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Seasonal field metabolic rate and water influx of captive-bred reintroduced 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. Reintroduced 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 reintroduced 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 reintroduced yellow-footed rock-wallabies (*Petrogale xanthopus celeris*), an endangered medium-sized marsupial that inhabits rocky outcrops across Australia's arid and semiarid rangelands. Captive-bred rock-wallabies were reintroduced 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).

Disciplines

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

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1 **Seasonal field metabolic rate and water influx of captive-bred re-introduced yellow-**
2 **footed rock-wallabies (*Petrogale xanthopus celeris*)**

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7

8 *Abstract*

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

24 **Introduction**

25 Re-introduced captive-bred animals must adapt to unfamiliar, wild situations following their release if
26 they are to survive. Arguably, a critical time for these animals is the first few days and weeks post-
27 release, when they may be more likely to succumb to unfamiliar predators and physiological stresses
28 associated with novel environments. However, the establishment of breeding populations from

29 released animals relies on the animals' abilities to adapt over the longer term. The ability of captive-
30 bred animals to adapt to new nutritional environments and to manage seasonal fluctuations in
31 resources post-release has not been extensively studied. Significant decreases in water consumption
32 post-release have been reported for some species (e.g. oryx *Oryx leucoryx*, Stanley Price 1986;
33 Przewalski horses *Equus przewalskii*, Pereladova *et al.* 1999), probably reflecting physiological
34 adjustments to a lack of *ad libitum* resources. Similar studies investigating the resource use by captive-
35 bred and released animals in Australia are lacking, despite reintroduction programs for many species
36 (e.g. see Serena 1994). This may be because one of the most successful means of evaluating resource
37 use in the field, the doubly labelled water method (Speakman 1997), is seen as an invasive technique,
38 requiring re-capture of animals and blood or other body fluid sampling. Nonetheless, without
39 comparative data on the resource patterns of re-introduced animals it is difficult to appreciate factors
40 important to the success of establishing breeding populations, like habitat quality, resource patch-use
41 and density, potential conflict with competing species, or other key threatening processes. As a first
42 step in evaluating the ability of captive-bred animals to adjust to free-living long-term, we investigated
43 the field metabolic rate and water use by captive-bred yellow-footed rock-wallabies (*Petrogale*
44 *xanthopus celeris*) re-introduced to an area within their former range.

45 Two sub-species of Yellow-footed rock wallaby are currently recognized, *P. x. xanthopus* occurring
46 in South Australia and New South Wales, and *P. x. celeris* occurring in Queensland. *P. x. xanthopus* is
47 currently listed as Near Threatened, a result of a declining and fragmented total population numbering
48 less than 10,000 individuals (Copley *et al.* 2008). *P. x. celeris* is not listed by IUCN presently, but was
49 assessed at Near Threatened in year 2000, with inferred populations of less than 10,000 individuals
50 (Lapidge 2001). These two sub-species of wallaby are thought to have diverged some 180, 000 years
51 ago (Eldridge 1997). Both sub-species have declined since European settlement, and their declines are
52 associated with excessive hunting from early European settlers (before their protection as a native
53 species), from competition with introduced domestic and feral herbivores, and predation by the
54 introduced European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*; Copley *et al.* 2008), though the
55 relative contribution of these features in explaining current wallaby population levels is unknown.
56 Consequently, understanding the role of resource acquisition and requirements to sustain breeding by
57 wallabies are crucial for evaluating release sites and for monitoring released populations with regard to

58 body condition and breeding success. For example, there is some evidence that indicates that *P.*
59 *xanthopus* require free-water during drought conditions, but many extant colonies do not occur near
60 permanent water, particularly in Queensland (P. McRae pers. comm.), suggesting that wild-type *P. x.*
61 *celeris* are able to survive without access to drinking water. Whether captive-bred and released *P. x.*
62 *celeris* share this (and other) abilities to ameliorate an arid environment is uncertain. We therefore
63 examined the energy and water metabolisms of captive-bred and released *P. x. celeris* over two
64 seasons, a wet summer and a dry winter, in a semi-arid rangelands site, southern Queensland,
65 Australia.

66

67 **Material and Methods**

68 *Study area and animals*

69 Twenty-four *P. x. celeris* bred at the Charleville compound of the Queensland Environmental Protection Agency
70 were re-introduced to Lambert Pastoral Station in the semi-arid Wallaroo Ranges (25°23'S, 145°51'E) on August
71 9, 1998, after a 20-year absence. Three releases, each comprising eight animals, occurred at three separate mesas
72 on the property. Mean age of released animals was 27 ± 10 (S.D. throughout) months and mean body mass $5.2 \pm$
73 1.1 kg. The re-introduction was undertaken in accordance with re-introduction guidelines (Kleiman 1989;
74 Stanley Price 1989; Short *et al.* 1992; Kleiman *et al.* 1994; IUCN 1998), and after extensive exotic predator
75 control (Lapidge 2001).

