Seasonal field metabolic rate and water influx of captive-bred reintroduced yellow-footed rock-wallabies (Petrogale xanthopus celeris)

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Lapidge, Steven J. and Munn, Adam J.: Seasonal field metabolic rate and water influx of captive-bred reintroduced yellow-footed rock-wallabies (Petrogale xanthopus celeris) 2012, 400-406.


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Disciplines
Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

Publication Details

This journal article is available at Research Online: https://ro.uow.edu.au/scipapers/4677
Seasonal field metabolic rate and water influx of captive-bred re-introduced yellow-footed rock-wallabies (*Petrogale xanthopus celeris*)

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Abstract

Captive breeding and release is a tool used by conservation biologists to re-establish populations of endangered or locally extinct species. Re-introduced animals that have been bred in captivity must learn to meet the challenges posed by free-living, and to adjust to local environmental conditions, food and water sources. How well re-introduced animals might meet these challenges is uncertain as few longitudinal studies have investigated the physiology of reintroduced animals or the implications of this for successful establishment of new populations. Here we have evaluated long-term, seasonal energy and water use by re-introduced yellow-footed rock-wallabies, *Petrogale xanthopus celeris*, an endangered medium-sized marsupial that inhabits rocky outcrops across Australia’s arid and semi-arid rangelands. Captive-bred rock-wallabies were re-introduced to an area within the known boundaries of their former range, in south-western Queensland, Australia. Post-release water turnover rates (WTR) and field metabolic rates (FMR) were measured during their first wet summer and dry winter, by means of the doubly labelled water method. Total body water (73.1%), FMR (1650.0 kJ day\(^{-1}\)), female fecundity (100%), and male and female body masses and survival were consistent between seasons, but rates of water turnover were significantly lower for all animals during the dry winter (174.3 mL day\(^{-1}\)) than during the wet summer (615.0 mL day\(^{-1}\)). There were no significant differences in WTR or FMR between males and lactating females (in either season).

Introduction

Re-introduced captive-bred animals must adapt to unfamiliar, wild situations following their release if they are to survive. Arguably, a critical time for these animals is the first few days and weeks post-release, when they may be more likely to succumb to unfamiliar predators and physiological stresses associated with novel environments. However, the establishment of breeding populations from
released animals relies on the animals’ abilities to adapt over the longer term. The ability of captive-bred animals to adapt to new nutritional environments and to manage seasonal fluctuations in resources post-release has not been extensively studied. Significant decreases in water consumption post-release have been reported for some species (e.g. oryx *Oryx leucoryx*, Stanley Price 1986; Przewalski horses *Equus przewalskii*, Pereladova *et al.* 1999), probably reflecting physiological adjustments to a lack of *ad libitum* resources. Similar studies investigating the resource use by captive-bred and released animals in Australia are lacking, despite reintroduction programs for many species (e.g. see Serena 1994). This may be because one of the most successful means of evaluating resource use in the field, the doubly labelled water method (Speakman 1997), is seen as an invasive technique, requiring re-capture of animals and blood or other body fluid sampling. Nonetheless, without comparative data on the resource patterns of re-introduced animals it is difficult to appreciate factors important to the success of establishing breeding populations, like habitat quality, resource patch-use and density, potential conflict with competing species, or other key threatening processes. As a first step in evaluating the ability of captive-bred animals to adjust to free-living long-term, we investigated the field metabolic rate and water use by captive-bred yellow-footed rock-wallabies (*Petrogale xanthopus celeris*) re-introduced to an area within their former range.

