were still attached to their umbilical cords.

### *Animal Husbandry*

Animals were maintained in outdoor enclosures (8 m  $\times$  10 m) grassed with *Phalaris tuberosa*. Enclosures were lined to 1.2 m with galvanized sheeting embedded in concrete and entirely enclosed with wire netting to prevent the entry of predators. Initially, pens were set up with three females and one male. Some young remained in the pens after weaning so that numbers increased until sub-adults were removed. These young did not appear to be harmed by the adults. Food was provided *ad libitum* as dog food (Harper's Puppy Chow; Arnott-Harper Pty Ltd) and occasionally sliced bread and apples. Animals also had access to whatever invertebrates or plant material they might find edible. The pens contained a plentiful supply of earthworms. Water was freely available at all times.

Shelter was provided in the form of low brick structures (1 m long  $\times$  0.5 m wide  $\times$  0.5 m high) open at one end only and covered by either wood or galvanized tin sheeting. Meadow hay was piled on top as insulation and also used as nest material inside. Animals usually preferred to build their own nests in the long grass but in winter tended to use the brick shelters more frequently.

### *Animal Handling*

When grass nests were located, a circular net (0.5 m diam.) was placed over the entire nest. The narrow end of the net had a drawstring so that it could be opened to handle animals in the nest or closed and used to catch bandicoots that were moving freely in the pen. Once the net was in place the nest was gently prised open and if a bandicoot was present it could usually be picked up in a small calico bag. If the animal did jump from the nest it was restrained by the net so that it could still be placed in the bag easily.

Before the animals were caught, the bags were tared on a balance so that it was a simple procedure to weigh the animal once caught. With gentle handling animals lay quietly and the pouch could be examined for the presence of young and the condition of the teats. Teats were numbered from 1 to 4 from the anterior position and given the prefix L for left or R for right.

To facilitate milk collection young were removed from the pouch for 4–5 h to allow milk to accumulate in the mammary glands. While the young were naked they were kept in a humid incubator at 35°C. When furred they were kept warm in calico bags. While out of the pouch they were weighed and measured. Milk was collected from the mothers after an intramuscular injection of oxytocin (Syntocinon; Sandoz, Australia) at a dosage of 0.8 i.u. kg<sup>-1</sup> body weight. Anaesthetic was not required as females, if gently handled, lay quietly during milking.

### *Milk Analyses*

The milk-solid content was determined gravimetrically to 0.1 mg on a Mettler balance (model K5T) by freeze-drying a known weight of milk, about 50–100 mg, in pre-weighed plastic vials. Very small samples, about 10 mg, were weighed in pre-weighed aluminium foil containers on a Cahn 21 Automatic Electrobalance to 0.001 mg and dried in a desiccator. All samples were subsequently reweighed to determine total solids.

Carbohydrate concentrations were determined as total hexose using the methods of Messer and Green (1979) and crude lipid determinations by the methods of Green *et al.* (1983). In the first 30–35 days of lactation the quantity of milk available for collection was small making analysis for lipid difficult. In this period lipid was estimated as the difference between total solids and the combined protein and carbohydrate, assuming an ash content of 5% of the solids fraction.

Total nitrogen was estimated using the dried residues of the total solids determinations, which were digested using the Kjeldahl procedure. Total nitrogen was estimated by a microdiffusion technique (Conway 1962) and converted to protein using a factor of 6.38. Small samples from early lactation, before 30 days, were analysed by the refined Coomassie blue method of Spector (1978).

The concentrations of the electrolytes sodium (Na<sup>+</sup>) and potassium (K<sup>+</sup>) were determined with a

Varian 1000 atomic absorption spectrophotometer using an acetylene-air gas mixture. The dilutions used were either 5  $\mu$ l or 10  $\mu$ l milk in 2 or 3 ml de-ionized water. The concentrations are expressed as mmol l<sup>-1</sup> of milk.

Analyses were based on 63 samples from 18 females, 10 of which contributed some data to Merchant (1989). These samples were used for determination of solids (% w/w, 61), carbohydrate (g 100 ml<sup>-1</sup>, 57), protein (% w/w, 36) and lipid (% w/w, 16); a further 18 lipid estimations were obtained by difference.

## Results

### Milk Solids

Early in lactation the milk was dilute (Fig. 1), with a total solids concentration of 7–9% (w/w). By midway through lactation, at 30 days, concentrations had reached 25–30% and by the time weaning began at 55 days they were as high as 45%. After 55 days solids concentrations dropped rapidly to around 10% (w/w) at 59 days. The increase in milk solids concentrations to 56 days was linear (Fig. 1).