76 Lambert Pastoral Station (25°23'S, 145°51'E) is located 140 km northwest of Charleville and 35 km southeast
77 of Lisburne Station, the origin of the founding stock for the captive Charleville colony. Lambert Station covers
78 17,000 ha, of which approximately 14% is rocky ranges likely to be suitable *P. x. celeris* habitat. The station
79 receives an annual rainfall of 415 ± 152 mm ($n = 43$), occurring predominantly in the summer monsoon season.
80 The area is characterised by low dissected residual tablelands of shallow, acid loamy lithosols with stone
81 (conglomerate-tillite) and rubble cover. Steep cliffs combined with exposed rock outcrops are common, along
82 with suitable gullies, terraces, caves and rock-piles for protection from the elements and from predators (Lim and
83 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;
84 these distances are substantially less than the distance *P. x. xanthopus* has been reported to travel to water (Lim
85 1987; Lim and Giles 1987). Scarps and tops of dissected tablelands are dominated by bendee, *Acacia catenulate*,
86 and mulga, *A. aneura*, open woodland with underlying green turkey bush, *Eremophila gilesii*, crimson turkey
87 bush, *E. latrobei*, twiggly sida, *Sida intricate*, and velvet potato-bush, *Solanum ellipticum*. The slope and base of

88 Site 1 also contain gidgee, *A. cambagei*, wilga, *Geijera parviflora*, and silver-leaved ironbark, *Eucalyptus*
89 *melanophloia*. The base of each site contains silver-tails, *Ptilotus obovatus*, and showy foxtail, *P. exaltatus*,
90 velvet lantern-bush, *Abutilon calliphllum*, *S. intricata*, and various chenopods including ruby saltbush,
91 *Enchylaena tomentosa*, and *Maireana*, *Sclerolaena*, and *Rhagodia* species. Although traditionally Mitchell grass
92 plains (*Astrebala* spp.), buffel grass, *Cenchrus ciliaris*, was sown in 1964 to improve the pasture (P. Bredhauer
93 pers. comm.).

94

95 *Sampling technique*

96 The doubly labelled water method (Lifson and McClintock 1966) was used to determine water turnover rate and
97 field metabolic rate following Nagy (1980, 1983, 1989). The technique is based on equilibration of ^{18}O with
98 oxygen in the body's water and bicarbonate pools, the latter through the carbonic anhydrase reaction. Hydrogen
99 is lost from the body in water, so the rate of loss of ^3H represents the WTR when the animal is in steady-state.
100 Oxygen is lost from the body in both water and CO_2 so the difference between the rates of loss of ^{18}O and ^3H
101 represents the rate of loss of CO_2 , or metabolic rate (Wallis and Green 1992). Potential errors in the doubly
102 labelled water technique have been reviewed (Nagy 1980, 1992; Nagy and Costa 1980; Speakman 1997; Green
103 1997; Gibson 1999).

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

114 Captured animals were transferred from traps into large pet-packs and carried to a vehicle for transport to the
115 field laboratory. Animals were weighed in hessian sacks using a hanging dial scale (± 0.05 kg) at initial capture
116 in summer, and at initial capture and recapture in winter; body masses were assumed to remain constant for
117 calculations (see below). Animals were placed in a darkened air-conditioned room prior to processing, during
118 isotope equilibration, and before being returned to the colony to minimise capture stress and dehydration. Blood
119 samples were obtained from a lateral tail vein using a 21 g x 1" needle (Terumo) and a 5 mL Luer syringe

120 (Terumo). An initial 2-mL blood sample was taken for measurement of background isotope levels. Blood was
121 stored in 5-mL dried Lithium Heparin vials, further sealed with Parafilm, and frozen. Each animal was injected
122 intramuscularly (hind-limb) with separate pre-weighed doses of H_2^{18}O and ^3HOH (tritiated water) in a 2.5 mL
123 syringe (with 25 g needle attached). Summer dose rates were $0.5 \text{ mL } ^3\text{HOH.kg}^{-1}$ body mass (8 MBq.mL^{-1}) and
124 $0.5 \text{ mL } \text{H}_2^{18}\text{O.kg}^{-1}$ body mass (98 atom%). Winter dose rates were reduced to $0.1 \text{ mL } ^3\text{HOH.kg}^{-1}$ body mass (8
125 MBq.mL^{-1}) and $0.3 \text{ mL } \text{H}_2^{18}\text{O.kg}^{-1}$ body mass (98 atom%) based on the summer results. The mass of the
126 injectate was determined by weighing the injection syringe on a digital balance (0.001 g) before and after
127 injection. Injectate mass was converted to volume by weighing 100 μl of each solution on a digital balance
128 (0.0001 g). Animals were left for 3 to 4 h to allow the isotopes to equilibrate with the body water pool, sufficient
129 time for a marsupial of the mass of adult *P. x. celeris* (Nagy 1983; Green 1989; Speakman 1997). A second 2-
130 mL blood sample was taken following equilibration. Once all equilibration samples were obtained, animals were
131 returned to the point of capture and released. Animals were recaptured between 5 and 9 days post-injection and
132 had a 2-mL blood sample taken at the point of capture.

