

# The physiology of the honey possum, *Tarsipes rostratus*, a small marsupial with a suite of highly specialised characters: a review

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**Abstract** Field and laboratory studies of the iconic nectarivorous and ‘pollenivorous’ honey possum, *Tarsipes rostratus*, are reviewed with the aim of identifying aspects of its physiology that are as yet poorly understood and needed to implement management strategies for its long-term conservation. Dietary specialisations include the loss of teeth, a modified gut with a high rate of passage, exceptionally low minimum nitrogen requirements, an apparently high basal metabolic rate and a permanently polyuric kidney. In contrast, its reproductive physiology is plesiomorphic, combining aspects such as a *post-partum* oestrus, embryonic diapause, photoperiodicity and extended maternal care that are usually separate characteristics of other marsupial groups. In common with a number of other marsupials, the honey possum has the potential for trichromatic colour vision and has been the subject of several studies attempting to correlate visual quality with ecological realities. Field physiological studies have established its high rates of nectar and pollen intake needed to maintain energy balance and highlight the need for a constant intake from floral sources. Early allometric studies suggesting that the honey possum’s relatively low reproductive rate may be linked to a diet limited in protein have not been supported and nitrogen intakes in the field exceed by a factor of 10 the animal’s basic requirements for balance. Measurements of rates of protein turnover in field-caught lactating females suggest that they divert nitrogen from the protein pool to

milk production by reducing rates of degradation, rather than by increasing rates of synthesis of protein. Although not yet an endangered species, the honey possum’s habitat has been drastically reduced since European occupation of Australia and future-targeted research on the animal’s unique physiology and habitat linkage is needed that can be translated into effective management practices. Only then will its long-term survival be assured.

**Keywords** Tarsipes · Physiology · Reproduction

## Abbreviations

|              |   |
|--------------|---|
| BMR          | Basal metabolic rate                    |
| SMR          | Standard metabolic rate                 |
| FMR          | Field metabolic rate                    |
| $T_{b\ min}$ | Minimal body temperature in torpor      |
| $k_b$        | Biological elimination rate             |
| DLW          | Doubly labelled water method            |
| CCK          | Cholecystokinin                         |
| BPP          | Bovine pancreatic polypeptide           |
| MRT          | Mean retention time                     |
| SNP          | Scott National Park                     |
| FRNP         | Fitzgerald River National Park          |
| OPR          | Offspring production rate               |
| N            | Nitrogen                                |
| MNR          | Maintenance nitrogen requirements       |
| MFN          | Metabolic faecal nitrogen               |
| EUN          | Endogenous urinary nitrogen excretion   |
| BV           | Biological value                        |
| MWP          | Metabolic water production              |
| TDN          | Truly digestible nitrogen intake        |
| $P_M$        | Progesterone metabolites (progestagens) |
| $E_2$        | Oestradiol-17 $\beta$                   |
| $C_{urea}$   | Clearance of urea                       |
| $C_{IN}$     | Clearance of inulin (=GFR)              |

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|                                 |                              |
|---------------------------------|------------------------------|
| $C_{\text{urea}}/C_{\text{IN}}$ | Clearance ratio of urea      |
| RMT                             | Relative medullary thickness |
| RMA                             | Relative medullary area      |
| JMN                             | Juxtaglomerular nephrons     |
| GFR                             | Glomerular filtration rate   |
| SWS                             | Short-wavelength sensitive   |
| MWS                             | Middle-wavelength sensitive  |
| LWS                             | Long-wavelength sensitive    |
| UVS                             | Ultraviolet sensitive        |
| MSP                             | Microspectrophotometry       |
| VMN                             | Vomer nasal organ            |

## Evolutionary relationships

The tiny honey possum (Fig. 1) is one of the most unusual of marsupials: adapted both morphologically and physiologically to a unique nectar and pollen diet (Richardson et al. 1986; Rosenberg and Richardson 1995; Van Tets and Whelan 1997) and, because of its extreme specialisation, only distantly related to other marsupial species (Kavanagh et al. 2004; Archer and Kirsch 2006; Nilsson et al. 2004). Taxonomically it is the sole member of the Family Tarsipedidae and in some classifications is placed in its own Super-Family, the Tarsipedoidea and is considered “the paragon of autapomorphic specialisation within Diprotodontia.” (Kirsch 1977a, b; Aplin and Archer 1987; Russell and Renfree 1989; Kirsch 1968). Apomorphic characters include a highly derived karyotype of  $2N = 24$  (Hayman and Sharp 1982), shared only by two macropodids, *Lagostrophus fasciatus* and *Potorous longipes*; extremely reduced dentition with correspondingly ill-formed maxillae and dentaries (Rosenberg and Richardson 1995); a specialised tongue (Baggett 1978) and palatal rugae adapted for the collection of pollen and nectar (Richardson et al. 1986); a complex stomach combined with a simple gut that lacks a caecum and the largest known sperm of any mammal (Harding et al. 1981; Woolley and Scarlett 1984; Harding et al. 1984).

## Metabolism

### Basal metabolic rate (BMR)

The reliance of the honey possum on fresh flowers for its food makes it a difficult animal to maintain and breed in captivity (Bradshaw et al. 2000; Vose 1973) and this has severely restricted, and perhaps distorted, laboratory studies of its physiology. Its basal or standard metabolic rate (BMR or SMR) was first reported in 1990 as  $2.9 \pm 0.3 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$  ( $\sim 14 \text{ kJ day}^{-1}$  or  $442 \text{ kJ kg}^{-0.75} \text{ day}^{-1}$  assuming a mean body mass of 10 g) (Withers et al. 1990), which is over twice the average marsupial rate of  $1.3 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$  or



**Fig. 1** Adult male honey possum, *Tarsipes rostratus* from Scott National Park in the southwest of Western Australia (body mass = 10 g) in torpor

$220 \text{ kJ kg}^{-0.75} \text{ day}^{-1}$  (Dawson and Hulbert 1970) and 158% of the averaged eutherian rate. This high value has been questioned (McNab 2005), given that marsupials traditionally have been found to have a BMR some 30% lower than that of similar-sized eutherian mammals (Dawson and Hulbert 1969; Dawson and Hulbert 1970). The question was re-examined by Cooper and Cruz-Neto (2009) who also reported a lower, but still elevated BMR of  $2.52 \pm 0.22 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$  ( $= 6.56 \text{ kJ day}^{-1}$  or  $329 \text{ kJ kg}^{-0.75} \text{ day}^{-1}$ ). This figure is 162% of that predicted allometrically from BMR values of other marsupial species and 118% of that predicted for an eutherian mammal of the same mass (McNab 2008).

Part of the reason for these unusual data may be that the seven animals in Cooper and Cruz-Neto's (2009) study, although listed as “adult honey possums” only weighed an average of 5.4 g. Male honey possums are not sexually mature until they reach 7–7.5 g, and typically weigh 8–12 g, with females being heavier at 10–14 g (Renfree et al. 1984; Russell and Renfree 1989; Bradshaw et al. 2000). The individuals in Cooper and Cruz-Neto's (2009) study were thus juveniles and their mass-specific rate of oxygen consumption in the thermoneutral zone could reasonably be expected to be higher than that of fully grown adults.

Honey possums are particularly stress-prone (Russell 1986; Vose 1972) and confining honey possums in small metabolism cages (600 mL in the case of Withers et al. 1990) is known to significantly elevate their energy expenditure that may persist for up to 72 h (Bradshaw and Bradshaw 2001). Honey possums have extremely large adrenal glands relative to their body mass, averaging  $1,603 \pm 223 \text{ mg kg}^{-1}$  (Oates et al. 2007), compared with adrenals from other marsupials and eutherian mammals that typically fall within the range of 100–200  $\text{mg kg}^{-1}$  (Chester Jones 1957; McDonald 1977). Resting faecal cortisol levels are also extremely high, averaging 4–6  $\mu\text{g g}^{-1}$  (Oates et al. 2007) some thousand times higher than levels of 2–10  $\text{ng g}^{-1}$ ,

for example, in Gilbert's potoroo (*Potorous gilbertii*) (Stead-Richardson et al. 2010). These levels increase up to  $30 \mu\text{g g}^{-1}$  following routine weighing and pouch inspection (Oates et al. 2007). It would thus appear that the question of the BMR of the Honey possum has not been resolved and further research is needed, using adult animals that have been carefully habituated to being held in small chambers.

#### Field metabolic rate (FMR)

The FMR of the honey possum was first measured in the Fitzgerald River National Park (FRNP) on the south coast of WA using the doubly labelled water method (DLW) (Nagy 1980; Speakman 1997) by Nagy et al. (1995). They reported a mean FMR of  $34.4 \pm 11.1 \text{ kJ day}^{-1}$  for 12 honey possums (6 male and 6 female) with an average mass of 9.9 g, which conformed closely to allometric expectations for marsupials (Nagy 1994, 1999, 2005; Riek 2008). The FMR varied from 14.2 to  $51.8 \text{ kJ day}^{-1}$  between individuals, however, and they attributed this large variation to some individuals utilising torpor during the measurement period in mid-winter. Citing Withers et al.'s (1990) BMR figure of  $2.9 \pm 0.3 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , they calculated the ratio of FMR/BMR as 2.7, significantly lower than the figure of 4.6–6.9 recorded for small insectivorous marsupials (Nagy 1987). The DLW method was also used to estimate daily rates of nectar and pollen intake in honey possums living in Scott National Park (SNP), in the extreme southwest of WA. The mean FMR of 12 females and 14 males, with an average mass of  $9.0 \pm 0.4 \text{ g}$ , was  $28.6 \pm 3.0 \text{ kJ day}^{-1}$  (corrected for isotopic fractionation, see Speakman 1997). No significant difference was found between measurements made in the wet and dry seasons of the year (Bradshaw and Bradshaw 1999). The radioactive isotope, rubidium-86 ( $^{86}\text{Rb}$ ), has also been used recently to estimate FMR in the honey possum and biological elimination rate constants ( $k_b$ ) correlated significantly with simultaneous measurements of the FMR using the DLW method (Bradshaw and Bradshaw 2007). Whatever the method employed, the FMR of the honey possum is clearly lower than that of similar-sized insectivorous marsupials of the Family Dasyuridae, such as *Sminthopsis crassicaudata* (Nagy et al. 1988) and *Antechinus stuartii* (now ascribed to *A. agilis*) (Nagy et al. 1978), indicating that its nectarivorous mode of foraging is less expensive. It is also lower than that of small nectarivorous bats, such as *Glossophaga commissarisii*, that receive only small nectar rewards per flower in contrast with *Tarsipes* feeding on *Bankisia* inflorescences (Voigt et al. 2006).