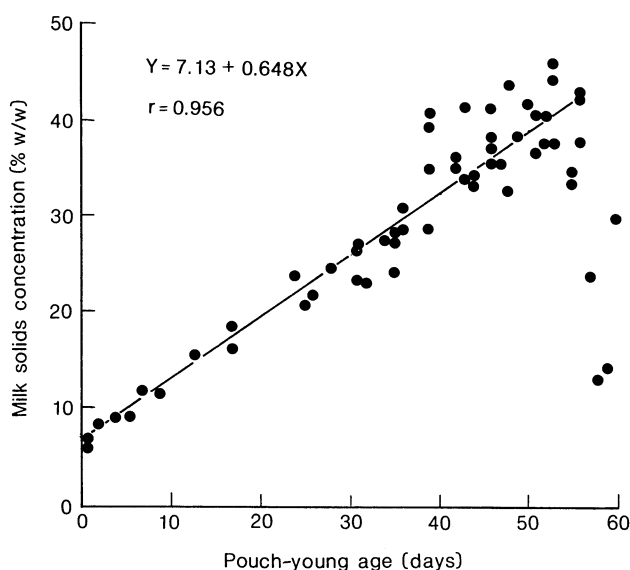


Fig. 1. Changes in total milk solids during lactation in *Isodon macrourus*. Regression equation represents data to 56 days.

### Carbohydrate

Carbohydrate concentrations (g 100 ml<sup>-1</sup>), expressed as total hexose, started at around 2 g 100 ml<sup>-1</sup> and rose to 6–8 g 100 ml<sup>-1</sup> by 30 days (Fig. 2). From 30 to 55 days there was a slight downward trend to values around 5–7 g 100 ml<sup>-1</sup>. Around 55–60 days values dropped rapidly to about 1 g 100 ml<sup>-1</sup>.

### Lipid

Lipid concentrations commenced at about 2% (w/w) and increased to around 10% by 30 days (Fig. 3). Thereafter they continued to increase and reached about 25% by 55 days.

The triglyceride fraction of the lipid was analysed to determine the fatty acid complement in 19 samples from seven females between 39 and 56 days of lactation. The concentrations (% w/w) of the various fatty acids showed no change over this time and are presented (Table 1) as averages for the period. Palmitic acid (C16:0) at 27.31% and oleic acid (C18:1) at 36.31% were present in the highest concentrations. Stearic (C18:0) and linoleic (C18:2) acids at 10.11% and 12.36% respectively also contributed significantly.

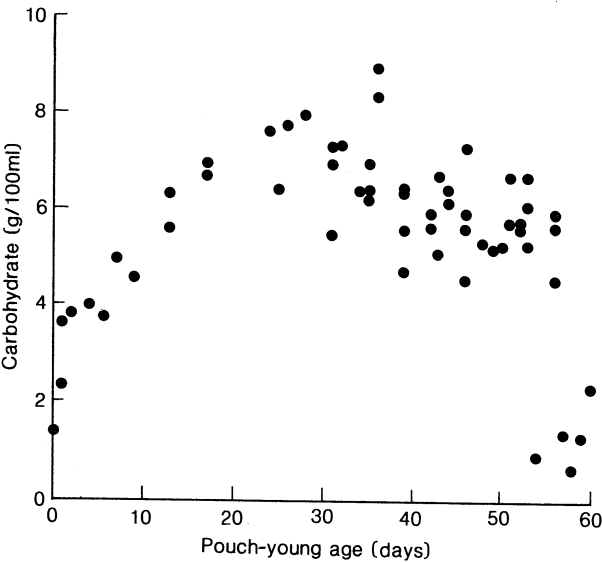


Fig. 2. Changes in carbohydrate concentration (g 100 ml<sup>-1</sup>) during lactation in *Isodon macrourus*.