133

134 *Sample analyses*

135 Pure water was extracted from blood samples by microdistillation (Nagy 1983). Liquid-scintillation
136 spectroscopy was used to determine ^3H activity. Subsamples (100- μl) of distilled water were pipetted
137 into plastic scintillation vials (Packard), to which 5 mL of scintillation fluid (Packard Ultima GoldTM)
138 was added. Specific activity of each sample, along with two vials of the standard dose and four blanks
139 (scintillation fluid only), was determined using a Packard 1600 TR liquid scintillation counter.
140 Samples from each collection period were analysed together to avoid bias in differential radioactive
141 decay of tritium. Isotope Ratio Mass Spectroscopy (Speakman *et al.* 1990) was used to determine ^{18}O
142 concentration by Metabolic Solutions Inc., Nashua, NH, U.S.A. WTR and FMR were calculated using
143 equations 1-4 of Nagy (1983; see Nagy 1983, Page 33 for description of equations when body masses
144 are unchanged). It was assumed that total body water did not change throughout the isotope decay
145 period or that any changes in total body water were linear. CO_2 production rates were then converted
146 to units of energy metabolism (kJ) using the calculated heat equivalent for a general herbivorous diet
147 of $21.2 \text{ kJ L}^{-1} \text{ CO}_2$ (Munks and Green 1995; Hume 1999). To allow comparison between animals of
148 different body mass, the allometric scaling exponents of 0.71 for water turnover rates of free-range

149 marsupials (Nagy and Peterson 1988; Hume 1999) and 0.58 for field metabolic rate (Nagy 1994;
150 Cooper et al. 2003) were used.

151

152 *Statistical analyses*

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

163

164 **Results**

165 *Seasonal conditions*

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

175

176 *Animal details and body mass*

177 Ten *P. x. celeris* were injected with doubly labelled water (H_2^{18}O and ^3HOH) within the first six days
178 of the winter measurement period, and nine were injected within the first six days of the summer
179 measurements period; one additional male was injected only with tritiated water in summer as the
180 chance of recapturing this transient male was deemed low. Eight of the ten animals were recaptured
181 during each measurement period. Four animals were sampled during both periods (3♂: 1♀) and eight
182 others sampled once (1♂: 7♀). Thus, 12 animals were sampled in total throughout the study (4♂: 8♀;
183 Table 1). Mean body mass of animals during each sample period is presented in Table 1. Changes in
184 body mass between initial capture and recapture were only assessed during winter, when average body
185 mass decline was negligible at $0.06 \pm 0.02\%$ day⁻¹. The four animals sampled in both seasons gained
186 313 ± 193 g between the summer and winter sampling. All females were lactating when captured,
187 having a mean age of pouch young of 105 ± 45 days (range 33-169 days), about half the pouch life of
188 a joey (Lapidge 2001).

189

190 *Total body water and water turnover rate*

191 Total body water (TBW) was not significantly different between males and females for either season
192 (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
193 1). Overall, mean TBW for re-introduced *P. x. celeris* at Lambert Station was $73.1 \pm 5.8\%$.

194 Water turnover rate (WTR) (Table 1) was significantly different between summer and winter
195 samples ($F_{1,14}=67.0$, $P<0.001$), with allometrically-adjusted summer WTRs being more than 3.5-fold
196 winter WTRs. The change in WTR between seasons was similar for both sexes (male: $F_{1,5}=30.1$,
197 $P=0.003$; female: $F_{1,8}=31.2$, $P=0.001$), and there was no significant difference between male and
198 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
199 independent of joey age in lactating females ($F_{1,7}=0.28$, $P=0.61$). Although sample sizes were low,
200 WTR did not vary between sites within either season (summer: $F_{1,7}=0.99$, $P=0.35$; winter: $F_{2,5}=2.50$,
201 $P=0.18$).

202

203 *Field metabolic rate*

204 Field metabolic rate (FMR) remained relatively constant between seasons at $593 \pm 229 \text{ kJ kg}^{-0.58} \text{ d}^{-1}$
205 (Table 1). Although there was a tendency for males to have a higher FMR than females ($F_{1,13}=3.52$,
206 $P=0.08$), there was no significant difference between the sexes within either season (summer:
207 $F_{1,5}=3.19$, $P=0.13$; winter: $F_{1,6}=0.48$, $P=0.51$). FMR did not differ for males ($F_{1,4}=0.29$, $P=0.62$) or
208 females ($F_{1,7}=0.75$, $P=0.42$) between seasons. FMR of lactating females was independent of joey age
209 ($F_{1,7}=0.001$, $P=0.97$). Although sample sizes were low, FMR did not vary significantly between sites
210 (summer: $F_{1,6}=0.01$, $P=0.91$; winter: $F_{1,6}=3.25$, $P=0.11$).