Two sub-species of Yellow-footed rock wallaby are currently recognized, *P. x. xanthopus* occurring in South Australia and New South Wales, and *P. x. celeris* occurring in Queensland. *P. x. xanthopus* is currently listed as Near Threatened, a result of a declining and fragmented total population numbering less than 10,000 individuals (Copley *et al.* 2008). *P. x. celeris* is not listed by IUCN presently, but was assessed at Near Threatened in year 2000, with inferred populations of less than 10,000 individuals (Lapidge 2001). These two sub-species of wallaby are thought to have diverged some 180,000 years ago (Eldridge 1997). Both sub-species have declined since European settlement, and their declines are associated with excessive hunting from early European settlers (before their protection as a native species), from competition with introduced domestic and feral herbivores, and predation by the introduced European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*; Copley *et al.* 2008), though the relative contribution of these features in explaining current wallaby population levels is unknown. Consequently, understanding the role of resource acquisition and requirements to sustain breeding by wallabies are crucial for evaluating release sites and for monitoring released populations with regard to
body condition and breeding success. For example, there is some evidence that indicates that *P. xanthopus* require free-water during drought conditions, but many extant colonies do not occur near permanent water, particularly in Queensland (P. McRae pers. comm.), suggesting that wild-type *P. x. celeris* are able to survive without access to drinking water. Whether captive-bred and released *P. x. celeris* share this (and other) abilities to ameliorate an arid environment is uncertain. We therefore examined the energy and water metabolisms of captive-bred and released *P. x. celeris* over two seasons, a wet summer and a dry winter, in a semi-arid rangelands site, southern Queensland, Australia.

**Material and Methods**

*Study area and animals*

Twenty-four *P. x. celeris* bred at the Charleville compound of the Queensland Environmental Protection Agency were re-introduced to Lambert Pastoral Station in the semi-arid Wallaroo Ranges (25°23'S, 145°51'E) on August 9, 1998, after a 20-year absence. Three releases, each comprising eight animals, occurred at three separate mesas on the property. Mean age of released animals was 27 ± 10 (S.D. throughout) months and mean body mass 5.2 ± 1.1 kg. The re-introduction was undertaken in accordance with re-introduction guidelines (Kleiman 1989; Stanley Price 1989; Short *et al.* 1992; Kleiman *et al.* 1994; IUCN 1998), and after extensive exotic predator control (Lapidge 2001).

Lambert Pastoral Station (25°23'S, 145°51'E) is located 140 km northwest of Charleville and 35 km southeast of Lisburne Station, the origin of the founding stock for the captive Charleville colony. Lambert Station covers 17,000 ha, of which approximately 14% is rocky ranges likely to be suitable *P. x. celeris* habitat. The station receives an annual rainfall of 415 ± 152 mm (n = 43), occurring predominantly in the summer monsoon season. The area is characterised by low dissected residual tablelands of shallow, acid loamy lithosols with stone (conglomerate-tillite) and rubble cover. Steep cliffs combined with exposed rock outcrops are common, along with suitable gullies, terraces, caves and rock-piles for protection from the elements and from predators (Lim and Giles 1987; Sharp 1997). Free water in dams is within 600 m of Site 1, 500 m of Site 2 and 1.4 km of Site 3; these distances are substantially less than the distance *P. x. xanthopus* has been reported to travel to water (Lim 1987; Lim and Giles 1987). Scarps and tops of dissected tablelands are dominated by bendee, *Acacia catenulate*, and mulga, *A. aneura*, open woodland with underlying green turkey bush, *Eremophila gilesii*, crimson turkey bush, *E. latrobei*, twiggy sida, *Sida intricata*, and velvet potato-bush, *Solanum ellipticum*. The slope and base of

**Sampling technique**

The doubly labelled water method (Lifson and McClintock 1966) was used to determine water turnover rate and field metabolic rate following Nagy (1980, 1983, 1989). The technique is based on equilibration of $^{18}$O with oxygen in the body’s water and bicarbonate pools, the latter through the carbonic anhydrase reaction. Hydrogen is lost from the body in water, so the rate of loss of $^3$H represents the WTR when the animal is in steady-state. Oxygen is lost from the body in both water and CO$_2$ so the difference between the rates of loss of $^{18}$O and $^3$H represents the rate of loss of CO$_2$, or metabolic rate (Wallis and Green 1992). Potential errors in the doubly labelled water technique have been reviewed (Nagy 1980, 1992; Nagy and Costa 1980; Speakman 1997; Green 1997; Gibson 1999).

*P. x. celeris* were sampled during the wet summer (January) and dry winter (July) of 2000. Animals were caught in treadle-operated wire cage traps (height 38 cm, width 38 cm, length 76cm; Mascot Wire Works, Sydney, and Crestware Industries, Adelaide). Traps were lined with high-density foam on the inside of doors, sides and roof to prevent injury to the animal once captured, and re-lined with 95% shade-cloth to protect the foam from damage by captured animals. Traps were positioned perpendicular to pathways to allow access from both directions in areas frequented by *P. x. celeris*, as established from radio-telemetry undertaken in the two months post-release. *P. x. celeris* faecal density in each identified area guided final trap placement. Traps were baited with macropod pellets and universal bait (peanut butter and rolled oats) and sprayed with diluted aniseed essence to attract distant animals. Trapping at the three sites was undertaken on a rotational nightly basis over a minimum of 12 nights with traps baited and set within two hours of dusk and checked the following dawn.