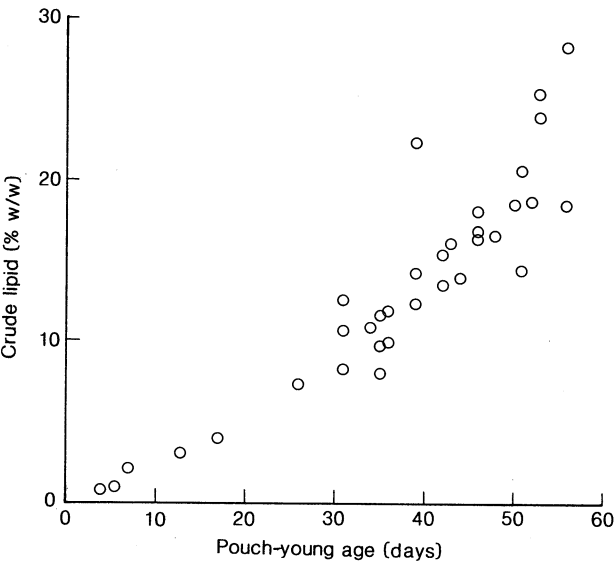


Fig. 3. Changes in crude lipid concentration (% w/w) during lactation in *Isodon macrourus*.

Table 1. Major fatty acids of the milk triglycerides over the period 39 to 56 days of lactation in *Isodon macrourus*  
Values expressed as mean percentages (w/w) of the total triglyceride fraction  $\pm$  1 s.d.

|      | Fatty acids |       |       |      |       |       |      |
|------|-------------|-------|-------|------|-------|-------|------|
|      | 14:0        | 16:0  | 18:0  | 16:1 | 18:1  | 18:2  | 18:3 |
| Mean | 2.88        | 27.31 | 10.11 | 5.03 | 36.31 | 12.36 | 1.22 |
| s.d. | 1.25        | 2.11  | 1.63  | 1.89 | 3.30  | 0.93  | 0.33 |
| n    | 19          | 19    | 19    | 19   | 19    | 19    | 19   |

### Protein

Protein concentrations began at about 2% (w/w), had increased to 8% by 30 days and then gradually rose to a maximum of 10–14% at 40–45 days (Fig. 4). By 50–55 days protein concentrations had fallen to around 8–10% and then declined further to about 2% (w/w) at the end of lactation. Milk of this protein content was obtained from both previously sucked and unsucked teats (Table 2).

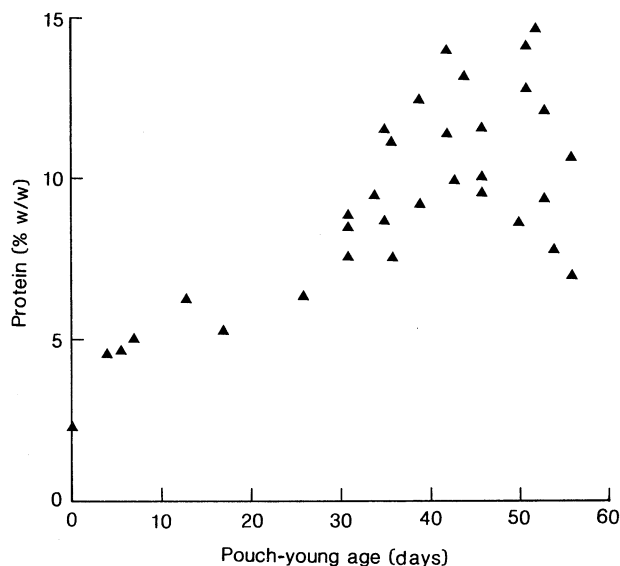


Fig. 4. Changes in protein concentration (% w/w) during lactation in *Isodon macrourus*.

Table 2. Milk composition in teats of different type close to parturition in *Isodon macrourus*

PU = previously unsucked; PS = previously sucked; + = with new young attached; – = no young

