



Ontogeny and allometry of metabolic rate and ventilation in the marsupial: Matching supply and demand from ectothermy to endothermy [☆]

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ABSTRACT

The 'supply' of substrates should match 'demand' for energy utilization and not limit it. Integration of supply to demand would be expected to occur during ontogeny. As a result of a short gestation and protracted lactation most development in marsupials occurs *ex utero* in a thermally stable pouch, hence there is an early reliance on atmospheric oxygen. This paper explores through allometry the matching of ventilation (supply) and rate of oxygen consumption (demand) in the tamar wallaby from birth to adulthood, covering four orders of magnitude and the transition from ectothermy to endothermy. The allometric exponent for the scaling equation for the rate of oxygen consumption in the ectothermic and endothermic phases of development was 0.78, the difference in intercept between the two equations being approximately 2.5-fold. A similar exponent and factorial increase in intercept was found for ventilation. Hence, convective requirement is mass independent throughout development, from ectothermy to endothermy, being similar to previously published values for the class Mammalia. Altogether, these results support the notion that, at rest, supply by ventilation is matched to demand for oxygen during postnatal development in the marsupial.

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1. Introduction

Are animals designed so that the supply of substrates matches the demand set by the rate of energy utilization? Current arguments hinge on supply limitation models (see Banavar et al., 2002; West and Brown, 2005) versus multilevel regulation of metabolic scaling (see Suarez and Darveau, 2005). Issues surrounding metabolic state (e.g. basal or maximal), digestive state (e.g. can a post-absorptive state be achieved in a herbivore relying on fermentation, a suckling young?), body temperature and four dimensional biology (time) all undoubtedly influence the allometric exponent determined for metabolic rate (see Weibel et al., 2004; Weibel and Hoppeler, 2005; White and Seymour, 2004, 2005; West et al., 1999).

The presence of excess capacities in many physiological systems (Diamond, 1998), most notably studied in the cardio-respiratory systems of mammals (Weibel, 1987; Jones and Lindstedt, 1993) and reptiles (Frappell et al., 2002), demonstrates that the supply of substances to the cells would not be expected to limit metabolic rate. Excess capacity is contrary to the concept of symmorphosis, that has animals designed so that capacities match maximum loads (Taylor and Weibel, 1981). Nevertheless, symmorphosis also requires capacities in a multi-step pathway to be matched and this is consistent with the

idea that allometry in capacities for the supply of substrates has been matched by allometry in capacities for energy utilization (Suarez et al 2004). Suarez and Darveau (2005) subsequently surmise that 'Supply and demand systems are better viewed as having coevolved with each other, as having developed as interacting systems during ontogeny, and as exerting acute regulatory influences upon each other in living animals'.

During its ontogeny the marsupial offers a unique opportunity to examine whether supply matches demand, at least in terms of oxygen delivery. As a result of a short gestation and protracted lactation most development in marsupials occurs *ex utero*, hence there is an early reliance on atmospheric oxygen. Indeed, it has been shown that in some very small newborn marsupials (dunnarts, genus *Sminthopsis*, birth weight ~12–17 mg) the lung serves no role in gas exchange at birth, instead the newborn is reliant entirely on cutaneous exchange of oxygen to meet its aerobic requirements (Mortola et al., 1999; Frappell and Mortola, 2000). In addition, marsupials are born ectothermic and the transition to endothermy occurs just prior to pouch vacating so that the young, once it vacates the pouch, is able to maintain adult body temperature (see Hulbert, 1988).

This paper explores the matching of resting ventilation (supply) and rate of oxygen consumption (demand) in the tamar wallaby (*Macropodidae*, *Macropus eugenii*) from birth, where there is approximately 30% reliance on cutaneous gas exchange (MacFarlane and Frappell, 2001), to adulthood, where the lungs are the sole gas exchange organ. The mass range from birth to adult covers four orders of magnitude and the transition from ectothermy to endothermy. Further, as for most macropods (kangaroos, wallabies and potoroids)

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development of the ectothermic tammar wallaby young occurs in the confines of a warm and thermally stable pouch maintained at maternal body temperature ($\sim 36.5^\circ\text{C}$). Subsequently, throughout development as the macropod transcends from ectothermy to endothermy, body temperature is maintained essentially constant (see Janssens and Rodgers, 1989). Use is made of this fact to remove the confounding effects that changes in body temperature may have on metabolic rate and hence scaling effects (see White and Seymour, 2005).