Captured animals were transferred from traps into large pet-packs and carried to a vehicle for transport to the field laboratory. Animals were weighed in hessian sacks using a hanging dial scale (± 0.05 kg) at initial capture in summer, and at initial capture and recapture in winter; body masses were assumed to remain constant for calculations (see below). Animals were placed in a darkened air-conditioned room prior to processing, during isotope equilibration, and before being returned to the colony to minimise capture stress and dehydration. Blood samples were obtained from a lateral tail vein using a 21 g x 1” needle (Terumo) and a 5 mL Luer syringe.
An initial 2-mL blood sample was taken for measurement of background isotope levels. Blood was stored in 5-mL dried Lithium Heparin vials, further sealed with Parafilm, and frozen. Each animal was injected intramuscularly (hind-limb) with separate pre-weighed doses of $\text{H}_2^{18}\text{O}$ and $\text{H}_2\text{O}$ (tritiated water) in a 2.5 mL syringe (with 25 g needle attached). Summer dose rates were 0.5 mL $\text{H}_2\text{O} \cdot \text{kg}^{-1}$ body mass (8 MBq.mL$^{-1}$) and 0.5 mL $\text{H}_2^{18}\text{O} \cdot \text{kg}^{-1}$ body mass (98 atom%). Winter dose rates were reduced to 0.1 mL $\text{H}_2\text{O} \cdot \text{kg}^{-1}$ body mass (8 MBq.mL$^{-1}$) and 0.3 mL $\text{H}_2^{18}\text{O} \cdot \text{kg}^{-1}$ body mass (98 atom%) based on the summer results. The mass of the injectate was determined by weighing the injection syringe on a digital balance (0.001 g) before and after injection. Injectate mass was converted to volume by weighing 100 $\mu\text{l}$ of each solution on a digital balance (0.0001 g). Animals were left for 3 to 4 h to allow the isotopes to equilibrate with the body water pool, sufficient time for a marsupial of the mass of adult $P. x. celeris$ (Nagy 1983; Green 1989; Speakman 1997). A second 2-mL blood sample was taken following equilibration. Once all equilibration samples were obtained, animals were returned to the point of capture and released. Animals were recaptured between 5 and 9 days post-injection and had a 2-mL blood sample taken at the point of capture.

**Sample analyses**

Pure water was extracted from blood samples by microdistillation (Nagy 1983). Liquid-scintillation spectroscopy was used to determine $\text{H}^3$ activity. Subsamples (100-$\mu\text{l}$) of distilled water were pipetted into plastic scintillation vials (Packard), to which 5 mL of scintillation fluid (Packard Ultima Gold™) was added. Specific activity of each sample, along with two vials of the standard dose and four blanks (scintillation fluid only), was determined using a Packard 1600 TR liquid scintillation counter. Samples from each collection period were analysed together to avoid bias in differential radioactive decay of tritium. Isotope Ratio Mass Spectroscopy (Speakman *et al.* 1990) was used to determine $^{18}\text{O}$ concentration by Metabolic Solutions Inc., Nashua, NH, U.S.A. WTR and FMR were calculated using equations 1-4 of Nagy (1983; see Nagy 1983, Page 33 for description of equations when body masses are unchanged). It was assumed that total body water did not change throughout the isotope decay period or that any changes in total body water were linear. CO$_2$ production rates were then converted to units of energy metabolism (kJ) using the calculated heat equivalent for a general herbivorous diet of 21.2 kJ L$^{-1}$ CO$_2$ (Munks and Green 1995; Hume 1999). To allow comparison between animals of different body mass, the allometric scaling exponents of 0.71 for water turnover rates of free-range...
marsupials (Nagy and Peterson 1988; Hume 1999) and 0.58 for field metabolic rate (Nagy 1994; Cooper et al. 2003) were used.