211

212 **Discussion**

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

222 The TBW values we measured in *P. x. celeris* are similar to those from the sympatric euro
223 (*Macropus r. erubescens*; $73.1 \pm 0.5\%$; Dawson *et al.* 1975), and to those of the eastern grey kangaroo
224 (*M. giganteus*; $73.5 \pm 0.4\%$; Blaney *et al.* 2000), red kangaroo (*M. rufus*; $67.8 \pm 0.7\%$; Munn *et al.*
225 2009), and tammar wallaby (*M. eugenii*; $73.3 \pm 4.7\%$; Nagy *et al.* 1990a). TBW can be an indicator of
226 body condition as it varies inversely with body fat, thus a high TBW percentage indicates poor body
227 condition (Holleman and Dieterich 1973; Bakker and Main 1980; Catt 1981; Reimer and Hindell
228 1996; Gibson and Hume 2000). In our study, *P. x. celeris* maintained TBW and thus body condition
229 during the dry winter. This finding, along with animals maintaining body mass between seasons,
230 suggests they are well adjusted to free-living conditions. In fact, four animals sampled in both seasons

231 gained body mass, and continuous breeding by all females throughout the year was observed (Lapidge
232 2001). The consistent across-season TBW and body mass therefore indicates re-introduced *P. x.*
233 *celeris* maintained body-fat reserves throughout the driest period post-release. This contrasts
234 somewhat with studies on other wild/free-range marsupials such as bilbies (*Macrotis lagotis*), which
235 lost body condition in summer possibly associated with reduced food availability or increased
236 thermoregulatory demands (Gibson and Hume 2000). Even among the largest marsupials, the red
237 kangaroo *M. rufus* body condition in winter was lower than other seasons, probably due to low rainfall
238 and reduced pasture biomass (Moss and Croft 1999). Thus, it appears that our captive-bred *P. x.*
239 *celeris* possessed the ability to cope with seasonal fluctuations in water and food availability, despite
240 the absence of similar stresses during captive rearing.

241 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)
242 we reported were somewhat different to those found for *P. x. xanthopus* (summer 101 mL kg^{-0.71} d⁻¹,
243 winter 276 mL kg^{-0.71} d⁻¹; Lim *et al.* 1987), and both studies found variation in WTRs followed local
244 rainfall. The higher WTRs in summer in *P. x. celeris* were likely the result of increased water required
245 for thermoregulation, as ambient temperatures regularly exceed 40°C throughout the species' range
246 (Dawson and Denny 1969; Withers 1992; BOM 2001), and also to increased water intake from forage,
247 as water content of consumed forage during the wet summer was higher than during the dry winter
248 (Allen 2001). In this regard, it is important to note that WTR itself may not reflect the water
249 requirements of the animal because water influxes for herbivores can be heavily influenced by forage
250 water contents. Consequently, it is difficult to draw conclusions about the definitive water
251 requirements of free range animals, and particularly their abilities to withstand water shortages, unless
252 these data can be collected from animals known to be water restricted. Of note, there was probably
253 also increased availability of surface water for the *P. x. celeris* during the wet summer as water tends
254 to accumulate within cracks and rock depressions in the rocky terrain they inhabit.

255 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
256 *Petrogale* species, and among the lowest recorded for any marsupial (Hume 1999; Nagy and
257 Bradshaw 2000; Bradshaw *et al.* 2001). Winter WTR in *P. x. celeris* is most akin to *Petrogale* species
258 occupying similar habitat and climatic niche in Western Australia, such as Rothschild's Rock-wallaby
259 (*P. rothschildi*; 68 mL kg^{-0.71} d⁻¹; Bradshaw *et al.* 2001) and Black-flanked rock-wallaby (*P. lateralis*;

260 77 mL kg^{-0.71} d⁻¹; Nagy and Bradshaw 2001) during a dry spring. Of note, our data for the winter WTR
261 in *P. x. celeris* was considerably lower than that reported for *P. x. xanthopus* in winter (276 mL kg^{-0.71}
262 d⁻¹; Lim *et al.* 1987). Similarly low WTRs to those of *P. x. celeris* (this study) have been reported for
263 dehydrated captive Spectacled Hare-wallaby (*L. conspicillatus*; 51 mL kg^{-0.71} d⁻¹; Bakker and Bradshaw
264 1983), and non-dehydrated wild Spectacled Hare-wallaby (30.1 mL kg^{-0.71} d⁻¹; Bradshaw *et al.* 2001),
265 and for free-ranging Brush-tailed Bettong (*Bettongia penicillata*; 57 mL kg^{-0.71} d⁻¹; Green 1989) and
266 Quokka (*Setonix brachyurus*; 57 mL kg^{-0.71} d⁻¹; Nagy *et al.* 1990a). This finding suggests that water
267 demands for macropods are more closely related to habitat than to phylogeny (see also Withers *et al.*
268 2006). For example, low WTR in *Petrogale* species are likely the result of animals sheltering by day
269 in rocky outcrops and minimising exposure to climatic variations, thus reducing evaporative cooling.
270 *Petrogale xanthopus* has also been reported to decrease faecal water loss and increase urine
271 concentration during dry periods (Lim *et al.* 1987).