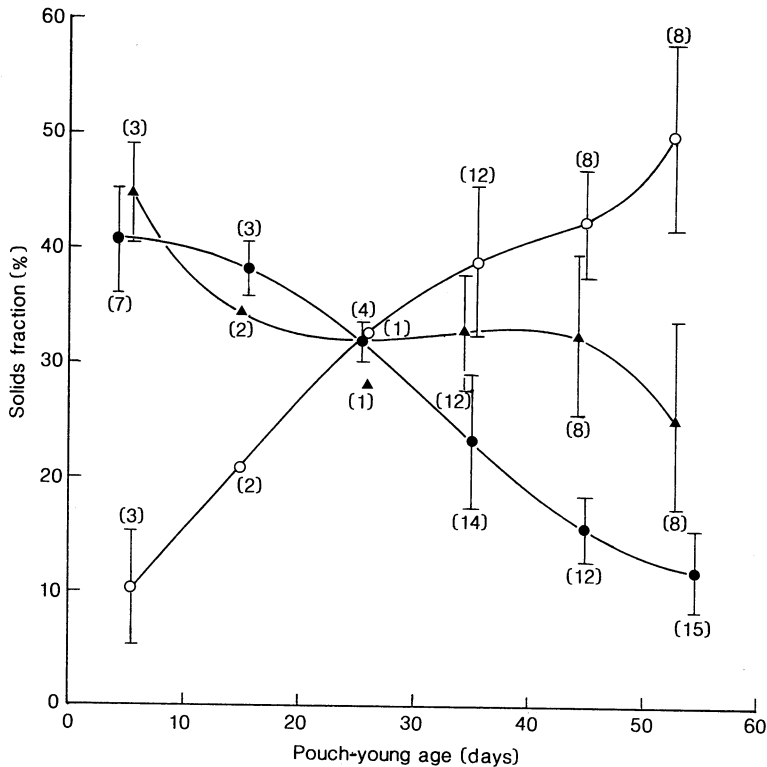
| Animal No. | PYage <sup>A</sup> (days) | Teats | Solids (% w/w) | Hexose (% w/w) | Protein (g 100 ml <sup>-1</sup> ) | Na (mm l <sup>-1</sup> ) | K (mm l <sup>-1</sup> ) |
|------------|---------------------------|-------|----------------|----------------|-----------------------------------|--------------------------|-------------------------|
| S44        | 2 h                       | PU+   | —              | 1.4            | 2.2                               | 91                       | 10                      |
| S44        | 2 h                       | PS+   | 7.05           | 1.2            | 2.3                               | 95                       | 9                       |
| S44        | 2 h                       | PU–   | 6.03           | 1.7            | 2.0                               | 90                       | 11                      |
| S33        | <1                        | PU+   | 6.67           | 2.37           | —                                 | 98                       | 17                      |
| S33        | <1                        | PS+   | 8.87           | 2.02           | —                                 | 108                      | 10                      |
| S33        | <1                        | PS–   | 9.55           | 2.23           | —                                 | 110                      | 8                       |
| S38        | 1                         | PU+   | 7.53           | 3.65           | —                                 | 77                       | 20                      |
| S38        | 1                         | PU–   | 7.55           | 0.56           | —                                 | —                        | —                       |
| S21        | 2                         | PU+   | 8.74           | 3.83           | —                                 | 62                       | 24                      |
| S21        | 2                         | PS+   | 9.06           | 3.27           | —                                 | 66                       | 21                      |
| S21        | 2                         | PS–   | 15.73          | 0.70           | —                                 | 124                      | 21                      |

<sup>A</sup> PYage = age of pouch young.

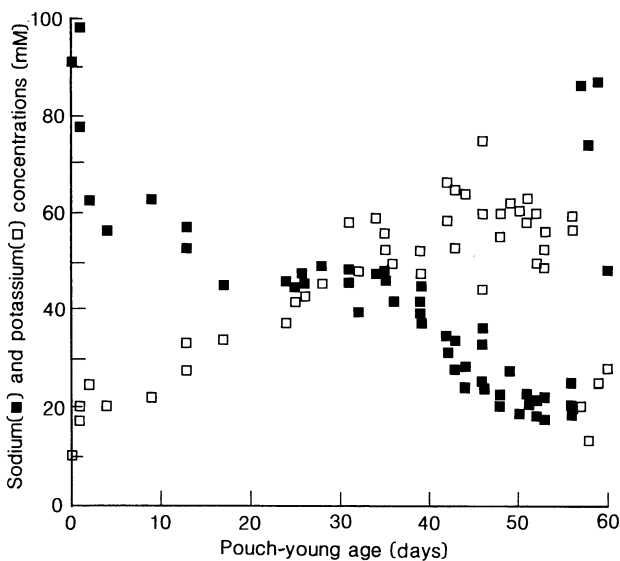
### Carbohydrate : Lipid : Protein Ratios

The relative contributions of carbohydrate, lipid and protein to the solids of the milk are presented in Fig. 5. Carbohydrate showed a consistent decline from about 40% to about 10% throughout lactation, whereas lipid, in contrast, increased from about 10% to around

50%. Protein values began at about 40–45% of the solids fraction but by 35 days they had declined to around 30–35%; these values were maintained between days 40 and 50. Values then began to decline, some individual values reaching 16% at the end of lactation.



**Fig. 5.** The relative proportions of carbohydrate (●), lipid (○) and protein (▲) throughout lactation in *Isoodon macrourus* expressed as a percentage of the solids fraction of the milk. Values are given as means  $\pm$  1 s.d. (n).