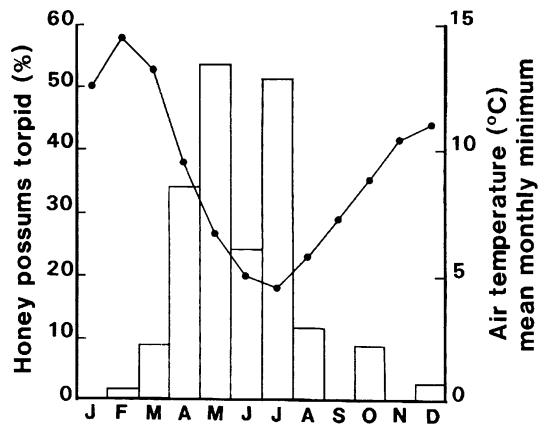
#### Torpor

The occurrence of torpor in the honey possum was first signalled by anecdotal reports of animals being found 'dead' by farmers on cold mornings in holes dug for fence posts,

which miraculously re-awakened when warmed (Glauert 1928, 1958). The incidence and depth of torpor was then documented in both field and laboratory in a study by Collins et al. (1987). These authors habituated adult honey possums to a metabolism cage with a volume of 3.1 l over a 3-day period before commencing measurements of the rate of oxygen consumption using a standard flow-through system. Rates of oxygen consumption were then monitored continuously for a period of 4 days and three nights with bouts of torpor identified by rates of oxygen consumption falling below the expected BMR calculated from Dawson and Hulbert (1970). Metabolic rates varied from 150 to  $350 \text{ J g}^{-1} \text{ h}^{-1}$  corresponding to an energy expenditure of 36–84  $\text{KJ day}^{-1}$  for a 10 g individual (their animals averaged 8.3 g). These rates exceed estimates of the FMR for *Tarsipes*, which range from 25.1 to  $34.4 \text{ kJ day}^{-1}$  [see "Field metabolic rate (FMR)"] and suggest that animals confined in metabolism cages may be stressed.

Torpor bouts were readily induced by withholding nectar and varied in duration from 2 to 15 h in Collins et al.'s (1987) study. Energy expenditure was reduced by approximately 70% and, in the field, animals were found in torpor in pitfall traps from March until September, with the frequency ranging from 14 to 34%. Torpor was also investigated by Withers et al. (1990) who recorded reductions in body temperature to as low as  $5^\circ\text{C}$  in torpid individuals. Torpor bouts averaged 10 h and were not found to last longer than 24 h without spontaneous arousal. Arousal times were negatively correlated with ambient temperature, ranging from 75 min at  $13^\circ\text{C}$  to 500 min at  $7^\circ\text{C}$ .

The subject of torpor in marsupials and small mammals has been extensively reviewed (Geiser et al. 1996; Geiser 2004) and two general patterns have been described: hibernation or prolonged torpor in hibernators and daily torpor in heterotherms. Small heterothermic dasyurids (e.g. *Antechinus*, *Sminthopsis*, *Planigale*, etc.) have short-term shallow bouts in which body temperatures decline by 10– $20^\circ\text{C}$ , but remain above  $12^\circ\text{C}$ . Small marsupial hibernators such as *Burramys*, *Cercartetus* and *Acrobates* have longer (up to 10 days) and deeper torpor bouts with body temperatures falling to 5– $6^\circ\text{C}$  (Geiser 1994). The honey possum appears to differ from other marsupial heterotherms in displaying short-term (<12 h) but deep ( $T_{b \text{ min}} 5^\circ\text{C}$ ) torpor. It is important to note, however, that long-term experiments have yet to be conducted with *Tarsipes* to establish whether the species is capable of prolonged torpor bouts. Geiser and Ruf (1995) found that torpor-bout duration was the most reliable parameter in separating hibernators from daily heterotherms. Apparent seasonal patterns in the frequency of torpor bouts were documented in FRNP by Withers et al. (1990) and varied inversely with the ambient temperatures, averaging approximately 50% of animals trapped in the cold winter months of May and June and 24% in June (Fig. 2). These data, however, record only the frequency of



**Fig. 2** Seasonal occurrence of torpor (bars) in relation to mean monthly minimum air temperature (filled circles) for honey possums (*Tarsipes rostratus*) captured in the field in Fitzgerald National Park on the south coast of Western Australia (from Withers et al. 1990 with permission)

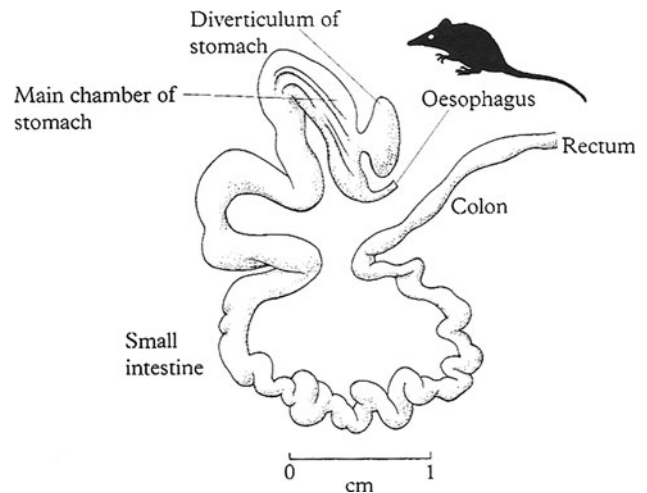
animals found in torpor in pitfall traps and do not necessarily reflect the animals' usage of torpor when unconfined in their natural habitat.

Daily cycles of torpor and basking have been documented, using radio-telemetry, in the small rock-dwelling marsupial, *Pseudantechinus macdonnellensis*, which assist in survival in the resource-poor environments frequented by this species (Geiser and Pavey 2007). This raises the possibility that honey possums could also use torpor to enhance survivorship during periods of low nectar production, which occur in late summer and autumn. Rates of nectar production by a suite of plants visited by honey possums in the FRNP were measured by Collins et al. (1987), using methods developed by Collins and Newland (1986), and found to vary from 1,548 kJ ha<sup>-1</sup> day<sup>-1</sup> in June to as low as 20 kJ ha<sup>-1</sup> day<sup>-1</sup> in September. In SNP, which has a lower floristic diversity than FRNP, late summer and early autumn are the most difficult times for honey possums with few nectar-producing plants in flower, including their primary food source, *Banksia ilicifolia*. This question was addressed by Bradshaw et al. (2007) in a field study in February 2004 using honey possums fitted with temperature-sensitive radio-transmitters. Only two instances, however, were recorded when body temperatures fell below 20°C, one early in the morning and the other late at night and there was no evidence of torpor being employed as a food-sparing mechanism in summer.

## Dietary physiology

### Gut morphology and rate of food passage

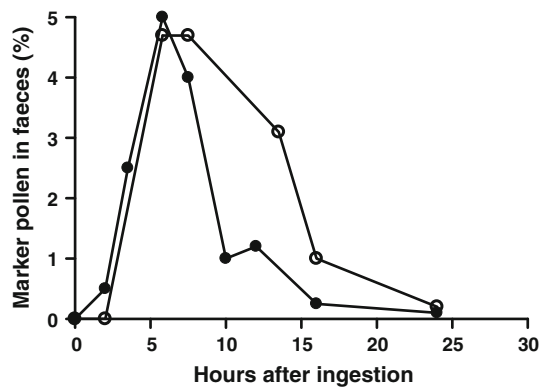
The gut of the honey possum is unusual (Fig. 3), both in lacking a caecum, where refractory food components are



**Fig. 3** Gastrointestinal tract of the honey possum, *Tarsipes rostratus*, showing the absence of a caecum and the bi-lobed stomach with a diverticulum (redrawn by Hume 1999, from Schultz 1976 with permission)

normally fermented (Hume 1982), and in possessing a bi-lobed stomach with a marked diverticulum (Schultz 1976). The distribution of gastrointestinal endocrine cells in the gut of the honey possum, using specific antibodies for eutherian gastro-entero-pancreatic hormones, was reported by Yamada et al. (1989). They found that several cell types including, somatostatin- and gastrin-immunoreactive cells, were less common than in the Virginia opossum, *Didelphis virginiana* (Krause et al. 1985) and there was also an absence of Chief cells (pepsinogen and renin secreting) in the stomach. Other major cell types involved in the production of cholecystokinin (CCK), secretin, pancreatic glucagon and bovine pancreatic polypeptide (BPP) were also not found in the honey possum.

The absence of Chief cells suggests that honey possums have lost the ability to secrete peptidases and thus hydrolyse proteins in the stomach. Interestingly, there are no reports to date of pH measurements throughout the gut, which would be of interest in this context and Hume (1999) notes that the question of whether exposure of pollen to acid conditions in the stomach is required for effective intestinal digestion is unresolved. Pollen is a rich source of nutrients and typically consists of 20% protein, 37% carbohydrate, 4% lipid and 3% minerals (Knox 1979). Pollen also contains a variety of essential amino acids, vitamins and fatty acids required by mammals (Heslop-Harrison 1973). Digestion of pollen grains in the honey possum appears confined to the intestine as very few of the pollen grains in the gastric stomach were devoid of contents (protoplast) and none had pollen tubes (Richardson et al. 1986). Digestion of pollen (as measured by the loss of protoplast) increased progressively as one moves down the gut, from <50% in the first quarter to 60–95% in the third quarter and with virtually all pollen grains in the faeces lacking their



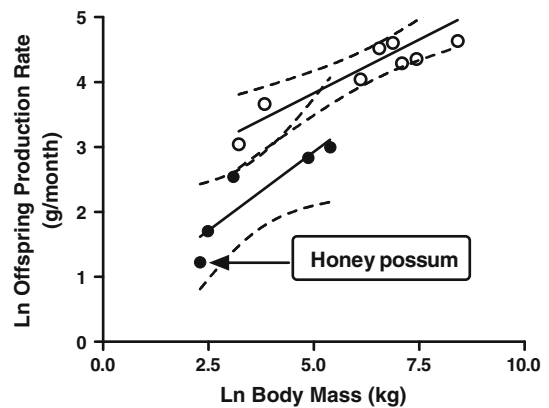
**Fig. 4** Pattern of faecal appearance of marked pollen grains in the honey possum, *Tarsipes rostratus*, fed either 25% (filled circles) or 60% (open circles) sucrose solutions (adapted from Richardson et al. 1986 with permission)

contents (Richardson et al. 1986). There has been speculation that pollen grains may germinate within the gut of the honey possum but although Turner (1984) reports the “presence of pollen grains with swollen protrusions”, she found no grains with actual pollen tubes in the gut of the single male *Tarsipes* examined by her.