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

286 The FMR of our captive-bred and released *P. x. celeris* was not significantly different between
287 summer and winter, and averaged 593 ± 229 kJ kg^{-0.58} d⁻¹. The tendency for a higher winter- ($607 \pm$
288 194 kJ kg^{-0.58} d⁻¹) than summer-FMR (576 ± 248 kJ kg^{-0.58} d⁻¹) was likely a result of higher

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

308 Three *P. x. celeris* deaths were recorded throughout 2000 (animal F36 in February, F15 in April and
309 F27 in November), after the DLW measurement periods, and all from suspected fox (*Vulpes vulpes*)
310 attacks. All deceased females were carrying pouch young at the time of death, and all died during
311 months with recorded rainfalls (Lapidge 2001). Of note, all females known or suspected to be killed
312 by foxes (n=5) were killed during months of high rainfall and were found on the plain (Lapidge and
313 Henshall 2001). However, no rain fell in the months two males died and their remains were found on
314 the hill. Greater foraging for free water by females than males may explain the slight female bias in
315 fox predation and why remains of each sex were found in different locations. Whether additional water
316 was required for lactation could not be statistically proven, and fresh-matter food intakes or
317 requirements are difficult to predict as differences in digestibility between males and females are

318 uncertain. Nonetheless, our data indicate that re-introduced captive-bred *P. x. celeris* were able to
319 survive without free water within two-years of release from captivity, if not sooner. *P. lateralis* has
320 also been reported to obtain nearly all their water from their diet during drought conditions and not
321 travel to free water, though available nearby (Nagy and Bradshaw 2000).

322

323 **Conclusion**

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

340

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354 **References**

- 355 Allen, C.B. (2001). Analysis of dietary overlap between three sympatric herbivores in semi-arid west
356 Queensland. Ph.D. Thesis, University of Sydney, Australia.
- 357 Bakker, H.R. and Bradshaw, S.D. (1983). Renal function in the Spectacled Hare-wallaby, *Lagorchestes*
358 *conspicillatus*: Effects of dehydration and protein deficiency. *Australian Journal of Zoology* **31**: 101-108.
- 359 Bakker, H.R. and Main, A.R. (1980). Condition, body composition and total body water estimation in the
360 quokka, *Setonix brachyurus* (Macropodidae). *Australian Journal of Zoology* **28**: 395-406.
- 361 Blaney, C.E., Dawson, T.J., McCarron, H.C.K., Buffenstein, R. and Krockenberger, A.K. (2000). Water
362 metabolism and renal function and structure in Eastern Grey Kangaroos (*Macropus giganteus*): responses to
363 water deprivation. *Australian Journal of Zoology* **48**: 335-345.
- 364 Bradshaw, S.D., Morris, K.D., and Bradshaw, F.J. (2001). Water and electrolyte homeostasis and kidney
365 function of desert-dwelling marsupial wallabies in Western Australia. *Journal of Comparative Physiology B*
366 **171**: 23-32.
- 367 Bureau of Meteorology (2001). Climate averages: tables of averages for specific locations.
368 (<http://www.bom.gov.au/climate/averages>). Bureau of Meteorology, Australia.
- 369 Carlson, G.P. (1997). Fluid, electrolyte, and acid-base balance. In *Clinical Biochemistry of domestic animals*, 5th
370 Ed: Kaneko, J.J., Harvey, J.W. and Bruss, M.L. (Editors). Academic Press, USA. pp 485-516.
- 371 Catt, D.C. (1981). Growth and condition of Bennetts wallaby (*Macropus rufogriseus fruticus*) in South
372 Canterbury, New Zealand. *New Zealand Journal of Zoology* **8**: 295-300.
- 373 Cooper, C.E., Withers, P.C. and Bradshaw, D. (2003) Field metabolic rate and water turnover of the numbat
374 (*Myrmecobius fasciatus*). *Journal of Comparative Physiology B*. **173**: 687-693.