Statistical analyses

Significance of differences in WTR and FMR between sexes and seasons were tested using two-factor ANOVA for unequal sample sizes. Dependence of WTR and FMR on reproductive status (joey age) was examined using simple linear regression. Minimum significance was defined as $P<0.05$. For all response variables, the significance of differences between sexes and seasons and the effect of individual animals were examined using REML (Residual Maximum Likelihood Estimation; Patterson & Thompson, 1971), with animal as a random effect and sex, season and sex*season as fixed effects. When there was no effect due to animal, the data were reanalysed as a two-way non-orthogonal analysis of variance with unequal sample sizes. Results are presented as season or sex means ± S.E. of mean, where the SEs are derived from the REML analysis or two-way ANOVA as appropriate. Dependence of water turnover rate and field metabolic rate on reproductive status (joey age) was examined using linear regression. All analyses were performed using GenStat (2003).

Results

Seasonal conditions

In the three months prior to the summer FMR measurements, 205 mm of rain had fallen on Lambert Station. During the sampling period a further 22 mm of rain fell. Daily ambient temperatures during summer sampling were regularly in excess of 40°C. Radio-telemetry of animals immediately after rain indicated that they were foraging on the plain, where they may have obtained free water that had collected in the hoof depressions of cattle (Lapidge 2001) or other depressions. No animal was radio-tracked in the vicinity of local dams or water tanks, although this possibility cannot be ruled out. No rain fell during the winter sampling period and the last rainfall recorded was 117 mm in mid-May, two months prior to the winter sampling. Daily ambient temperatures during the winter sampling period were generally in the mid-20°C range.
Animal details and body mass

Ten *P. x. celeris* were injected with doubly labelled water (H$_2$O$^{18}$O and $^3$HOH) within the first six days of the winter measurement period, and nine were injected within the first six days of the summer measurements period; one additional male was injected only with tritiated water in summer as the chance of recapturing this transient male was deemed low. Eight of the ten animals were recaptured during each measurement period. Four animals were sampled during both periods (3♂: 1♀) and eight others sampled once (1♂: 7♀). Thus, 12 animals were sampled in total throughout the study (4♂: 8♀; Table 1). Mean body mass of animals during each sample period is presented in Table 1. Changes in body mass between initial capture and recapture were only assessed during winter, when average body mass decline was negligible at 0.06 ± 0.02% day$^{-1}$. The four animals sampled in both seasons gained 313 ± 193 g between the summer and winter sampling. All females were lactating when captured, having a mean age of pouch young of 105 ± 45 days (range 33-169 days), about half the pouch life of a joey (Lapidge 2001).

Total body water and water turnover rate

Total body water (TBW) was not significantly different between males and females for either season (summer: $F_{1,5}=0.28$, $P=0.62$; winter: $F_{1,4}=0.33$, $P=0.59$), or between seasons ($F_{1,13}=0.04$, $P=0.85$; Table 1). Overall, mean TBW for re-introduced *P. x. celeris* at Lambert Station was 73.1 ± 5.8%.

Water turnover rate (WTR) (Table 1) was significantly different between summer and winter samples ($F_{1,14}=67.0$, $P<0.001$), with allometrically-adjusted summer WTRs being more than 3.5-fold winter WTRs. The change in WTR between seasons was similar for both sexes (male: $F_{1,5}=30.1$, $P=0.003$; female: $F_{1,8}=31.2$, $P=0.001$), and there was no significant difference between male and female WTRs within either season (summer: $F_{1,7}=0.02$, $P=0.88$; winter: $F_{1,6}=0.12$, $P=0.74$). WTR was independent of joey age in lactating females ($F_{1,7}=0.28$, $P=0.61$). Although sample sizes were low, WTR did not vary between sites within either season (summer: $F_{2,7}=0.99$, $P=0.35$; winter: $F_{2,5}=2.50$, $P=0.18$).
Field metabolic rate

Field metabolic rate (FMR) remained relatively constant between seasons at 593 ± 229 kJ kg\(^{-0.58}\) d\(^{-1}\) (Table 1). Although there was a tendency for males to have a higher FMR than females \((F_{1,13}=3.52, P=0.08)\), there was no significant difference between the sexes within either season (summer: \(F_{1,5}=3.19, P=0.13\); winter: \(F_{1,6}=0.48, P=0.51\)). FMR did not differ for males \((F_{1,4}=0.29, P=0.62)\) or females \((F_{1,7}=0.75, P=0.42)\) between seasons. FMR of lactating females was independent of joey age \((F_{1,7}=0.001, P=0.97)\). Although sample sizes were low, FMR did not vary significantly between sites (summer: \(F_{1,6}=0.01, P=0.91\); winter: \(F_{1,8}=3.25, P=0.11\)).