The rate of passage of pollen through the gut of the honey possum is very rapid with marker pollen first appearing after 2–4 h after ingestion and peaking at 6 h (Fig. 4). The concentration of sugar in the diet tested by Richardson et al. (1986) had a small effect on the rate of passage of pollen grains with a mean retention time (MRT) of 9.2 h with 60% sucrose versus a MRT of 6.7 h with 25% sucrose calculated by Hume (1999). Hume (1999) also reports unpublished MRTs of 7.8 and 8.3 h for sucrose and honey diets, respectively, fed to *Tarsipes* by G. Lundie-Jenkins and A. Smith (cited in Hume 1999). Different sugar solutions were offered to honey possums by Landwehr et al. (1990) who found that sucrose was preferred to fructose, and both to glucose, although there was no evidence that the animals could discriminate between these sugars, other than by their odour.

#### Nitrogen metabolism

An early allometric study comparing the reproductive strategies of Australian possums and gliders, speculated that diet may be a major factor in shaping the diverse patterns observed in life-history traits (Smith and Lee 1984). Their comparative analysis revealed that honey possums have a reduced offspring production rate (OPR) when compared with similar-sized possums and in relation to allometric expectations (Fig. 5). They noted that this pattern of lower OPRs is also common to other exudate-feeding possums and gliders when compared with folivores, and suggested



**Fig. 5** Regression of calculated mean offspring production rates (OPR) in grams per month as a function of maternal body mass in leaf-eating (open circles) folivorous and species feeding on sap gum, nectar and pollen (filled circles), including the nectarivorous honey possum, *Tarsipes rostratus*. Equations for the regressions as follows: folivores,  $y = 0.329x + 2.180$  where  $y = \text{OPR}$  and  $x = \text{body mass in kg}$ ,  $r^2 = 0.774$ ,  $P = 0.0017$ ; non-folivores,  $y = 0.483x + 0.5076$ ,  $r^2 = 0.801$ ,  $P = 0.04$  (adapted from Smith and Lee 1984)

that their rich carbohydrate diets may be correspondingly deficient in protein, with low nitrogen intakes limiting their reproductive potential.

Dietary and truly digestible maintenance nitrogen requirements (MNR) have been determined in laboratory feeding trials, regressing nitrogen balance against nitrogen intake for a variety of marsupials (Table 1) and most estimates fall within the range of 150–300 mg N kg<sup>-0.75</sup> day<sup>-1</sup> (Hume 1999), which is approximately half that recorded for eutherian mammals (Robbins 1993). Although no explicit mechanism has ever been identified, the assumption has been that this is a phylogenetic trait and the low MNRs are a consequence of the substantially lower BMR of marsupials. A very low MNR of 87 mg N kg<sup>-0.75</sup> day<sup>-1</sup> was reported for the sugar glider, *Petaurus breviceps*, fed a pollen and honey diet (Smith and Green 1987) that was attributed to an unusually low value for metabolic faecal nitrogen (MFN) on a roughage-free diet, and a low value for endogenous urinary nitrogen excretion (EUN) (Hume 1999). An even lower value of 46 mg N kg<sup>-0.75</sup> day<sup>-1</sup> for the MNR was reported for the pygmy possum, *Cercartetus nanus*, when fed a pollen diet suspended in an agar/sugar gel (van Tets and Hulbert 1999). The MNR increased to 147 mg N kg<sup>-0.75</sup> day<sup>-1</sup>, however, when the possums were fed a diet of mealworms (*Tenebrio molitor*) and the difference was attributed to the higher biological value (BV) of the pollen.

A preliminary study reported an MNR for the honey possum of 230 mg N kg<sup>-0.75</sup> day<sup>-1</sup>, (Wooller et al. 1999) which fell within the range for larger herbivorous species. Urine and faeces were not separated in this study, however, which is necessary to distinguish between MFN and EUN,

**Table 1** Comparative aspects of nitrogen metabolism in marsupial and eutherian mammals

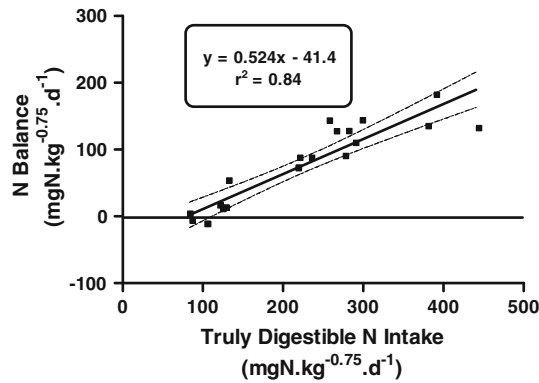
| Species                          | EUN<br>(mg kg <sup>-0.75</sup><br>day <sup>-1</sup> ) | MFN<br>(mg g DMI <sup>-1</sup> ) | Dietary MNR<br>(mg kg <sup>-0.75</sup><br>day <sup>-1</sup> ) | Truly digestible MNR<br>(mg kg <sup>-0.75</sup><br>day <sup>-1</sup> ) | References   |
|----------------------------------|---|----------------------------------|---|--|--|
| <b>Marsupials</b>                |   |                                  |   |  |  |
| <i>Macropus r. robustus</i>      |   |                                  | 300   | 240  | Foley et al. (1980)                                  |
| <i>Macropus r. erubescens</i>    | 34  | 27                               | 290   | 160  | Brown and Main (1967)                                |
| <i>Macropus eugenii</i>          | 60  | 41                               | 240–290   | 230–250  | Barker (1968); Hume (1977)                           |
| <i>Macropus giganteus</i>        |   |                                  | 350   | 270  | Foley et al. (1980)                                  |
| <i>Setonix brachyurus</i>        | 44  | 29                               | 189   | 186  | Brown (1968)   |
| <i>Thylogale thetis</i>          |   |                                  | 600   | 530  | Hume (1977)  |
| <i>Trichosurus vulpecula</i>     |   | 8–33                             | 203–560   | 189–420  | Wellard and Hume (1981);<br>Foley and Hume (1987)    |
| <i>Pseudocheirus peregrinus</i>  |   | 24                               | 380   | 290  | Chilcott and Hume (1984)                             |
| <i>Petaroides volans</i>         |   |                                  | 700   | 560  | Foley and Hume (1987)                                |
| <i>Petaurus breviceps</i>        | 25  | 7                                | 87  | 73   | Smith and Green (1987)                               |
| <i>Cercartetus nanus</i>         | 23–37   | 0.5–1.8                          | 50–147  | 41–127   | Van Tets and Hulbert (1999)                          |
| <b><i>Tarsipes rostratus</i></b> | <b>42</b>   | <b>35</b>                        | <b>89</b>   | <b>79</b>  | Bradshaw and Bradshaw (2001)                         |
| <i>Caluromys philander</i>       |   |                                  | 176   | 146  | Foley et al. (2000)                                  |
| <i>Phascolarctos cinereus</i>    |   | 6                                | 283   | 271  | Cork (1986)  |
| <i>Vombatus ursinus</i>          | 31  |                                  | 158   | 71   | Barboza et al. (1993)                                |
| <i>Lasiiorhinus latifrons</i>    | 42  |                                  | 201–205   | 116  | Barboza et al. (1993)                                |
| <b>Eutherians</b>                |   |                                  |   |  |  |
| <i>Sus scrofa</i>                | 131   | 104                              |   |  | Du Toit and Smuts (1941)                             |
| <i>Rattus rattus</i>             | 137   | 135                              |   |  | Brody (1945)   |
| <i>Ammospermophilus leucurus</i> | 157   | 200                              |   | 263  | Karasov (1982)                                       |
| <i>Cavia porcellus</i>           | 145   |                                  |   |  | Brody (1945)   |
| <i>Oryctolagus cuniculus</i>     | 148   |                                  |   |  | Brody (1945)   |
| <i>Ovis aries</i>                | 87  | 550                              | 390–489   | 340–452  | Smuts and Marais (1938);<br>Moir and Williams (1950) |
| <i>Camelus dromedarius</i>       | 67  |                                  |   |  | Schmidt-Nielsen et al. (1957)                        |
| <i>Capra hircus</i>              | 115   |                                  |   |  | Hutchinson and Morris (1936)                         |
| <i>Procavia habessinica</i>      |   | 369                              | 311   | 209  | Hume et al. (1980)                                   |

and data were included from animals in negative nitrogen balance, which are known to inflate estimates of the MNR (Manatt and Garcia 1992).

In a separate study, a total of 17 honey possums (10 male and 7 female) were fed a range of diets when housed in metabolism cages fitted with a small refuge area where the animals could retreat in an effort to reduce the stress of confinement (Bradshaw and Bradshaw 2001). Measurements of nitrogen intake and excretion were made over a 5-day period with calculations based on data collected from days 2 to 5 when dietary intake and urine volumes had stabilised. The dietary maintenance nitrogen requirement (MNR) was estimated to be  $89 \pm 21$  mg N kg<sup>-0.75</sup> day<sup>-1</sup> (2.6 mg day<sup>-1</sup> for a 9 g individual) and the truly digestible MNR was 79 mg N kg<sup>-0.75</sup> day<sup>-1</sup> (Fig. 6). Regressing nitrogen balance on intake separately for the ten males and seven females gave MNR estimates of 130 and 70 mg N kg<sup>-0.75</sup> day<sup>-1</sup>, respectively, but the difference in

intercepts for the two regressions was not statistically significant, with  $P = 0.06$ , but warrants further analysis with larger sample sizes.