**Fig. 6.** Changes in the concentrations of sodium (■) and potassium (□) during lactation in *Isoodon macrourus*.

### Electrolytes

Sodium concentrations in the milk at parturition were between 78–98 mmol l<sup>-1</sup> (Fig. 6). There was an initial sharp decrease to about 50–60 mmol l<sup>-1</sup> over the next 2 days followed by a gradual decline to about 45 mmol l<sup>-1</sup> at 30 days. The levels were maintained between 30 and 40 days, after which a more rapid decrease became evident so that by 50–55 days sodium concentrations had fallen to around 20 mmol l<sup>-1</sup>. After 55 days sodium concentrations increased to the values observed around parturition.

Potassium concentrations in the milk generally showed the reverse of sodium with initial values around 10–20 mmol l<sup>-1</sup> rising to about 45 mmol l<sup>-1</sup>, the same concentration as sodium, by 30 days. Potassium concentrations continued to increase to around 60 mmol l<sup>-1</sup> although there was considerable variability in these later values. After 55 days values dropped markedly to concentrations around 10–20 mmol l<sup>-1</sup>, very similar to those observed at the beginning of lactation. The curves for the two electrolytes cross at about 30 days and again between 55 and 60 days.

### Newly Lactating and Previously Suckled Teats

Newborn young entering the pouch may encounter either teats that have not previously and recently been sucked or teats that were sucked by members of the previous litter as recently as the day before. In one case (animal S33), three young aged 56 days were present in the pouch and white milk could be expressed from the sucked teats on the day prior to the birth of her next litter. On the following morning six newborn young were attached to teats in the pouch. Three of these young were attached to large and previously sucked teats (PS). One of these young and two young from small previously unsucked teats (PU) were removed to allow collection of milk. Milk was also collected from two large teats, which did not have new young attached. The small teats without young did not give sufficient milk for analysis. The composition of the milk from these teats and also samples from other females with two types of teat are presented in Table 2. These data suggest that by the time newborn young have attached to the teats there is little difference in milk composition between the PU teats and the PS teats, i.e. between the early milk produced by a newly activated mammary gland and that produced by a gland that has undergone regression over the preceding few days. When new young were found in the pouch, members of the previous litter were seldom found in the same nest as their mother.

### Discussion

The milk of the northern brown bandicoot exhibits a pattern of change during the course of lactation similar to that shown for other marsupials (Green 1984; Green *et al.* 1987; Crowley *et al.* 1988). The bandicoot, however, accomplishes these changes over a much shorter period of time than the other species. As lactation ends there is a dramatic decrease in milk solids concentration and in a few days the composition once more resembles that of very early milk. There is no overlapping period of suckling when the mother is producing milk of two types as in some of the macropodids, e.g. the red kangaroo, *M. rufus* (Sharman and Calaby 1964) and the grey kangaroo, *Macropus giganteus* (Poole 1973).

Ideally, milk sampling should reflect the removal of milk from the mammary gland during normal suckling behaviour (Oftedal 1984). The frequency of suckling by young is not known for the bandicoot nor for marsupials generally. In the present study, therefore, separation of young from their mothers to allow milk accumulation may not approximate the normal interval between suckling bouts, and milk samples may not represent precisely the milk extracted by a suckling young. Oftedal (1984) discusses also the influence of oxytocin injection on milk composition in eutherian mammals. It is not known if oxytocin exerts the same influence in marsupials; however, its use is essential in order to obtain sufficient milk for analysis. The methods used here are similar to those used in other

marsupial milk composition studies (Green *et al.* 1980; Green *et al.* 1987; Crowley *et al.* 1988 and Smolenski and Rose 1988).

The maximum concentration of milk solids, about 45% (w/w), is generally higher than in other marsupials; e.g. 30% in *D. viverrinus* (Green *et al.* 1987), 40% in *M. eugenii* (Green *et al.* 1980), 25% in *T. vulpecula* (P. Cowan pers. comm.) and 23% in *M. rufus* (Lemon and Barker 1967). It is probable that the rapid increase to high concentrations of milk solids in *I. macrourus* accounts, in part, for the fast growth of young bandicoots (Mackerras and Smith 1960; Lyne 1964).

Milk carbohydrate concentrations reached peak values of around 8 g 100 ml<sup>-1</sup> and are similar to those measured for *D. viverrinus* (Green *et al.* 1987) but about half those found in *M. eugenii* (Messer and Green 1979).