Discussion

Lapidge (2000) reported captive-bred \(P. x. xanthopus\) at Aroona Sanctuary, Flinders Ranges, South Australia assumed a diet similar to that of free-ranging counterparts within 2-3 months of release. Such a finding strongly suggests that the captive-bred and subsequently released animals were able to adjust to their new environment, and they were capable of foraging successfully to meet their minimum nutrient requirements, and indeed to begin breeding. The findings presented here further support that conclusion, as the captive-bred, released animals were apparently capable of meeting their daily water and energy needs to maintain body mass within each season, and to support breeding. Although we do not know exactly how many young survived post-weaning, the captive-bred females were certainly capable of rearing young to at least mid-pouch life stages.

The TBW values we measured in \(P. x. celeris\) are similar to those from the sympatric euro \((Macropus r. erubescens; 73.1 ± 0.5\%; Dawson et al. 1975)\), and to those of the eastern grey kangaroo \((M. giganteus; 73.5 ± 0.4\%; Blaney et al. 2000)\), red kangaroo \((M. rufus; 67.8 ± 0.7\%; Munn et al. 2009)\), and tammar wallaby \((M. eugenii; 73.3 ± 4.7\%; Nagy et al. 1990a)\). TBW can be an indicator of body condition as it varies inversely with body fat, thus a high TBW percentage indicates poor body condition (Holleman and Dieterich 1973; Bakker and Main 1980; Catt 1981; Reimer and Hindell 1996; Gibson and Hume 2000). In our study, \(P. x. celeris\) maintained TBW and thus body condition during the dry winter. This finding, along with animals maintaining body mass between seasons, suggests they are well adjusted to free-living conditions. In fact, four animals sampled in both seasons...
gained body mass, and continuous breeding by all females throughout the year was observed (Lapidge 2001). The consistent across-season TBW and body mass therefore indicates re-introduced *P. x. celeris* maintained body-fat reserves throughout the driest period post-release. This contrasts somewhat with studies on other wild/free-range marsupials such as bilbies (*Macrotris lagotis*), which lost body condition in summer possibly associated with reduced food availability or increased thermoregulatory demands (Gibson and Hume 2000). Even among the largest marsupials, the red kangaroo *M. rufus* body condition in winter was lower than other seasons, probably due to low rainfall and reduced pasture biomass (Moss and Croft 1999). Thus, it appears that our captive-bred *P. x. celeris* possessed the ability to cope with seasonal fluctuations in water and food availability, despite the absence of similar stresses during captive rearing.

The seasonal WTR patterns for *P. x. celeris* (summer 175.4 mL kg$^{-0.71}$ d$^{-1}$; winter 49.0 mL kg$^{-0.71}$ d$^{-1}$) we reported were somewhat different to those found for *P. x. xanthopus* (summer 101 mL kg$^{-0.71}$ d$^{-1}$, winter 276 mL kg$^{-0.71}$ d$^{-1}$; Lim et al. 1987), and both studies found variation in WTRs followed local rainfall. The higher WTRs in summer in *P. x. celeris* were likely the result of increased water required for thermoregulation, as ambient temperatures regularly exceed 40°C throughout the species’ range (Dawson and Denny 1969; Withers 1992; BOM 2001), and also to increased water intake from forage, as water content of consumed forage during the wet summer was higher than during the dry winter (Allen 2001). In this regard, it is important to note that WTR itself may not reflect the water requirements of the animal because water influxes for herbivores can be heavily influenced by forage water contents. Consequently, it is difficult to draw conclusions about the definitive water requirements of free range animals, and particularly their abilities to withstand water shortages, unless these data can be collected from animals known to be water restricted. Of note, there was probably also increased availability of surface water for the *P. x. celeris* during the wet summer as water tends to accumulate within cracks and rock depressions in the rocky terrain they inhabit.