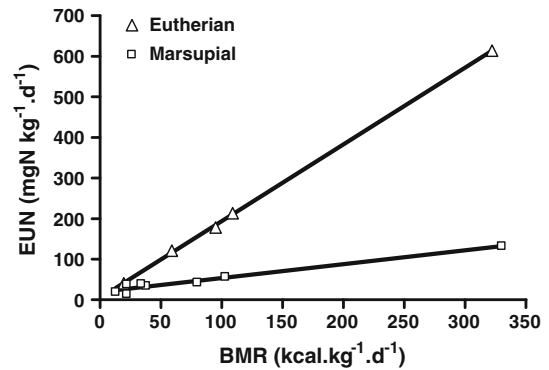
The BV is calculated as the ratio of retained nitrogen to truly digestible nitrogen intake (TDN) and did not vary significantly between the four diets, averaging  $58 \pm 2.2\%$ . This BV for the honey possum is lower than the figure of 68% reported for the sugar glider (Smith and Green 1987) and 72% for the pygmy possum (van Tets and Hulbert 1999) and reflects a higher rate of nitrogen loss in the case of the honey possum. The EUN in the honey possum was estimated at 42 mg N kg<sup>-0.75</sup> day<sup>-1</sup> compared with the 25 and 22 mg N kg<sup>-0.75</sup> day<sup>-1</sup> in the case of the sugar glider and pygmy possum, respectively. Bradshaw and Bradshaw (2001) speculated that the high water content of the nectar/pollen diet fed the honey possum results in extremely high rates of urine production (polyuria) with obligatory losses



**Fig. 6** Relationship between truly digestible nitrogen intake (TDN) and nitrogen balance in the honey possum, *Tarsipes rostratus*. Truly digestible maintenance nitrogen requirement for balance (MNR) from this relationship (when  $y = 0$ ) is  $79 \text{ mg N kg}^{-0.75} \text{ day}^{-1}$ , confidence limits indicated by *broken lines* (from Bradshaw and Bradshaw 2001 with permission)

of nitrogen. The clearance ratio of urea ( $C_{\text{urea}}/C_{\text{IN}}$ ) was found to be positively correlated with the rate of urine production in spectacled hare wallabies by Bakker and Bradshaw (1983) and a similar mechanism could function in *Tarsipes*. The digestibility of the dietary nitrogen in the honey possum varied from 67.4 to 81.6%, averaging 76% and the digestibility of the pollen in the diets was 75%. The proportion of nitrogen contained in the exine of the pollen that was not digested could also be estimated and averaged 24.8%. From these data it appears that approximately 25% of the nitrogen content of pollen is located in the exine and 75% is available for assimilation (Bradshaw and Bradshaw 2001).

Rates of nitrogen excretion in mammals have been known to be linked to levels of energy expenditure since the pioneering work of Smuts (1935) who proposed a loss of approximately 2 mg of nitrogen for every kilocalorie of energy expended, with protein turnover thus accounting for some 15–20% of the resting metabolic rate (Welle and Nair 1990). Given that the BMR in marsupials is generally lower than that of eutherians (with some exceptions, such as small insectivorous marsupials) one might therefore expect rates of protein turnover also to be lower in marsupials and this was confirmed in the case of three species of wallabies by White et al. (1988) who found that protein synthesis only made a 7–8% contribution to fed metabolic rates in contrast to a figure of 17–25% in the case of eutherian mammals. Plotting EUN versus BMR for both marsupials and eutherians (Fig. 7) reveals two very different regressions, however, with the production of 4.184 kJ of heat (1 kcal) being associated with the excretion of only 0.34 mg of N in the case of a marsupial, instead of 2 mg N for an eutherian (Bradshaw and Bradshaw 2001). Obligatory nitrogen losses in marsupials (EUN and MFN) are indeed lower than in eutherians, (Table 1), but these cannot be due to lower BMRs as the



**Fig. 7** Relationship between endogenous urinary nitrogen excretion (EUN in  $\text{mg N kg}^{-1} \text{ day}^{-1}$ ) and basal metabolic rate (BMR in  $\text{kcal kg}^{-1} \text{ day}^{-1}$ ) in eutherian (*open triangles*) and marsupial (*open squares*) mammals. Linear regression equation for eutherians is  $\text{EUN} = 0.45\text{BMR} + 4.44$ ,  $r^2 = 0.999$  and for marsupials is  $\text{EUN} = 0.08\text{BMR} + 19.24$ ,  $r^2 = 0.96$  (from Bradshaw and Bradshaw 2001 with permission)

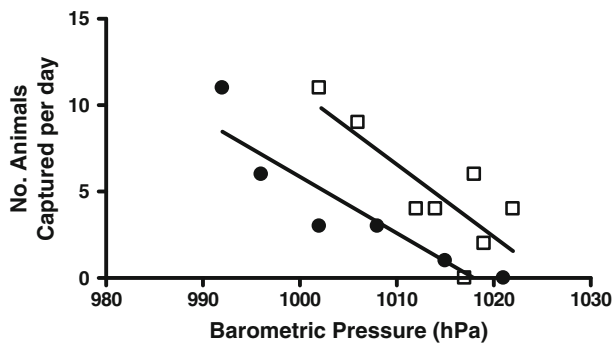
relationship in Fig. 7 reflects the EUN for a given BMR in the two taxa.

## Ecophysiology

### Activity and turnover studies

Numerous field studies have highlighted the important role thought to be played by *Tarsipes* as a pollinator of native vegetation as it pursues its unique diet of nectar and pollen (Wooller et al. 1983b; Wiens et al. 1979; Hopper 1980; Barret 1995; Carthew and Goldingay 1997). These studies have documented pollen loads carried by *Tarsipes* and suggest that their nocturnal behaviour enables them to exploit the evening peak of nectar production that is not available to diurnal avian honeyeaters (Barret 1995). Details of the honey possums' movements and the frequency and duration of flower visitations could thus provide valuable information on their efficacy as pollinators (Hopper and Burbidge 1982; Heinrich 1975). Capture rates of animals in FRNP have been found to be positively correlated both with estimates of nectar production (Wooller et al. 1993) and annual rainfall in the preceding year (Wooller et al. 1998). One interesting correlation observed in SNP was a significant negative correlation between capture rates and barometric pressure during the passage of rain-bearing low pressure systems (Fig. 8) (Bradshaw et al. 2007). It is unclear why their activity is stimulated by the passage of a storm. It is possible that nectar production by flowers may be stimulated by a fall in barometric pressure, or the passage of a violent storm may reduce the activity of predators.

Early field studies on honey possums reported high rates of recapture of marked individuals and exceptional levels



**Fig. 8** Correlation between daily capture rates of honey possums and change in barometric pressure recorded during the passage of two rain-bearing low pressure systems in Scott National Park (SNP). *Filled circles* September 2005, *open squares* October 2006. Pearson  $r$  for September 2005 =  $-0.911$ ,  $P = 0.012$  and for October 2006 =  $-0.795$ ,  $P = 0.018$ . Equations for the regressions are, September 2005,  $y = -0.326x + 332.6$ ,  $r^2 = 0.829$ ,  $P = 0.0117$ , where  $y$  = number of animals captured and  $x$  = barometric pressure in hPa; October 2006,  $y = -0.418 + 428.6$ ,  $r^2 = 0.631$ ,  $P = 0.0185$  (from Bradshaw et al. 2007 with permission)

of site fidelity (Wooller et al. 1981). These were characterised by movement patterns of “<30 m even over several months” and translated into correspondingly small home range sizes of 0.13 ha for males and 0.07 ha for females (Garavanta et al. 2000). Such levels of philopatry are, however, inconsistent with reports of low levels of genetic divergence between widely geographically separated populations of *Tarsipes* in Western Australia (Bryant et al. 2000; Spencer and Bryant 2000). Home ranges calculated solely from trapping data, however, seriously underestimate actual movements as was made clear when radio-tracking was employed. When small, 700 mg, radio-transmitters were fitted to both male and female honey possums and movements monitored in SNP over a 10-day period, ‘utilisation areas’ were some 18 times larger than home ranges calculated from long-term trapping data, averaging  $0.79 \pm 0.24$  ha in males and  $0.14 \pm 0.08$  ha in females (Bradshaw and Bradshaw 2002). Males were found to move as much as 500 m between feeding and refuge sites each night, whilst females tended to remain localised within feeding areas.

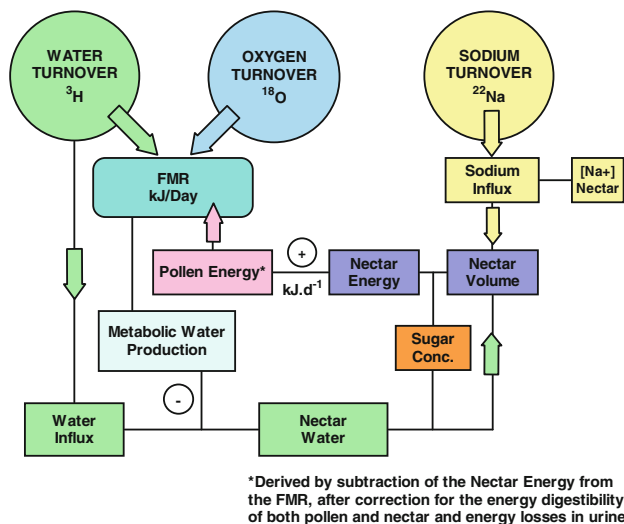
Such large displacements for a 10 g animal would be expected to involve high turnover rates, especially of water. A mean rate of water turnover of  $9.1 \pm 9.2$  mL day<sup>-1</sup> was reported for 10 g honey possums by Nagy et al. (1995) using tritiated water. The influence of weather conditions on rates of water turnover was explored by Bradshaw and Bradshaw (1999) working in SNP and, although influx and efflux rates were lower in summer at 8.5 and 8.9 mL day<sup>-1</sup>, respectively, when compared with 11.3 and 11.6 mL day<sup>-1</sup> in winter, the differences were not statistically significant. Water turnover rates in the honey possum thus approximate

the animal’s own body mass per day. Rates of sodium turnover, using sodium-22, were also measured in honey possums by Bradshaw and Bradshaw (1999) and influxes ranged from 0.134 to 0.155 mmol day<sup>-1</sup> with no effect of season.