- 375 Copley, P., Ellis, M. and van Weenen, J. (2008). *Petrogale xanthopus*. In: IUCN 2011. IUCN Red List of
376 Threatened Species. Version 2011.1. <www.iucnredlist.org>. Downloaded on **22 June 2011**.
- 377 Copley, P.B. and Robinson, A.C. (1983). Studies on the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray
378 (Marsupialia: Macropodidae) II. Diet. *Australian Wildlife Research* **10**: 63-76.
- 379 Dawson, T.J. and Denny, M.J.S. (1969). Seasonal variation in the plasma and urine electrolyte concentration of
380 the arid zone kangaroos *Megaleia rufa* and *Macropus robustus*. *Australian Journal of Zoology* **17**: 777-784.
- 381 Dawson, T.J. and Ellis, B.A. (1979). Comparison of the diets of yellow-footed rock-wallabies and sympatric
382 herbivores in western New South Wales. *Australian Wildlife Research* **6**: 245-54.
- 383 Dawson, T.J., Denny, M.J.S., Russell, E.M. and Ellis, B.A. (1975). Water usage and diet preferences of free
384 ranging kangaroos, sheep and feral goats in the Australian arid zone during summer. *Journal of Zoology*
385 (*London*) **177**: 1-23.
- 386 Dellow, D.W. and Hume, I.D. (1982). Studies on the nutrition of macropodine marsupials. IV. Digestion in the
387 stomach and the intestine of *Macropus giganteus*, *Thylogale thetis* and *Macropus eugenii*. *Australian Journal*
388 *of Zoology* **30**: 767-777.
- 389 GenStat for Windows (2003). Seventh Edition, VSN International Ltd, UK.
- 390 Gibson, L.A. (1999). Nutritional ecology of the Greater Bilby, *Macrotis lagotis*, in far south-western
391 Queensland. PhD Thesis, University of Sydney, Australia.
- 392 Gibson, L.A. and Hume, I.D. (2000). Seasonal field energetics and water influx rates of the Greater Bilby
393 (*Macrotis lagotis*). *Australian Journal of Zoology* **48**: 225-239.
- 394 Green, B. (1989). Water and energy turnover in free-living macropodoids. In *Kangaroos, Wallabies and Rat*
395 *Kangaroos*: 223-229. Grigg, G., Hume, I. and Jarman, P. (Eds.). Surrey Beatty and Sons, New South Wales,
396 Australia.
- 397 Green, B. (1997). Field energetics and water fluxes in marsupials. In *Marsupial Biology: Recent research, new*
398 *perspectives*: pp 143-162. Saunders, N.R. and Hinds, L.A. (Eds.). University of New South Wales Press:
399 Sydney.
- 400 Holleman, D.F and Dieterich, R.A. (1973). Body water content and turnover in several species of rodents as
401 evaluated by the tritiated water method. *Journal of Mammalogy* **54**: 456-465.
- 402 Hume, I.D. (1999). *Marsupial nutrition*. Cambridge University Press, UK.
- 403 IUCN (1998). *Guidelines for Re-introductions*. Prepared by the IUCN/SSC Re-introduction Specialist Group.
404 IUCN, Gland, Switzerland and Cambridge, U.K. 10pp

- 405 Kennedy, P.M. and Heinsohn, G.E. (1974). Water metabolism of two marsupials- the brush-tailed possum,
406 *Trichosurus vulpecula* and the rock-wallaby, *Petrogale inornata* in the wild. *Comparative Biochemistry and*
407 *Physiology A* **47**: 829-834.
- 408 Kleiman, D.G. (1989). Reintroductions of captive mammals for conservation: guidelines for reintroducing
409 endangered species into the wild. *BioScience* **39**: 152-161.
- 410 Kleiman, D.G., Stanley Price, M.R., Beck, B.B. (1994). Criteria for reintroductions. In *Creative conservation:*
411 *Interactive management of wild and captive animals*: 287-303. Onley, P.J.S., Mace, G.M. and Feistner,
412 A.T.C. (Eds). London: Chapman and Hall.
- 413 Lapidge, S.J. (2000). Dietary adaptation of reintroduced yellow-footed rock-wallabies, *Petrogale xanthopus*
414 *xanthopus* (Marsupialia: Macropodidae), in the northern Flinders Ranges, South Australia. *Wildlife Research*
415 **27**: 195-201.
- 416 Lapidge, S.J. (2001). Reintroduction biology of Yellow-footed Rock-wallabies (*Petrogale xanthopus celeris* and
417 *P. x. xanthopus*). Ph.D. thesis, University of Sydney, Australia.
- 418 Lapidge, S.J. and Henshall, S. (2001). Diet of foxes and cats, with evidence of predation on yellow-footed rock-
419 wallabies (*Petrogale xanthopus celeris*) by foxes, in southwestern Queensland. *Australian Mammalogy* **23**:
420 47-51.
- 421 Lifson, N. and McClintock, R. (1966). Theory of use of the turnover rates of body water for measuring energy
422 and material balance. *Journal of Theoretical Biology* **12**: 46-74.
- 423 Lim, T.L. (1987). Ecology and management of the rare yellow-footed rock-wallaby *Petrogale xanthopus* Gray
424 (Macropodidae). Ph.D. thesis, Macquarie University, Australia.
- 425 Lim, T.L. and Giles, J.R. (1987). Studies on the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray
426 (Marsupialia: Macropodidae) III. Distribution and management in western New South Wales. *Australian*
427 *Wildlife Research* **14**: 147-161.
- 428 Lim, T.L., Robinson, A.C., Copley, P.B., Gordon, G., Canty, P.D. and Reimer, D. (1987). The Conservation and
429 Management of the Yellow-footed Rock-wallaby *Petrogale xanthopus* Gray, 1854. *Department of*
430 *Environment and Planning, South Australia, Special Publication* **4**: 1-94.
- 431 Moss, G.L. and Croft, D.B. (1999). Body condition of the red kangaroo (*Macropus rufus*) in arid Australia: The
432 effect of environmental condition, sex and reproduction. *Australian Journal of Ecology* **24**: 97-109.
- 433 Munks, S.A. (1990). Ecological energetics and reproduction in the Common Ringtail Possum, *Pseudocheirus*
434 *peregrinus*. Ph.D. Thesis, University of Tasmania, Australia.
- 435 Munks, S.A. and Green, B. (1995). Energy allocation for reproduction in a marsupial arboreal folivore, the
436 common ringtail possum (*Pseudocheirus peregrinus*). *Oecologia* **101**: 94-104.