The winter WTR of *P. x. celeris* in the current study (49.0 mL kg$^{-0.71}$ d$^{-1}$) is the lowest recorded for a *Petrogale* species, and among the lowest recorded for any marsupial (Hume 1999; Nagy and Bradshaw 2000; Bradshaw et al. 2001). Winter WTR in *P. x. celeris* is most akin to *Petrogale* species occupying similar habitat and climatic niche in Western Australia, such as Rothschild’s Rock-wallaby (*P. rothschildi*; 68 mL kg$^{-0.71}$ d$^{-1}$; Bradshaw et al. 2001) and Black-flanked rock-wallaby (*P. lateralis*;
77 mL kg\(^{-0.71}\) d\(^{-1}\); Nagy and Bradshaw 2001) during a dry spring. Of note, our data for the winter WTR in \(P. x. celeris\) was considerably lower than that reported for \(P. x. xanthopus\) in winter (276 mL kg\(^{-0.71}\) d\(^{-1}\); Lim et al. 1987). Similarly low WTRs to those of \(P. x. celeris\) (this study) have been reported for dehydrated captive Spectacled Hare-wallaby (\(L. conspicillatus\); 51 mL kg\(^{-0.71}\) d\(^{-1}\); Bakker and Bradshaw 1983), and non-dehydrated wild Spectacled Hare-wallaby(30.1 mL kg\(^{-0.71}\) d\(^{-1}\); Bradshaw et al. 2001), and for free-ranging Brush-tailed Bettong (\(Bettongia penicillata\); 57 mL kg\(^{-0.71}\) d\(^{-1}\); Green 1989) and Quokka (\(Setonix brachyurus\) 57 mL kg\(^{-0.71}\) d\(^{-1}\); Nagy et al. 1990a). This finding suggests that water demands for macropods are more closely related to habitat than to phylogeny (see also Withers et al. 2006). For example, low WTR in \(Petrogale\) species are likely the result of animals sheltering by day in rocky outcrops and minimising exposure to climatic variations, thus reducing evaporative cooling. \(Petrogale xanthopus\) has also been reported to decrease faecal water loss and increase urine concentration during dry periods (Lim et al. 1987).

Generally, WTR and FMR in reproductive female marsupials are related to age of pouch young and thus lactational demands (Green 1989, 1997; Munks 1990; Hume 1999). We found no significant difference in allometrically-adjusted WTR or FMR between males and lactating females in either season (Table 1). Comparison with non-lactating females was not possible as all females carried pouch young. However, we found that both WTR and FMR were independent of joey age in lactating females. These findings suggest no significant water or energy demands of lactation on \(P. x. celeris\), and differ from that reported by Kennedy and Heinsohn (1974), who demonstrated a 17% higher WTR in lactating compared with non-lactating unadorned rock-wallaby (\(P. inornata\)). Nevertheless, other studies have reported little or no significant increase in WTR during lactation for other macropodid marsupials, including rufous bettong (\(A. rufescens\); Wallis and Green 1992), brush-tailed bettong and tammar wallaby(Green 1997). Green (1997) suggested that this may be due to the macropods usually supporting only a single, small pouch young, and thus rates of milk production are low when compared to eutherians mammals, even during mid-pouch life. However, total investment in reproduction by eutherians and marsupials is similar by late lactation (Tyndale-Biscoe 2005).