#### Measurement of nectar and pollen intake in free-ranging animals

Turner (1984) used the equation of Smuts (1935), relating daily protein requirements for the maintenance of body mass in eutherians, to predict daily protein requirements for honey possums and quoted a figure of 110 mg protein (=17.6 mg N) for a 15 g individual. A re-examination shows that this calculation is in error and the correct figure should be 6.45 mg N for a 15 g animal, or 4.4 mg for a 9 g individual (Bradshaw and Bradshaw 2001). Smuts (1935) emphasised, however, that his equation only estimated the amount of N needed to replace obligatory endogenous losses associated with metabolism and the figure of 4.4 mg N would need to be increased to account for the biological value of pollen and for activity levels above basal.

A direct approach was made using a combination of stable and radioactive isotopes (<sup>3</sup>H, <sup>22</sup>Na and <sup>18</sup>O) to develop a method for the estimation of rates of food intake of free-ranging honey possums (Bradshaw and Bradshaw 1999; Bradshaw et al. 1987). This method was based on a number of assumptions, including (1) that animals do not drink free water, (2) nectar is the primary source of sodium in their diet, and (3) they are in energy balance during the period of measurement. The rationale of the method (Fig. 9) involves determining firstly the FMR, using the DLW method, from which metabolic water production (MWP) is calculated and subtracted from the total water influx to estimate the water intake from nectar. Pollen grains are harvested from each animal to identify the plants on which they have been feeding (Beattie 1971; Wooller et al. 1983a) and nectar from flowers of these plants is then collected and sugar content is measured. The water intake from nectar is converted to nectar volume and its energy content subtracted from the FMR to determine the energy derived from pollen, and hence pollen intake (after correcting for the energy digestibility of both pollen and nectar and energy losses in the urine). Sodium-22 was used to provide a second independent estimate of nectar volume from the measured sodium concentration of the nectar ingested. The assumption that sodium in the diet is sourced from nectar rather than from pollen was tested experimentally by leaching and then digesting pollen. Most of the sodium was found to be in the exine, with <10% available for absorption and calculations were adjusted accordingly (Bradshaw and Bradshaw 1999). Sensitivity analysis suggested that the model was most



**Fig. 9** Schema outlining the rationale underlying the measurement of rates of intake of nectar and pollen in free-ranging honey possums (*Tarsipes rostratus*) (from Bradshaw and Bradshaw 1999 with permission)

sensitive to variations in nectar sugar concentration, which falls during wet periods of the year.

An analysis of the effect of season on rates of pollen and nectar intake found that nectar volume was the only variable that changed, increasing from  $5.6 \text{ mL day}^{-1}$  in dry seasons to  $10.1 \pm 1.2 \text{ mL day}^{-1}$  in wet periods of the year. There was no difference in nectar energy intake between the two seasons, however, and it was evident that the honey possums were auto-regulating nectar intake to compensate for the lower sugar concentrations in winter. There was no correlation between the intakes of pollen and nectar, suggesting that they feed selectively for each food source (Goldingay 1990).

Nectar intake of the 26 individuals in the study averaged  $5.9 \pm 0.6 \text{ mL day}^{-1}$  but average weight loss was  $-2.7 \pm 0.7\% \text{ day}^{-1}$  and regressing nectar intake against daily change in body mass enables one to predict that an intake of 7 mL of nectar would be needed to maintain mass balance in these animals. Similarly, the actual mean pollen intake of  $660 \text{ mg day}^{-1}$  would need to be increased to approximately  $1 \text{ g day}^{-1}$  if the honey possums are to remain in mass balance (Bradshaw and Bradshaw 1999). An intake of 1 g of pollen with a nitrogen content of 4% would result in the assimilation of approximately 30 mg of nitrogen, given that the nitrogen digestibility of the pollen diet given to honey possums in feeding trials was 76% (Bradshaw and Bradshaw 2001).

#### Protein metabolism

The impetus for the field and laboratory studies on the honey possum detailed in “Gut morphology and rate of

food passage” and “Measurement of nectar and pollen intake in free-ranging animals” came from the hypothesis proposed by Smith and Lee (1984) that the relatively low OPRs of nectar, sap- and gum-feeding possums may be a consequence of their high carbohydrate diets being deficient in protein. In a recent review of life history variation in marsupials, dietary deficiencies were again advanced as possible factors limiting reproductive potential (Fisher et al. 2001). The fact that pollen grains are encased in a hard exine that is extremely resistant to chemical breakdown (Raven et al. 1986) has led to a perception that pollen is indigestible and of little nutritional value to small mammals (Smith 1982).

Pollen is, however, a very rich and easily assimilated source of nitrogen with a digestibility of 76% and a BV of 58% in the case of the honey possum. The field data have shown that, on average, honey possums absorb 30 mg of nitrogen daily, which is over ten times their MNR of 2.6 mg for a 9 g individual. Honey possums are thus not deprived of nitrogen in their diet. However, the apparently lower rates of protein synthesis in marsupials (Welle and Nair 1990) could limit their reproductive potential when the increased burden of producing milk is added to what already may be a low rate of protein synthesis in the mother.

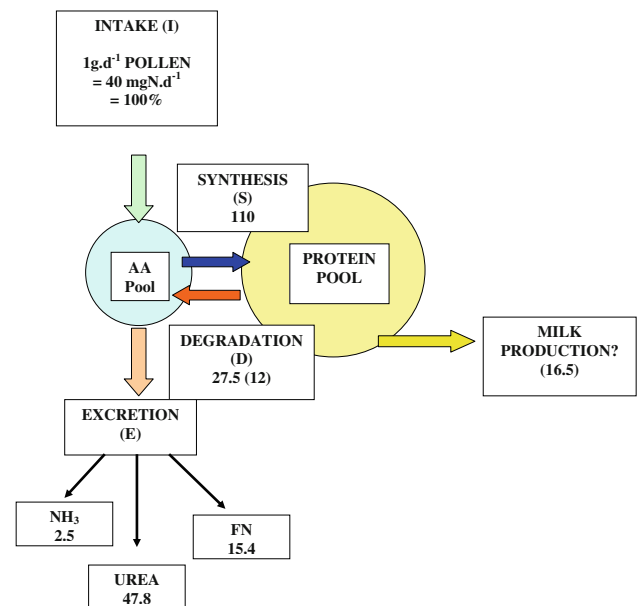
Rates of nitrogen synthesis and protein turnover have traditionally been measured in man and a number of domestic animals in laboratory situations (Waterlow et al. 1978; Young et al. 1991) with some studies extending to a number of marsupials (Barboza et al. 1993; Freudemberger and Nolan 1993; White et al. 1988). In these studies, the animals have been fed laboratory diets and rates of protein measured under standard laboratory conditions whereas, in the case of the honey possums, what is needed are measurements on animals living in their natural environment and feeding on nectar and pollen. This is almost impossible to achieve but was approximated in a field-based study in SNP with animals captured and held overnight for the measurement of rates of protein turnover and synthesis (Bradshaw and Bradshaw 2009).

A single-injection protocol (Golden and Jackson 1981; Stein 1981) was chosen with ammonia ( $\text{NH}_3$ ) as the nitrogenous end product as it is excreted within 24 h, compared with 72 h in the case of urea. Animals were injected with  $^{15}\text{N}$ -glycine and placed in metabolism cages for the collection of urine and faeces (Bradshaw and Bradshaw 2009). Rates of nitrogen flux and protein metabolism were calculated following the protocol of White et al. (1988) based on a two-pool model for amino acids and protein in the body (Picou and Taylor-Roberts 1969). Whole body rates of nitrogen turnover, nitrogen synthesis and protein synthesis in  $\text{mg day}^{-1}$  did not vary between males and females with and without pouch young, with protein synthesis averaging

$7.7 \pm 0.5 \text{ g kg}^{-0.75} \text{ day}^{-1}$ . Whole body rates of protein degradation, however, were significantly lower in females carrying pouch young, once the correction was made for the mass of the young. Protein degradation in lactating females averaged  $0.7 \pm 0.5 \text{ g kg}^{-0.75} \text{ day}^{-1}$  compared with  $2.1 \text{ g kg}^{-0.75} \text{ day}^{-1}$  in non-lactating females and  $3.9 \text{ g kg}^{-0.75} \text{ day}^{-1}$  in males.

A model of nitrogen flow based on these data is shown in Fig. 10 based on the assumption that nitrogen needed for milk production is diverted from the protein pool by a decrease in the rate of degradation, rather than from an increase in the rate of synthesis. As a result,  $6.6 \text{ mg N day}^{-1}$  can be diverted to milk production, resulting in the production of  $0.52 \text{ mL day}^{-1}$  of milk, with an average nitrogen concentration of 4%, assuming 50% incorporation. It can be calculated that a total of 128 mg of nitrogen is needed to produce two *Tarsipes* young of mass 2.5 g at weaning, and that this would be provided by 20 mL of milk secreted in 38 days at the above rate. As pouch life in the honey possum normally lasts for 60–70 days (Russell 1982) these rates are more than adequate and suggest that the diversion of quite small amounts of nitrogen are all that is needed to support the growth of the young in the pouch. Nothing is known of the composition of milk in the honey possum, however, and it would be of interest to know whether it changes with the age of the young, as has been observed in other marsupials (Krockenberger 2006).

The various studies undertaken on the nitrogen metabolism of the honey possum over the last decade thus do not support the proposal of Smith and Lee (1984) that its relatively low OPR is the consequence of a dietary deficiency. Recent theoretical studies have explored correlations between body size, energy metabolism and life span in mammals (Speakman 2005a, b) with marsupials recording low life spans for their body masses (Austad and Fischer 1991). Longevity in the honey possum has been estimated at 1–2 years by Russell and Renfree (1989) and field recapture data record maximum longevity of 1.6 years for males and 4 years for females (Bradshaw et al. 2007). Austad and Fischer (1991) discount metabolic ‘rate of living’ theories of ageing and focus on environmental vulnerability, noting that life span is significantly enhanced in arboreal (volant) compared with terrestrial species of marsupials. Honey possums have evolved in and adapted to an environment that is rich in floral diversity and nectar and pollen production and their relatively lower reproduction rate may reflect the reliability of this unique food supply. They are also unusual amongst marsupials in retaining the young for a significantly longer period of time before weaning than similar-sized phalangeroids (Russell 1982; Wooller et al. 1984) which may provide the young with a longer learning experience (Croft and Eisenberg 2006) and exposure to potential hazards.