Protein concentrations in *I. macrourus* milk peaked at about 12% compared with 8% for *D. viverrinus* (Green *et al.* 1987), 13% for *M. eugenii* (Green *et al.* 1988), 10% for *T. vulpecula* (Gross and Bolliger 1959) and 6–8% for *M. rufus* (Lemon and Barker 1967).

The rise in crude lipid levels throughout lactation reflects the general increase in milk solids. This pattern is seen in *D. viverrinus* (Green *et al.* 1987) and *M. eugenii* as well as other marsupials (Green 1984). The analyses of the triglyceride fraction of the milk for the fatty acid composition was carried out over 39–56 days of the lactational cycle and did not show sequential changes during this time. As in other marsupials (Griffiths *et al.* 1972; Green *et al.* 1983), palmitic and oleic acids were the major fatty acids, with oleic acid the most predominant. Whether, as in the other marsupials, palmitic acid predominates in early lactation is not known.

In *I. macrourus* milk, stearic and linoleic acids (10% and 12% w/w respectively) occur in amounts similar to those found in *D. viverrinus* (7% and 15%) (Green *et al.* 1987); in *M. eugenii* the respective concentrations are 18% and 7%. The significance of these differences is not known but Green *et al.* (1987) suggest that diet may be implicated as shown by the greater amounts of arachidonic acid (C20:4) in the milk of *D. viverrinus*, which probably reflects the insectivorous diet of this species. Griffiths *et al.* (1973) show that the fatty acid composition of the milk of the echidna, *Tachyglossus aculeatus*, can be altered by diets of different fatty acid composition.

Sodium and potassium concentrations in *I. macrourus* are inversely related, with sodium higher for the first half of lactation. A crossover point occurs at about 30 days into lactation, which is close to the time at which pouch young first release the teat. This pattern of change is similar to that found in *D. viverrinus* (Green *et al.* 1987), *M. eugenii* (Green *et al.* 1980) and *S. brachyurus* (Bentley and Shield 1962).

Linzell and Peaker (1971) note that it appears necessary for milk to be isosmotic with plasma and that its osmolarity is regulated predominantly by its carbohydrate and salt content. Messer *et al.* (1987) observe that the oligosaccharides of *D. viverrinus* milk are of larger molecular size than those of *M. eugenii* and therefore exert lower osmotic pressures. They postulated that this should allow *D. viverrinus* milk to have a higher concentration of sodium plus potassium than the milk of *M. eugenii* and the study by Green *et al.* (1987) showed this to be the case. The concentration of electrolytes in *D. viverrinus* mid-lactation milk was 83 mM (Green *et al.* 1987) compared with 37 mM in *M. eugenii* (Green *et al.* 1980) and 40 mM in *S. brachyurus* (Bentley and Shield 1962). The electrolyte concentration in mid-lactation *I. macrourus* milk is 95 mM, which is similar to that of *D. viverrinus*. Consequently it appears probable that the oligosaccharides of *I. macrourus* milk are of similar molecular size to those of *D. viverrinus*.

One of the major differences between the peramelids and other marsupials of similar size is that the duration of lactation is much shorter. In *Perameles nasuta* the young were weaned at 61–63 days (Stodart 1966), in *I. macrourus* at about 56–58 days (Gordon 1971, 1974; this study) and in *P. gunnii* at about 60 days (Heinsohn 1966). In the eastern quoll, *Dasyurus viverrinus*, an animal of similar body weight to the bandicoots, the young are weaned at about 150 days (Merchant *et al.* 1984), almost three times the age of newly



weaned bandicoot young. The reproductive pattern in *I. macrourus* is such that the female returns to oestrus and mates in late lactation so that the termination of pouch occupancy by one litter may be very closely followed by the birth of, and attachment to the teats by, the next. This rapid replacement of one litter by another raises the possibility that new young, entering the pouch immediately after its vacation by the previous litter, do not have the choice of all teats for attachment since some teats may be too large for their mouths or, on attachment, they might find that the milk is of an inappropriate composition. In the macropodids it is not uncommon for there to be a period of overlapping suckling by young of different ages (Sharman and Calaby 1964; Merchant and Calaby 1981). In *Perameles nasuta*, however, both Lyne (1964) and Stodart (1966) concluded that weaning was complete by the time that the new litter was born. The same applies in *I. macrourus* but the possible problems with regard to teat size and milk composition remain. Hall (1983) reported that the recently sucked teats remained too large to allow attachment of newborn young for up to 1 month. Merchant (1989) has shown that it is not uncommon for new young to attach to a recently sucked teat (18 of 74 young from 17 litters) and that their survival rate was no different from that of young attaching to previously unsucked teats, which is contrary to the statement in Tyndale-Biscoe and Renfree (1987).