The FMR of our captive-bred and released \(P. x. celeris\) was not significantly different between summer and winter, and averaged 593 ± 229 kJ kg\(^{-0.58}\) d\(^{-1}\). The tendency for a higher winter- (607 ± 194 kJ kg\(^{-0.58}\) d\(^{-1}\)) than summer-FMR (576 ± 248 kJ kg\(^{-0.58}\) d\(^{-1}\)) was likely a result of higher
thermoregulatory demands resulting from night-time temperatures near freezing, and to an increase in foraging activity during the dry winter. A similar finding was reported for rufus bettong (A. rufescens; Wallis and Green 1992). Green (1989) reported a comparable FMR (622 kJ kg$^{-0.58}$ d$^{-1}$) for one specimen of P. x. xanthopus. FMR of P. xanthopus spp. (Green 1989; this study) is considerably higher than similarly sized macropods from more mesic environments (e.g. 488 kJ kg$^{-0.58}$ d$^{-1}$ for tammar wallaby, M. eugeni, and 578 kJ kg$^{-0.58}$ d$^{-1}$ for Tasmanian pademelon (Thylogale. billardieri; Nagy and Bradshaw 2000), and that of the smaller black-flanked rock wallaby (P. lateralais) during the dry season (386 kJ kg$^{-0.58}$ d$^{-1}$; Nagy and Bradshaw 2000). This finding is inconsistent with Nagy and Bradshaw (2000), who reported FMRs of arid-zone marsupials to be 35% less than those of non-arid-zone marsupials. However, it is important to recognise that the animals in this study were not wild, and we have no way of knowing how captive-rearing may have impacted their basic physiology. As far as we are aware, there are no data available for the FMR (or WTR) of wild P. x. celeris, making it difficult to determine whether our animals are representative of the species generally, or whether other factors are involved. Interestingly, the generally higher FMR of P. xanthopus and P. x. celeris compared with similar-sized plains-dwelling macropods, or marsupials generally, may be associated with their habitat. For example, P. xanthopus spp. may use more energy to transverse complex rocky terrains, but the costs of locomotion for this species are unknown. It is also worth noting that the FMRs of black-flanked rock wallaby (P. lateralais), which inhabit similar rocky terrains, are not especially high compared with marsupials generally.

Three P. x. celeris deaths were recorded throughout 2000 (animal F36 in February, F15 in April and F27 in November), after the DLW measurement periods, and all from suspected fox (Vulpes vulpes) attacks. All deceased females were carrying pouch young at the time of death, and all died during months with recorded rainfalls (Lapidge 2001). Of note, all females known or suspected to be killed by foxes (n=5) were killed during months of high rainfall and were found on the plain (Lapidge and Henshall 2001). However, no rain fell in the months two males died and their remains were found on the hill. Greater foraging for free water by females than males may explain the slight female bias in fox predation and why remains of each sex were found in different locations. Whether additional water was required for lactation could not be statistically proven, and fresh-matter food intakes or requirements are difficult to predict as differences in digestibility between males and females are
uncertain. Nonetheless, our data indicate that re-introduced captive-bred *P. x. celeris* were able to survive without free water within two-years of release from captivity, if not sooner. *P. lateralis* has also been reported to obtain nearly all their water from their diet during drought conditions and not travel to free water, though available nearby (Nagy and Bradshaw 2000).

### Conclusion

Results from this study indicate that there may be a difference in free water usage between *P. x. celeris* and *P. x. xanthopus*. For example, our re-introduced *P. x. celeris* at Lambert Station, Queensland, did not travel 500 m (Site 2) to free water, whereas *P. x. xanthopus* under similar rainfall conditions at Middle Gorge, South Australia, travelled up to 2 km to access water (Lim 1987; Lim *et al.* 1987). Furthermore, the high incidence of rainfall in summer throughout the range of *P. x. celeris*, when animals are more likely to require water for thermoregulation, would reduce this sub-species’ need to travel to free water. Such differences in rainfall patterns throughout the range of *P. x. celeris* than *P. x. xanthopus* may explain why extant *P. x. celeris* colonies do not necessarily occur near free water. Nonetheless, the possibility that re-introduced *P. x. celeris* may need to travel to free water during droughts cannot be ruled out. Overall, further studies on the interactions of diet and water use, and differences between males and lactating versus non-lactating females would be useful. More importantly, further research on wild-type animals is necessary to determine whether captive-rearing has any impact on individual FMRs or WTRs. Such studies on vulnerable or endangered animals would likely face resistance because of the need to capture and re-capture of animals, but without that information it is not possible to fully appreciate how captive rearing might influence the basic physiology of species.

### Acknowledgments

The authors thank the Bredhauer family of Lambert Pastoral Station and the Atkinson family of Lisburne Pastoral Station for the use of their property, David Blyde and Western Plains Zoo for the loan of pet-paks used during the sampling, Warren Müller for statistical advice and the volunteers that assisted with field sampling. This study is part of the Yellow-footed Rock-wallaby Reintroduction
project, which is financially and logistically supported by I.D. Hume, the Queensland Environmental
Protection Agency, the Royal Zoological Society of South Australia, NRG Flinders, the Nature
Conservation Foundation of South Australia, the Zoological Parks Board of New South Wales, and
Australian Geographic. The authors also thank two anonymous reviewers for their comments and
contribution to improving the manuscript. This study was undertaken with the approval of the Animal
Ethics Committee of the University of Sydney (L04/4-98/3/2749) and Queensland Environmental
Protection Agency (W0/002083/98/SAA).