**Fig. 10** A model of nitrogen flow in relation to dietary intake of 1 g of pollen ( $\approx 4\%$  nitrogen) for the honey possum, *Tarsipes rostratus*. Dietary intake is set at  $40 \text{ mg day}^{-1} = 100\%$  with other parameters shown as percentage values of this. *I* nitrogen intake, *E* nitrogen excretion, *S* rate of nitrogen synthesis to the protein pool and *D* rate of nitrogen degradation from the pool, *FN* faecal nitrogen excretion, *Urea* urinary urea excretion, and *NH<sub>3</sub>* urinary ammonia excretion. The value for *D* in parentheses (12) represents the lower nitrogen degradation rate measured in females carrying pouch young (from Bradshaw and Bradshaw 2009 with permission)

## Reproductive physiology

The life-history details of both sexes have been reviewed and described as ‘opportunistic’ (Wooller et al. 1984, 2000; Renfree et al. 1984). As early as 1928, attention was drawn to the unusually large “male generative apparatus” of the honey possum (Rotenberg 1928) which, at just over 4% of the body size, is regarded as the largest relative to body mass of any mammal. The general anatomy of the testis and epididymis has been described (Scarlett and Woolley 1980; Woolley and Scarlett 1984) and there is a detailed information on the ultrastructure of the spermatozoa (Harding et al. 1984; Cummins et al. 1986).

Females experience 2–3 breeding periods a year, as determined by the frequency of young in the pouch; four are usually born but only 2–3 survive (Wooller and Richardson 1992; Wooller et al. 1984). The presence of spermatozoa and recently fertilised eggs together in the uterus indicate a *post-partum* oestrus in the female (Renfree 1981), the established paradigm for embryonic diapause in macropodid marsupials (Sharman 1955a, b). The nature of the delay in the honey possum, however, appeared to differ from that in macropodids, as removing the young from the

pouch was reported not to reactivate quiescent blastocysts, suggesting that lactational inhibition is absent, or incomplete (Renfree 1981; Renfree and Shaw 2000; Russell and Renfree 1989).

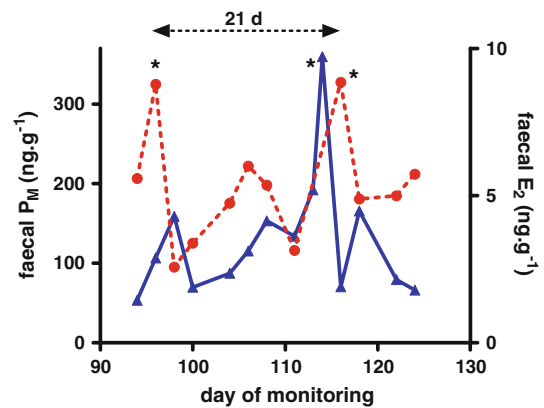
Two experimental approaches have provided extensive new data on the honey possum's reproductive physiology and its hormonal control: captive breeding and faecal steroid profiling, the latter which has been used widely to investigate reproductive profiles of oestradiol-17 $\beta$  ( $E_2$ ) and progesterone metabolites ( $P_M$ ) in mammals (Schwarzenberger et al. 1997; Wasser et al. 1994). Plasma progesterone is excreted in the faeces of *Tarsipes* principally as the metabolised isomers 5 $\alpha$ - and 5 $\beta$ -pregnan-3 $\beta$ -ol-20-one and 5 $\beta$ -pregnan-3 $\beta$ ,20 $\beta$ - and 20 $\alpha$ -diols. Oestradiol is measured in the unmetabolised and unconjugated form (Bradshaw et al. 2004).

### Oestrous cycling and gestation

Females, monitored long term and in the absence of males, exhibited cycles of regularly repeated spikes of  $E_2$  in the faeces, ranging from 21–28 days with a mean of 24 days  $\pm$  1.2 SE (Oates et al. 2007). An oestrous cycle of this length is present in many other species of marsupial within the Families Dasyuridae (Woolley 1990), Didelphidae (Harder and Fleming 1981), Peramelidae (Gemmell 1988; Lyne 1976), Phalangeridae (Lyne et al. 1959) and Potoridae (Rose 1987).

Within the luteal cycle of the honey possum, levels of  $P_M$  rise during the final week, but a second peak is also present that is associated with each ovulatory rise in  $E_2$  (Fig. 11). This unusual feature has also been reported in the squirrel glider, *Petaurus norfolcensis* (Woodd et al. 2006) and is present just prior to ovulation in the western quoll (*Dasyurus geoffroii*) (Bradshaw and Bradshaw 2011; Stead-Richardson et al. 2001). Although largely unexplored in Australian marsupials, progesterone elicits the onset of sexual receptivity and plays a role in ovulation in the American didelphid marsupial, *Monodelphis domestica* (Harder et al. 2008). The timing of the peak in the *Tarsipes* may indicate a role for progesterone in behavioural changes around the time of oestrus.

The length of gestation is not known, but has been estimated to last between 21 and 28 days, based on capture and re-capture data (Renfree et al. 1984; Russell and Renfree 1989). The actual gestation length may prove difficult to determine in the honey possum as mating may be observed, but the day of birth is elusive, with a newborn weighing only 4 mg. Births have been recorded in caged animals, but these appear to have resulted from matings in the natural environment (Russell 1986). An estimate, however, of the length of pregnancy can be deduced from the length of the oestrous cycle. As a *post-partum* oestrus occurs approxi-



**Fig. 11** Faecal concentrations (ng g<sup>-1</sup>) of oestradiol-17 $\beta$  ( $E_2$  filled circles) and progestagens ( $P_M$  filled triangles) in the final 21-day oestrous cycle of a female honey possum, *Tarsipes rostratus*, maintained on a short-day length (10 h L:12 h D). Five ova were present in the uterus on dissection. Asterisks indicate values >4 SD above baseline levels (adapted from Oates et al. 2007)

mately 2–4 days after birth (Bryant 2004), it is likely that the length of the gestation period is 2–4 days shorter than the oestrous cycle.

The egg, with a diameter of 0.15 mm is surrounded by three egg coats, the *zona pellucida*, a mucoid layer and the shell. After fertilisation, the mucoid layer thins and the blastocyst develops to the unilaminar stage when it is arrested at diapause, with an average diameter of 1.8 mm and approximately 2,000 cells, (Oates et al. 2007; Bryant 2004). This size and number of cells closely resemble the blastocysts of the feather-tailed glider, *Acrobates pygmaeus* (Ward and Renfree 1988), but are larger than those of *Cercartetus concinnus* (Ward 1990) and all macropodid marsupials (Smith 1981). Blastocysts in *Tarsipes* are, however, quite variable in size at arrest, ranging from 0.5 to 2.9 mm in diameter (Renfree 1980; Oates et al. 2007), and even in the uterus of a single female, five blastocysts varied from 1.6 to 2.8 mm. Their rate of development to the unilaminar stage is also unusual, being longer than in other marsupials examined to date. At least 2 weeks is required in *Tarsipes*, compared with 2–3 days in the quokka, *Setonix brachyurus*, (Sharman 1955a), 7 days in the tammar, *Macropus eugenii*, (Tyndale-Biscoe 1979), 9 days in *Potorous tridactylus* (Rose 1989; Shaw and Rose 1979) and 11 days in the dasyurid marsupial, *A. stuartii* (now *agilis*) (Selwood 1980).

Within the postulated gestation period of 19–21 days, a minimum period of 2 weeks to reach the unilaminar blastocyst stage would allow approximately 5 days to complete the gestation. The final stages of embryogenesis have been described as of “brief duration” (Renfree et al. 1984) and may even be, as in *Dasyurus viverrinus*, as short as 2–3 days (Hill 1910).

## Embryonic arrest or diapause

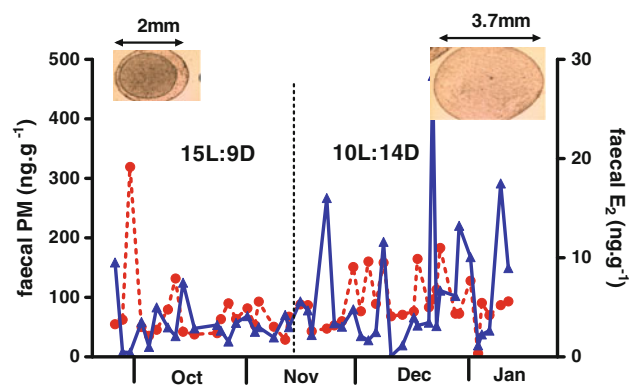
Embryonic arrest before implantation is widespread in mammals, occurring in about 100 species from 17 Families, including three marsupial Families (Renfree 1978; Renfree 1981; Sandell 1990). The term ‘diapause’ best describes the phenomenon in marsupials as implantation does not immediately follow the termination of delay, unlike the eutherian mammal. The two principal causes of arrest are photoperiod and lactation. Both forms of inhibition act on the ovary to suppress the *corpus luteum*, which, in turn, initiates the delay in embryonic growth, probably via the absence of stimulatory cytokines secreted by the uterus (Lopes et al. 2004; Dey et al. 2004).

The factors involved are not well understood and, as evolution of photoperiodic inhibition may have occurred separately 17 times (Ridley 1983), it is not surprising that no single path of control has emerged between species. For example, prolactin initiates diapause during lactational inhibition in the tammar wallaby (Tyndale-Biscoe and Hawkins 1977), but in mustelid carnivores, prolactin terminates diapause with subsequent implantation (Murphy et al. 1981). In mice, oestrogen injection terminates diapause (Weichert 1940) and implantation (Whitten 1958), whereas in the marsupial, progesterone alone reactivates the blastocyst (Berger and Sharman 1969).

There is also variation in the extent of stasis on the embryo during the arrest. The female bat, *Artibeus jamaicensis*, experiences two reproductive periods in the year. The embryo is arrested in each gestation of 4 months and is prevented from implanting in the first, but implants during the second, undergoing a further 2.5 months of arrested development while implanted (Fleming 1971). This suggests the imposition of a seasonal inhibition during the second pregnancy.