The present study has shown that recently sucked teats and their respective mammary glands can produce milk of a composition similar to that produced by teats and glands sucked for the first time. This fact reinforces the finding of Merchant (1989) that the survival rates of young attaching to the two types of teat are no different. Merchant (1989), however, described a situation in which three young, in separate litters, attaching to previously sucked teats, did not thrive initially. Two were permanently removed from the teats so that their potential was not known, and the third young subsequently grew to be indistinguishable from its siblings. This latter situation has been observed again but in this case the young was attached to a previously unsucked teat. Retarded growth is therefore not necessarily attributable solely to the inability of some recently suckled teats to respond quickly and produce milk appropriate for the newborn but may also occur as an apparent breakdown of normal mechanisms in previously unsucked teats.

The pattern of changes in milk components is similar in the northern brown bandicoot to that seen in other marsupials although the duration of lactation is short by marsupial standards. This reinforces the view that lactation in the various marsupial groups has a common pattern. It remains possible, however, that variations on this pattern remain to be found in terms of lactational duration, the concentration of milk solids and the individual components of the major milk constituents, and that these may occur in a way that is related to the lifestyle of particular species.

### Acknowledgments

We would like to thank Brian Green and Keith Newgrain for helpful criticism; Phil Cowan, DSIR, New Zealand for helpful criticism and laboratory expertise and Ray Leckie for lipid and triglyceride analyses.

### References

- Bentley, P. J., and Shield, J. W. (1962). Metabolism and kidney function in the pouch young of the macropod marsupial *Setonix brachyurus*. *J. Physiol.* **164**, 127-37.
- Conway, E. J. (1962). 'Microdiffusion Analysis and Volumetric Error.' (Crosby Lockwood & Son Ltd: London.)
- Crowley, H. M., Woodward, D. R., and Rose, R. W. (1988). Changes in milk composition during lactation in the potoroo, *Potorous tridactylus* (Marsupialia : Potoroinae). *Aust. J. Biol. Sci.* **41**, 289-96.