- 437 Munn, A.J., Dawson, T.J., McLeod, S.R. Croft D.B., Thompson, M.B. and Dickman, C.R. (2009) Field
438 metabolic rate and water turnover of red kangaroos and sheep in an arid rangeland: an empirically derived
439 dry-sheep-equivalent for kangaroos. *Australian Journal of Zoology* **57**, 23–28
- 440 Murphy, K.J. (1985). Some aspects of the ecology, digestive physiology and nutrition of the Yellow-footed
441 Rock-wallaby, *P. xanthopus*. B. Nat. Res. Thesis, University of New England, New South Wales.
- 442 Nagy, K.A. (1980). CO₂ production in animals: analysis of potential errors in the doubly labelled water method.
443 *American Journal of Physiology* **238**: R466-473.
- 444 Nagy, K.A. (1983). The doubly labelled water (³HH¹⁸O) method: a guide to its use. University of California, Los
445 Angeles, Publication No. 12-1417.
- 446 Nagy, K.A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecological*
447 *Monographs* **57**: 111-128.
- 448 Nagy, K.A. (1989). Doubly-labelled water studies of vertebrate physiological ecology. In *Stable Isotopes in*
449 *Ecological Research*: pp 270-287. Rundel, P.W., Ehleringer, J.R. and Nagy, K.A. (Eds.). Springer-Verlag,
450 New York.
- 451 Nagy, K.A. (1992). The doubly-labelled water method in ecological energetics studies of terrestrial vertebrates.
452 *Bulletin of Society of Ecophysicologists, Supplement XVII*: 9-14.
- 453 Nagy, K.A. (1994). Seasonal water, energy and food use by free-living, arid-habitat mammals. *Australian*
454 *Journal of Zoology* **42**: 55-63.
- 455 Nagy, K.A. and Bradshaw, S.D. (2000). Scaling of energy and water fluxes in free-living arid-zone Australian
456 marsupials. *Journal of Mammalogy* **81**: 191-199.
- 457 Nagy, K.A. and Costa, D.P. (1980). Water flux in animals: analysis of potential errors in the tritiated water
458 method. *American Journal of Physiology* **238**: R454-465.
- 459 Nagy, K.A. and Peterson, C.C. (1988). Scaling of water flux rate in animals. University of California
460 Publications in Zoology No. 120.
- 461 Nagy, K.A., Bradley, A.J. and Morris, K.D. (1990a). Field metabolic rates, water fluxes and feeding rates of
462 Quokkas, *Setonix brachyurus*, and Tammars, *Macropus eugenii*, in Western Australia. *Australian Journal of*
463 *Zoology* **37**: 553-560.
- 464 Nagy, K.A., Girand, I.A., and Brown, T.K. (1999). Energetics of free-ranging mammals, reptiles, and birds.
465 *Annual Review of Nutrition* **19**: 247-277.
- 466 Nagy, K.A., Sanson, G.D. and Jacobsen, N.K. (1990b). Comparative field energetics of two macropod
467 marsupials and a ruminant. *Australian Wildlife Research* **17**: 591-199.