During diapause, the level of development reached by the embryo at arrest is commonly the unilaminar blastocyst stage, although in the bat, the blastocysts reach the uterus with a precociously developed trophoblast and inner cell mass before arrest (Fleming 1971). The effect of suppressed uterine growth factors is the arrest of the mitotic cell cycle in the blastocyst, although, in the northern fur seal, *Callorhinus ursinus*, there is a very slow incidence of mitosis, with cells taking 50–60 days to double their number (Daniel 2004). It is unclear whether this is during a lactational or a seasonal arrest. There is a general agreement, however, that lactational inhibition arrests the mitotic cell cycle in the blastocyst but hypertrophy through fluid absorption may occur (Renfree and Shaw 2000; Lopes et al. 2004).

Faecal steroid concentrations in *Tarsipes* display a pattern of episodic  $P_M$  and  $E_2$  secretion that appears to represent the constitutive regime during diapause, with levels fluctuating between 200 and 800  $\text{ng g}^{-1}$  of  $P_M$  and 2–5  $\text{ng g}^{-1}$



**Fig. 12** Faecal concentrations ( $\text{ng g}^{-1}$ ) of oestradiol-17 $\beta$  ( $E_2$ , filled circles) and progestagens ( $P_M$ , filled triangles) in a female honey possum, *Tarsipes rostratus*, maintained in long day length (15 h L:9 h D) from July and switched to short day length (10 h L:14 h D) in mid-November. An elevation in steroid levels is associated with an increase in size and number of cells of the blastocyst (adapted from Oates et al. 2004)

for  $E_2$ . Alterations in these levels occur under differing light regimes. Long day-length (12 h L:12 h D) is inhibitory on the ovary, lowering steroid secretion (with cessation of oestrous cycling) but with short photoperiods (10 h L:14 h D) steroid levels rise and cycling occurs (Bradshaw et al. 2004). These are absolute photoperiodic conditions, but a response to natural photoperiodic change was uncovered when monitoring births in an outdoor captive population. All five females in the colony gave birth in the mid-2 weeks of February; three of which had retained blastocysts that were conceived the previous September (Bradshaw et al. 2000). Their arrest occurred during the 10-week lactation (Russell 1986) and continued throughout the lengthening days until some 7 weeks after the summer solstice, when days are shortening.

The hormonal basis underlying this apparent response was investigated in females subjected to altered light regimes (Oates et al. 2004). Females were habituated to a long day (15 h L:9 h D) and then switched to a short photoperiod of 10 h L:14 h D in November. Under the long-day regimen, the levels of both  $P_M$  and  $E_2$  were damped down in all females, but in those exposed to the short day, there were significant increases in levels of both hormones (Oates et al. 2004) (Fig. 12). In addition, there was a two-fold increase in size and number of cells in the blastocysts, a response not apparent in the females maintained on long days.

Extensive studies on photoperiod as a reproductive cue in the *Antechinus* genus have demonstrated that it is *changing* photoperiod (rather than an absolute one) that is critical for synchronising an underlying endogenous rhythm (Dickman 1985; McAllan and Dickman 1986; McAllan and Geiser 2006). The results with *Tarsipes* suggest that the shortening day-length after the summer solstice in December

sends a signal for resumption of blastocyst growth after diapause, not unlike the photoperiodic response of *M. eugenii* (Sadler and Tyndale-Biscoe 1977).

Births also occur, however, during September and October when day length is increasing, both in natural populations (Wooller et al. 1981) and in a captive population under natural photoperiod (Bradshaw et al. 2000). Females monitored during these months all displayed a marked modulation in both steroids. Oestrogen levels rose, and  $P_M$  levels fell significantly in all females, suggesting an underlying endogenous rhythm (Oates 2005).

Contrary to previous reports (Renfree and Shaw 2000), a lactational inhibition also occurs in *Tarsipes* and was demonstrated in two females maintained in the outdoor colony which lost their young prematurely. Pouch inspection less than a month later revealed the presence of new young, the age of which showed that their birth had occurred some days after the loss of the previous young (Oates et al. 2007). Embryonic diapause in the honey possum thus appears under the control of both photoperiodic and lactational inhibitions, as well as unknown seasonal factors (Bradshaw et al. 2007; Wooller et al. 2000). Diapause may last for as long as 13 months (Oates et al. 2004), similar to embryonic diapause in two species of macropodids, *M. eugenii* and *M. rufogriseus*, in which blastocysts may resume development after a year-long diapause (Walker and Rose 1981; Berger 1966).

During diapause, whether under lactational or seasonal inhibition, the number of cells in the blastocyst remains constant at approximately 2,000, once it reaches the unilaminar stage (Oates et al. 2007; Bryant 2004). The size, however, is quite variable and should not be taken as a measure of age. When stimulated, for example, expansion to 3.4 mm diameter was measured in one blastocyst containing approximately 10,900 cells; whereas blastocysts containing only 5,000 cells had expanded to 3.7 mm in diameter (Oates et al. 2007). Development up to the unilaminar stage in macropodids is autonomous and independent of ovarian conditions (Tyndale-Biscoe 1986) and appears similar in *Tarsipes*. If autonomous development is slow, as it is in the honey possum, the embryo may give the impression that it is 'growing' during lactation (Renfree and Shaw 2000). Careful distinction needs to be made in a lactating female between the mitotic division in the autonomously developing blastocyst and cell division in a blastocyst already at the unilaminar stage, before such a conclusion can be reached. The pygmy possum, for example, has a long oestrous cycle of 40 days (Oates 2005) and, during a lengthy gestation of a day or two shorter, it is likely that the early stage of autonomous development in the embryo, formed at the *post-partum oestrus*, would be slow and could be mistaken for growth during lactation.

## Reproduction in males

Examination of testis, scrotal length and prostate width in museum specimens of male honey possums, collected in all months of the year, indicated a non-seasonal pattern of breeding with spermatogenesis occurring throughout the year (Scarlett and Woolley 1980). These authors noted the production of sperm in the urine of three males only when the scrotum containing the testis and epididymis reached a length of 16 mm and a width of 9 mm (Scarlett and Woolley 1980). In a wild population of 170 males, these dimensions were correlated with a body mass of approximately 7 g (Renfree et al. 1984). These data indicate that the male honey possum is not sexually mature until it reaches a body mass of 7 g. Plasma testosterone concentrations have been measured in males, and range between 3 and 8 ng mL<sup>-1</sup>, with the smaller males having the lowest levels (Bradshaw, unpublished).

The mating strategy of the male, given its short life-span and the continuous production of spermatozoa when sexually mature, is an interesting one. The evidence based on morphological grounds (Scarlett and Woolley 1980) and population studies (Renfree et al. 1984), indicates a continuous breeding season on the part of the male. Sperm competition has been investigated using DNA analysis of the embryos (Bryant 2004). Multiple paternities were found in 86% of the litters, with the number of sires in a single litter often reaching three or four, indicating the prevalence of sexual selection.

## Kidney function

Details of kidney structure and function in marsupials are scanty, covering primarily dasyurids, macropodids and peramelids (Hulbert and Dawson 1974; Denny and Dawson 1977). Gross morphological features in the opossum *D. virginiana* and a number of species of West Australian kangaroos and wallabies in relation to renal concentrating ability were reported in the 1970s (Yadav 1979; Purohit 1974; Krause et al. 1979) and variations in renal medullary thickness (RMT) were related to environmental aridity in 25 species of dasyurids by Brooker and Withers (1994). An allometric study by Beuchat (1990) relating variations in RMT and urine osmolality to body mass in mammals included 25 marsupial species and a detailed study of renal vasculature in two dasyurids, *Sminthopsis dolichura* and *S. crassicaudata* by Brooker et al. (1995) complement early observations by Reid and McDonald (1967) and Pak Poy (1957).

The only published study of kidney morphology and function of the honey possum is that of Slaven and Richardson (1988), in which six individuals were examined for

glomerular number and volume, relative medullary area (RMA) and urine concentrating ability. The kidney differs markedly from that of other marsupials with a large cortex and very small medulla showing no evidence of differentiation into an inner and outer stripe (Sperber 1944; Beuchat 1990). The volume of the glomeruli of juxtglomerular nephroi (JMN) is given as  $535.4 \mu\text{m}^3$ , larger than that of cortical glomeruli at  $402.5 \mu\text{m}^3$ , which is substantially smaller (by a factor of 1,000) than the glomerular volumes reported for *A. stuartii*, which range from  $1.46$  to  $2.87 \times 10^5 \mu\text{m}^3$  (McAllan et al. 1996). Closer examination of the data of Slaven and Richardson (1988) suggests that they may have misinterpreted the standard equation used to estimate glomerular volume (Weibel 1979). The undivided medulla of the honey possum kidney suggests that the JMN lack long thin Loops of Henle that are involved in the elaboration of hyperosmotic urine (Bradshaw 2003; Bankir and de Rouffignac 1985). No details of nephron length and structure are given, however, but urine collected from animals in the laboratory varied in osmolality from  $208 \pm 15 \text{ mOsm kg}^{-1}$  on a 92% water diet to  $1,333 \pm 122 \text{ mOsm kg}^{-1}$  on a 60% water diet. The RMA was very low at 0.30 and the predicted maximum urinary concentration based on the equation of Brownfield and Wunder (1976) was  $1,469 \text{ mOsm kg}^{-1}$ . Slaven and Richardson (1988) concluded that the kidneys of the honey possum are very similar in form to those of frugivorous bats (Studier et al. 1983) with a large renal cortex in relation to the renal medulla and high rates of urine production.

In the laboratory, honey possums consumed twice their body mass per day when fed very dilute solutions (92% water) and produced urine at the rate of  $780 \pm 100 \text{ ml kg}^{-1} \text{ day}^{-1}$ . These high rates of water turnover are very similar to those reported recently by Goldstein and Newland (2004) in the tiny eutherian shrew, *Cryptotis parva*, that has a similar kidney to the honey possum with a small undifferentiated medulla. Rates of glomerular filtration (GFR) and the handling of filtrate, electrolytes and other solutes in the nephron of the honey possum are yet to be investigated and compared with values from other small mammals (McAllan et al. 1998a, b; Hewitt et al. 1981).

## Vision

Mature retinal projections of the honey possum using unicellular injections of horseradish peroxidase and tetramethylbenzidine processing were first reported by Harman et al. (1990) with the pattern of input to the brain being similar to that seen in other marsupials (Sanderson et al. 1987; Mark 1997).