References


Bakker, H.R. and Main, A.R. (1980). Condition, body composition and total body water estimation in the

metabolism and renal function and structure in Eastern Grey Kangaroos (*Macropus giganteus*): responses to

Bradshaw, S.D., Morris, K.D., and Bradshaw, F.J. (2001). Water and electrolyte homeostasis and kidney
function of desert-dwelling marsupial wallabies in Western Australia. *Journal of Comparative Physiology B*
171: 23-32.


IUCN, Gland, Switzerland and Cambridge, U.K. 10pp
Kennedy, P.M. and Heinsohn, G.E. (1974). Water metabolism of two marsupials - the brush-tailed possum, 
*Trichosurus vulpecula* and the rock-wallaby, *Petrogale inornata* in the wild. *Comparative Biochemistry and 
Physiology A* 47: 829-834.


Interactive management of wild and captive animals*: 287-303. Onley, P.J.S., Mace, G.M. and Feistner, 

xanthopus* (Marsupialia: Macropodidae), in the northern Flinders Ranges, South Australia. *Wildlife Research* 
27: 195-201.

Lapidge, S.J. (2001). Reintroduction biology of Yellow-footed Rock-wallabies (*Petrogale xanthopus celeris* and 
*P. x. xanthopus*). Ph.D. thesis, University of Sydney, Australia.

Lapidge, S.J. and Henshall, S. (2001). Diet of foxes and cats, with evidence of predation on yellow-footed rock- 
wallabies (*Petrogale xanthopus celeris*) by foxes, in southwestern Queensland. *Australian Mammalogy* 23: 
47-51.


(Marsupialia: Mocropodidae) III. Distribution and management in western New South Wales. *Australian 
Wildlife Research* 14: 147-161.

Management of the Yellow-footed Rock-wallaby *Petrogale xanthopus* Gray, 1854. *Department of 
Environment and Planning, South Australia, Special Publication* 4: 1-94.


Munks, S.A. and Green, B. (1995). Energy allocation for reproduction in a marsupial arboreal folivore, the 


Table 1. Seasonal body mass (BM), total body water, water turnover rate and field metabolic rate of reintroduced yellow-footed rock-wallabies at Lambert Station. Data are shown as means ± standard deviation with sample size indicated in parentheses next to sex. * Sample size of 4 relates to BM and water turnover rate, other values relate to three animals. †Within columns, pooled means differ significantly at \( P < 0.0001 \).

<table>
<thead>
<tr>
<th>Animal</th>
<th>BM</th>
<th>Total Body Water</th>
<th>Water Turnover Rate</th>
<th>Field Metabolic Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g</td>
<td>g</td>
<td>( \text{mL d}^{-1} )</td>
<td>( \text{mL kg}^{-0.71} \text{ d}^{-1} )</td>
</tr>
<tr>
<td>WET SUMMER</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males (3-4)*</td>
<td>6450 ± 666</td>
<td>4603.9 ± 412.0</td>
<td>73.3 ± 2.0</td>
<td>625.4 ± 78.7</td>
</tr>
<tr>
<td>Females (4)</td>
<td>5362 ± 188</td>
<td>3884.3 ± 150.9</td>
<td>72.4 ± 1.6</td>
<td>604.7 ± 44.5</td>
</tr>
<tr>
<td>Total</td>
<td>5906 ± 731</td>
<td>4192.7 ± 461.1</td>
<td>72.8 ± 1.8</td>
<td>615.0 ± 64.8</td>
</tr>
<tr>
<td>DRY WINTER</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males (3)</td>
<td>6713 ± 622</td>
<td>5193.2 ± 571.6</td>
<td>77.3 ± 4.1</td>
<td>201.9 ± 63.0</td>
</tr>
<tr>
<td>Females (5)</td>
<td>5268 ± 446</td>
<td>4010.8 ± 293.7</td>
<td>71.1 ± 8.2</td>
<td>157.8 ± 26.5</td>
</tr>
<tr>
<td>Total</td>
<td>5810 ± 871</td>
<td>4454.2 ± 710.0</td>
<td>73.4 ± 7.6</td>
<td>174.3 ± 48.8</td>
</tr>
</tbody>
</table>