- Gemmell, R. T. (1982). Breeding bandicoots in Brisbane (*Isodon macrourus* Marsupialia, Peramelidae). *Aust. Mammal.* **5**, 187-93.
- Gordon, G. (1971). A study of island populations of the short-nosed bandicoot, *Isodon macrourus* Gould. Ph.D. Thesis, University of New South Wales, Sydney.
- Gordon, G. (1974). Movements and activity of the short-nosed bandicoot *Isodon macrourus* Gould (Marsupialia). *Mammalia* **38**, 405-31.
- Green, B. (1984). Composition of milk and energetics of growth in marsupials. In 'Physiological strategies in lactation'. (Eds M. Peaker, R. G. Vernon and C. H. Knight.) pp. 369-87. (Academic Press: London.)
- Green, B., Griffiths, M., Leckie, R. M. C. (1983). Qualitative and quantitative changes in milk fat during lactation in the tammar wallaby (*Macropus eugenii*). *Aust. J. Biol. Sci.* **36**, 455-61.
- Green, B., Merchant, J. C., and Newgrain, K. (1987). Milk composition in the eastern quoll, *Dasyurus viverrinus* (Marsupialia: Dasyuridae). *Aust. J. Biol. Sci.* **40**, 379-87.
- Green, B., Merchant, J. C., and Newgrain, K. (1988). Milk consumption and energetics of growth in pouch young of the tammar wallaby *Macropus eugenii*. *Aust. J. Zool.* **36**, 217-27.
- Green, B., Newgrain, K., and Merchant, J. C. (1980). Changes in milk composition during lactation in the tammar wallaby (*Macropus eugenii*). *Aust. J. Biol. Sci.* **33**, 35-42.
- Griffiths, M., Elliott, M., Leckie, R. M. C., and Schoeffl, G. I. (1973). Observations of the comparative anatomy and ultrastructure of mammary glands and on the fatty acids of the triglycerides in platypus and echidna milk fats. *J. Zool. (Lond.)* **167**, 255-79.
- Griffiths, M., McIntosh, D. L., and Leckie, R. M. C. (1972). The mammary glands of the red kangaroo with observations on the fatty acid components of the milk triglycerides. *J. Zool. (Lond.)* **166**, 265-75.
- Gross, M. R., and Bolliger, A. (1959). Composition of milk of the marsupial *Trichosurus vulpecula*. *Am. Med. Ass. J. Dis. Children* **98**, 768-75.
- Hall, L. S. (1983). Observations on body weights and breeding of the northern brown bandicoot, *Isodon macrourus*, trapped in south-east Queensland. *Aust. Wildl. Res.* **10**, 467-76.
- Heinsohn, G. E. (1966). Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunnii* and *Isodon obesulus*). *Univ. Calif. Publ. Zool.* **80**, 1-107.
- Hill, J. P., and O'Donoghue, C. H. (1913). The reproductive cycle in the marsupial *Dasyurus viverrinus*. *Q. J. Microsc. Sci.* **59**, 133-74.
- Lemon, M., and Barker, S. (1967). Changes in milk composition of the red kangaroo, *Megaleia rufa* (Desmarest) during lactation. *Aust. J. Exp. Biol. Med. Sci.* **47**, 283-5.
- Linzell, J. L., and Peaker, M. (1971). Mechanism of milk secretion. *Physiol. Rev.* **51**, 564-97.
- Lyne, A. G. (1964). Observations on the breeding and growth of the marsupial *Perameles nasuta* Geoffroy, with notes on other bandicoots. *Aust. J. Zool.* **12**, 322-9.
- Lyne, A. G. (1974). Gestation and birth in the marsupial *Isodon macrourus*. *Aust. J. Zool.* **22**, 303-9.
- Mackerras, M. J., and Smith, R. H. (1960). Breeding the short-nosed marsupial bandicoot, *Isodon macrourus* (Gould), in captivity. *Aust. J. Zool.* **8**, 371-82.
- Merchant, J. C. (1989). Aspects of lactation in the brown bandicoot, *Isodon macrourus*. In 'Bandicoots'. (Eds A. G. Lyne and P. Brown.) (Surrey Beatty: Sydney.)
- Merchant, J. C., and Calaby, J. H. (1981). Reproductive biology of the red-necked wallaby (*Macropus rufogriseus banksianus*) and Bennett's wallaby (*M. r. rufogriseus*) in captivity. *J. Zool. (Lond.)* **194**, 203-17.
- Merchant, J. C., Newgrain, K., and Green, B. (1984). Growth of the eastern quoll, *Dasyurus viverrinus* (Shaw), (Marsupialia) in captivity. *Aust. Wildl. Res.* **11**, 21-9.
- Messer, M., and Green, B. (1979). Milk carbohydrates of marsupials II. Quantitative and qualitative changes in milk carbohydrates during lactation in the tammar wallaby (*Macropus eugenii*). *Aust. J. Biol. Sci.* **32**, 519-631.
- Messer, M., FitzGerald, P. A., Merchant, J. C., and Green, B. (1987). Changes in milk carbohydrates during lactation in the eastern quoll, *Dasyurus viverrinus* (Marsupialia). *Comp. Biochem. Physiol.* **88**, 1083-6.
- Oftedal, O. T. (1984). Milk composition, milk yield and energy output at peak lactation: a comparative review. In 'Physiological Strategies in Lactation'. (Eds M. Peaker, R. G. Vernon and C. H. Knight.) (Academic Press: London.)
- Poole, W. E. (1973). A study of breeding in grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest), in central New South Wales. *Aust. J. Zool.* **21**, 183-212.

- Sharman, G. B., and Calaby, J. H. (1964). Reproductive behaviour in the red kangaroo, *Megaleia rufa*, in captivity. *CSIRO Wildl. Res.* **9**, 58-85.
- Smolenski, A. J., and Rose, R. W. (1988). Comparative lactation in two species of rat-kangaroo (Marsupialia). *Comp. Biochem. Physiol.* **90**, 459-63.
- Spector, T. (1978). Refinement of the Coomassie blue method of protein quantitation. *Anal. Biochem.* **86**, 142-6.
- Stodart, E. (1966). Management and behaviour of breeding groups of the marsupial *Perameles nasuta* Geoffroy in captivity. *Aust. J. Zool.* **14**, 611-23.
- Tyndale-Biscoe, H., and Renfree, M. (1987). 'Reproductive Physiology of Marsupials.' (Cambridge University Press: Cambridge.)

Manuscript received 14 December 1987, revised 2 September 1988, accepted 5 September 1988