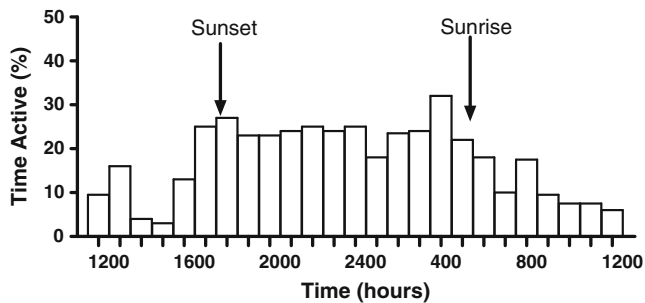
The first detailed study of the honey possum's visual capabilities (Arrese et al. 2002a) reported a visual acuity of

$0.60 \text{ cycles deg}^{-1}$  in moonlight and starlight, lower than the figure of  $0.75 \text{ cycles deg}^{-1}$  earlier attributed by Dunlop et al. (1994). Visual acuity in daylight was slightly higher at  $0.63 \text{ cycles deg}^{-1}$  and an ultrastructural analysis revealed a rod:cone ratio in the outer retina of 20:1 (Arrese et al. 2002a). The location of the eyes, high on the head, give it a very wide field of view, approaching  $240^\circ$ , and a binocular overlap of  $80^\circ$  in the horizontal plane equips it with an apparently well-developed visual predator-avoidance system. Overall, however, the honey possum has low visual acuity, placing it at the lower end of the marsupial scale, as would be expected from the absence of any retinal specialisation such as a visual streak.

Colour vision in most mammalian species is dichromatic, being mediated by two classes of cones, S and L, with either a short-wavelength sensitive (SWS) or a middle-wavelength to long-wavelength sensitive (MWS/LWS) pigment (Jacobs 1993, 2009). Early behavioural studies with the tammar wallaby, indicated the capacity for dichromatic colour vision based on SWS and MWS pigments with peak sensitivities ( $\lambda_{\text{max}}$ ) at 420 and 539 nm, respectively, (Hemmi 1999). Marsupials have traditionally been described as nocturnal, with the numbat, *Myrmecobius fasciatus*, being the only completely diurnal species (Christensen et al. 1984). In fact, most marsupials are crepuscular, emerging from their daytime refugia to feed at dusk, then continuing throughout the night, usually with a pause in activity after midnight followed by a resumption in the early hours of the morning (Lentle et al. 1998). A similar pattern of activity has been observed in the honey possum (Bradshaw et al. 2007; Russell 1986) with sporadic observations of their feeding on *Banksia* inflorescences during daylight hours under cold and cloudy conditions in mid-winter on the south coast of Western Australia (Hopper and Burbidge 1982).

The first report of the presence of medium wavelength (M) cones, in addition to S and L cones in marsupials—which would provide for trichomacy—was in the honey possum and the fat-tailed dunnart, *S. crassicaudata* (Arrese et al. 2002b). This study was based on microspectrophotometric data (MSP) and identified three cones with absorbance maxima at 557, 505 and 350 nm in the honey possum and at 535, 509 and approximately 350 nm in the dunnart (Arrese et al. 2006). These maxima imply the presence of LWS, MWS and ultraviolet (UVS) pigments, respectively, and data were subsequently extended to include the quokka, *S. brachyurus*, and bandicoot, *Isodon obesulus* (Arrese et al. 2005). Attempts, however, to identify this third cone pigment have failed, despite extensive efforts in two laboratories (Strachan et al. 2004; Cowling et al. 2008).

Jacobs (2009) in a recent review of the evolution of colour vision in mammals, mentioned that ...“The pigment gene/cone photopigment picture for the marsupials thus



**Fig. 13** Hourly activity of honey possums, *Tarsipes rostratus*, recorded over three 24-h periods in a captive population (adapted from Russell 1986)

remains somewhat clouded. It appears that at least some marsupials feature three different types of cone pigment, but confirmation that the third of these is a product of the Rh2 gene family is lacking... It may instead be that this pigment ... is the product of a second LWS gene, so far undetected, or ... an Rh1 rod pigment expressed in a class of cone." Further research in this rapidly developing field is likely to be informative.

There has been some attempt to relate the retinal physiology of the honey possum to its ecology with the suggestion that its optimal foraging periods are at dawn and dusk (Arrese et al. 2002a) when red and yellow flowers are thought to be the most prominent (Endler 1993). In an interesting study, Sumner et al. (2005) attempted to identify the presumed functional advantage of the additional middle-wave M cones of the honey possum by comparing its ability to detect flowers in a field situation with a hypothetical dichromatic animal possessing only S and L cones. Surprisingly, the dichromat was able to detect mature *Banksia attenuata* and *B. ilicifolia* flowers equally as well as the trichromat. Discrimination between flowers was also not improved by the presence of M cones with there being ... "no clear and consistent disadvantage in being dichromatic for discriminating between the target and non-target flower species in the honey possum's environment." The only situation where M cones appeared to be an advantage was in discriminating immature from mature inflorescences. The light conditions under which the study was undertaken varied from sun, cloud, early dusk, sunset and post sunset. Peak levels of activity of honey possums, however, occur between sunset and sunrise (Fig. 13)—usually in complete darkness—when any discrimination would depend on rods rather than cones.

Nectar of *Banksia* trees and other native flowers is highly aromatic and it seems reasonable that smell rather than vision would play a major part in honey possums locating their preferred food sources. In this context, Kratzing (1982) noted the significant development of the rostral nasal cavity and the vomeronasal organ (VMN) in the

honey possum and commented that .... "This together with the other anatomical evidence, suggests a close integration between oral and nasal structures in securing food, and indicates that the vomeronasal organ is likely to be involved in a sensory monitoring process."

## Conclusion and future directions

This review of the physiology of the honey possum highlights the species' unusual combination of a suite of highly specialised characters, contrasted with generalised features shared by many other marsupials (Table 2). Its diet, restricted to nectar and pollen, is unique amongst non-flying mammals and finds its only equivalent in a small group of nectarivorous bats.

There are many gaps in our knowledge of this species that need to be filled. The question of whether it has a high BMR, and thus a reduced metabolic scope, needs to be resolved. The maximum duration of torpor is unknown and there are as yet no field studies documenting the frequency of torpor in the field, as opposed to its incidence in trapped animals. It is also not known whether torpor is used to prolong survival during poor flowering periods. Its unusual gut morphology invites future research—the function of the marked diverticulum is unknown and pH measurements throughout the gut have yet to be reported. It is also unclear how the species manages to digest pollen and precisely where this occurs in the gut. Of fundamental interest is the significance of the markedly different relationship between BMR and EUN uncovered in the honey possum and common to other marsupials when compared with eutherians.

There has been only one study of kidney structure and function and it is not known whether honey possums possess a functional juxtaglomerular apparatus and juxta-medullary nephroi with long Loops of Henle having a developed thin segment. The rate of glomerular filtration has yet to be measured and standard renal parameters have yet to be reported. Given that the species appears to be in a constant state of polyuria and polydipsia with high levels of glucose in the urine (personal observation), such studies should prove most rewarding. Standard approaches for measuring renal parameters are not possible with such a small animal, but GFR could be measured using implanted mini-osmotic pumps as has proven successful with small birds (Goldstein and Bradshaw 1998).

Further research is needed on the species' sensory capabilities—both visual and olfactory. Its visual discrimination is poor and suggestions that it locates its food solely by colour, conflict with the fact that it feeds primarily at night. Nectar is highly aromatic, often containing aliphatic ketones that attract small mammals (Johnson et al. 2011), and would appear to be an obvious signal that could reli-

**Table 2** Reproductive features of the honey possum (*Tarsipes rostratus*) shared with other marsupial Families

| Feature   | Shared with   |                                   |
|---|---------------|-----------------------------------|
|   | Family        | References                        |
| Female  |               |                                   |
| Length of oestrous cycle                          | Didelphidae   | Hartman (1923)                    |
|   | Peramelidae   | Gemmell (1988)                    |
|   | Potoroidae    | Smith (1994); Rose (1987)         |
|   | Phalangeridae | Lyne et al. (1959)                |
|   | Thylacomyidae | McCracken (1986)                  |
| <i>Post-partum</i> oestrus and embryonic diapause | Macropodidae  | Sharman (1955a, b)                |
|   | Potoroidae    | Shaw and Rose (1979)              |
|   | Acrobatidae   | Ward and Renfree (1988)           |
|   | Burramyidae   | Ward (1990)                       |
| Slow development of unattached embryo             | Dasyuridae    | Selwood (1980)                    |
|   | Potoroidae    | Shaw and Rose (1979); Rose (1989) |
| Raised progesterone at oestrus                    | Petauridae    | Woodd et al. (2006)               |
|   | Dasyuridae    | Stead-Richardson et al. (2001)    |
|   | Didelphidae   | Hinds and Smith (1992)            |
| Cycle inhibited by long day                       | Dasyuridae    | McAllan and Geiser (2006)         |
| Cycle stimulated by short day                     | Macropodidae  | Sadlier and Tyndale-Biscoe (1977) |
| Male  |               |                                   |
| Axoneme maturation                                | Macropodidae  | Renfree et al. (1984)             |
|   | Phalangeridae | Cummins et al. (1986)             |
| Sperm mid-piece                                   | Dasyuridae    | Cummins et al. (1986)             |
| Flagellum   | Peramelidae   | Renfree et al. (1984)             |

ably be used by honey possums in locating sources of food in the dark.

There are many features of the reproductive physiology that also invite further research. Because of their small body size and fragility, information on hormone levels is very limited and progress may be achieved with the advent of more sensitive hormonal techniques, perhaps utilising different sources such as fur, saliva etc. (Davenport et al. 2006). An intriguing feature is the female's apparent ability to control the length of embryonic diapause and there is much to be learned regarding the interaction between dietary intake and photoperiod in controlling reproductive activity in the field. The question of whether lactational inhibition of diapausing blastocysts occurs in honey possums, as in macropodids, needs further research and is linked with the stage at which the developing zygote actually becomes a unilaminar blastocyst. Detailed studies of the embryological development of honey possums, acrobatids, petaurids and burramyids, similar to those published on *Antechinus*, are urgently needed to clarify these issues and should prove a promising terrain for future research.

Although not yet an endangered species, the honey possum's habitat has been drastically reduced since European occupation of Australia and future-targeted research on the animal's unique physiology and habitat linkage is needed

that can be translated into effective management practices. Only then will its long-term survival be assured.

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