- 468 Patterson, H.D. & Thompson, R. (1971). Recovery of inter-block information when block sizes are unequal.
469 *Biometrika* **58**: 545-554.
- 470 Perelodova, O.B., Sempéré, A.J., Soldatova, N.V., Dutov, V.U., Fisenko, G. and Flint, V.E. (1999). Przewalski's
471 horse- adaptation to semi-wild life in desert conditions. *Oryx* **33**: 47-58.
- 472 Reimer, A.B. and Hindell, M.A. (1996). Variation in body condition and diet of the Eastern Barred Bandicoot
473 (*Perameles gunnii*) during the breeding season. *Australian Mammalogy* **19**: 47-52.
- 474 Serena, M. (1994). *Reintroduction biology of Australian and New Zealand Fauna*. Surrey Beatty & Sons,
475 Chipping Norton.
- 476 Sharp, A. (1997). Insights into the dispersal patterns of yellow-footed rock-wallabies, *Petrogale xanthopus*.
477 *Australian Mammalogy* **19**: 229-238.
- 478 Short, J., Bradshaw, S.D., Giles, J., Prince, R.I.T., and Wilson, G.R. (1992). Reintroduction of macropods
479 (Marsupialia: macropodidae) in Australia- a review. *Biological Conservation* **62**: 189-204.
- 480 Speakman J.R. 1997. Doubly Labeled Water. Chapman & Hall, New York NY, USA
- 481 Speakman, J.R., Nagy, K.A., Masman, D., Mook, W.G., Poppitt, S.D., Strathearn, G.E. and Racey, P.A. (1990).
482 Interlaboratory comparison of different analytical techniques for the determination of oxygen-18 abundance.
483 *Analytical Chemistry* **62**: 703-707.
- 484 Stanley Price, M.R. (1986). The reintroduction of the Arabian oryx, *Oryx leucoryx* into Oman. *International Zoo*
485 *Yearbook* **24/25**: 179-188.
- 486 Stanley Price, M.R. (1989). *Animal reintroductions: the Arabian oryx in Oman*. New York: Cambridge
487 University Press.
- 488 Strahan, R. (1995). *The Mammals of Australian*. Reed Books, Sydney.
- 489 Tyndale-Biscoe, H. (2005). *Life of marsupials*. CSIRO Publishing, Collingwood, Victoria, Australia
- 490 Wallis, I.R. and Green, B. (1992). Seasonal field energetics of the Rufous Rat-kangaroo *Aepyprymnus rufescens*.
491 *Australian Journal of Zoology* **40**: 279-290.
- 492 White, R.G., Hume, I.D. and Nolan, J.V. (1988). Energy expenditure and protein turnover in three species of
493 wallabies (Marsupialia: Macropodidae). *Journal of Comparative Physiology B* **158**: 237-246.
- 494 Withers, P.C. (1992). *Comparative Animal Physiology*. Saunders College Publishing, U.S.A.
- 495 Withers, P.C., Cooper, C.E. and Larcombe, A.N. (2006) Environmental correlates of physiological variables in
496 marsupials. *Physiological and Biochemical Zoology* **79**: 437-53
- 497 Zar, J.H. (1984). *Biostatistical analysis*, 2nd Ed. Prentice-Hall, New Jersey.

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 \pm standard deviation with sample size indicated in parentheses next to sex. * Sample size of 4 relates to BM and water turnover

500 rate, other values relate to three animals. [†]Within columns, pooled means differ significantly at $P < 0.0001$.

Animal	BM	Total Body Water		Water Turnover Rate			Field Metabolic Rate	
	g	g	%	mL d ⁻¹	mL kg ^{-0.71} d ⁻¹	mL CO ₂ g ⁻¹ h ⁻¹	kJ d ⁻¹	kJ kg ^{-0.58} d ⁻¹
WET SUMMER								
Males (3-4)*	6450 \pm 666	4603.9 \pm 412.0	73.3 \pm 2.0	625.4 \pm 78.7	168.5 \pm 22.7	0.667 \pm 0.164	2194.5 \pm 728.7	742.5 \pm 210.8
Females (4)	5362 \pm 188	3884.3 \pm 150.9	72.4 \pm 1.6	604.7 \pm 44.5	183.4 \pm 10.6	0.438 \pm 0.188	1196.4 \pm 520.0	451.3 \pm 194.6
Total	5906 \pm 731	4192.7 \pm 461.1	72.8 \pm 1.8	615.0 \pm 64.8[†]	175.4 \pm 19.4[†]	0.536 \pm 0.211	1624.1 \pm 791.2	576.1 \pm 247.9
DRY WINTER								
Males (3)	6713 \pm 622	5193.2 \pm 571.6	77.3 \pm 4.1	201.9 \pm 63.0	53.1 \pm 18.4	0.550 \pm 0.121	1870.2 \pm 431.2	621.0 \pm 136.5
Females (5)	5268 \pm 446	4010.8 \pm 293.7	71.1 \pm 8.2	157.8 \pm 26.5	46.5 \pm 9.7	0.590 \pm 0.220	1559.5 \pm 577.9	599.2 \pm 221.4
Total	5810 \pm 871	4454.2 \pm 710.0	73.4 \pm 7.6	174.3 \pm 48.8[†]	49.0 \pm 14.0[†]	0.575 \pm 0.190	1676.0 \pm 548.7	607.4 \pm 194.2