2. Materials and methods

The data presented were collected over a 15 year period and apart from a few individuals that formed parts of other studies have not

previously been published. A total of 156 tammar wallabies (*Macropus eugenii*) from birth (~ 360 mg) to adulthood (~ 8 kg) comprising both sexes were measured for their rate of oxygen consumption ($\dot{V}\text{O}_2$), ventilation (\dot{V}_E) and breathing pattern at their normal body temperature ($\sim 36.5^\circ\text{C}$); body temperature (T_b) and body mass (M_b) were measured immediately prior to measurement in all animals. The above measurements on post-pouch animals were made at adult thermoneutrality (ambient temperature $26\text{--}28^\circ\text{C}$, Frappell and Baudinette, 1995) with the animal fully enclosed in a flow through respirometer. Small pouch young were either removed, weighed, fitted with a small face mask (see MacFarlane and Frappell, 2001) and enclosed in a water jacketed chamber at pouch temperature ($\sim 36.5^\circ\text{C}$, unpublished observations and Janssens and Rogers, 1989) or, alternatively, the mother was sedated (3:1 alphaxalone/alphadolone

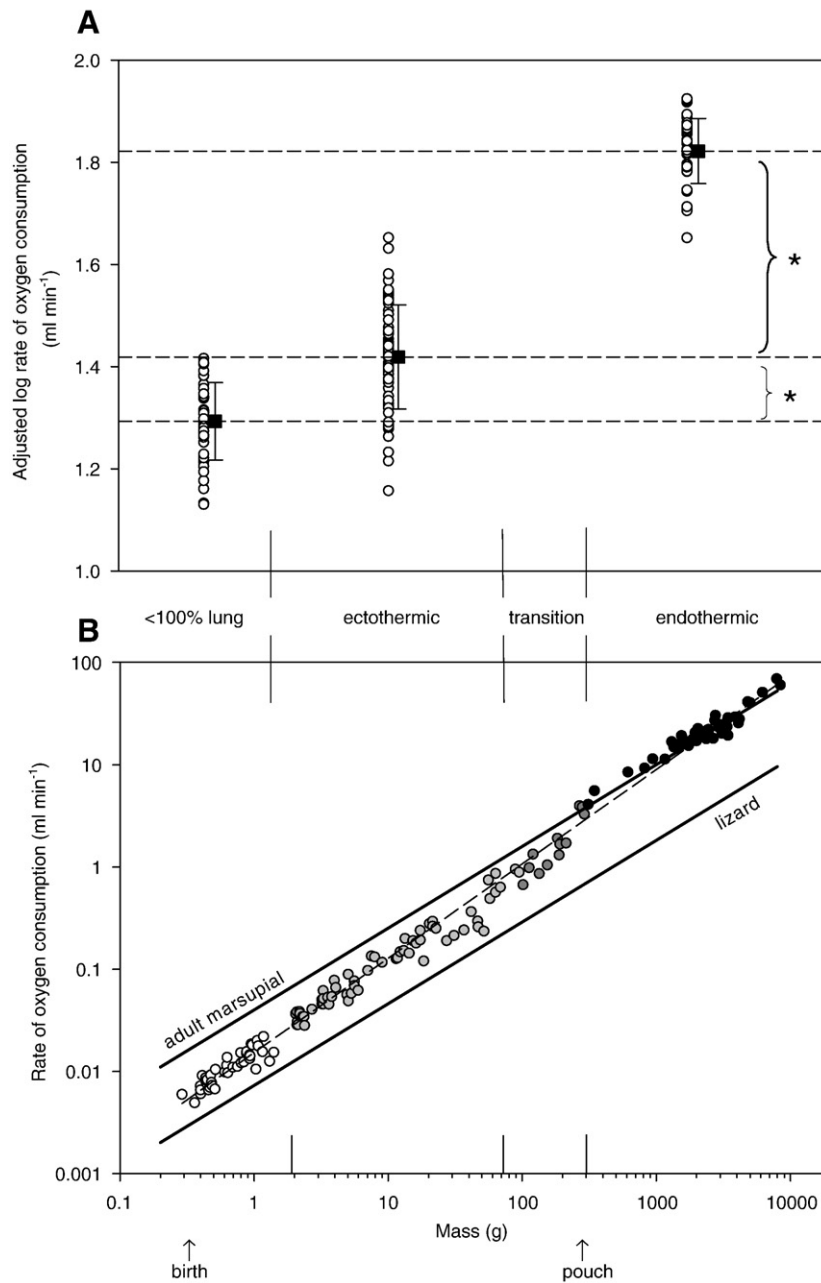


Fig. 1. Rate of oxygen consumption during postnatal development in the tammar wallaby. (A) Log adjusted values following standardisation of the covariate to the grand mean for each identifiable developmental age; \circ individual values, \blacksquare mean value ± 1 S.E.M. (B) Rate of oxygen consumption as a function of mass. Prediction lines (solid) are indicated for resting lizards (Andrews and Pough, 1985) and adult marsupials (Frappell and Baudinette 1995), the dashed line is the overall regression for all the data; see Table 1 for actual regressions. Symbols are individual values, shading represents developmental stages: \circ <100% lung \bullet ectothermic, \bullet transition, and \bullet endothermic.

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