

Letter

Are endotherms emancipated? Some considerations on the cost of reproduction

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Using allometric equations Wieser (1985) showed that the daily energy requirement for the production of a litter or clutch (up to birth or hatching) was only 6% of average daily metabolic rate (ADMR) for mammals and 2% for birds. He calculated this cost for two ectotherms (a fish and a nematode) as 35% and 100% of daily energy consumption, respectively and concluded that endotherms have much lower reproductive costs relative to ADMR than do ectotherms. Thus endotherms were emancipated from the cost of reproduction when they evolved endothermy. While his calculations are certainly correct they do not take into account that the production of a litter to the time of birth or of young to hatching is only part of reproduction in most mammals and birds. As Pond (1984) (see also Millar 1977) has stated “the two major features of mammalian reproduction are viviparity and lactation” (emphasis mine). The parental effort (Hirschfield and Tinkle 1975) of most mammals and birds, unlike that of many (though by no means all) ectotherms, *must* continue after birth or hatching of young in order to produce surviving offspring. Only physiological and behavioral processes which, at least potentially, lead to an individual’s genetic representation in future generations can be called reproduction (Wilson 1975).

Although the time of birth or hatching is a conspicuous breakpoint in development, costs incurred up to this time do not permit meaningful comparisons of the cost of reproduction in evolutionary terms. An example will make this point more clear: a 10 kg marsupial gives birth to a ca. 580 mg litter (calculated from Russell’s (1982) allometric equation) while a placental mammal of the same size produces a ca. 710 g litter. This clearly does not mean that the cost of reproduction of placental mammals is 1,000 times that of marsupials. Instead we are dealing with different strategies of reproduction: marsupials are opportunistic breeders making good use of an unpredictable environment where quick replacement of lost young is more important than even an augmented energetic cost by increasing the duration of lactation (Low 1978, May and Rubenstein 1984, Hayssen et al. 1985). Similarly, r-strategists produce many small offspring in which they invest a minimum of parental care, while K-strategists produce only a few and expend considerable effort in raising them to independence (MacArthur and Wilson 1967, see also May and Rubenstein 1984 for a discussion of the usefulness of this concept). At the time of parturition or egg-laying the r-strategist may well have invested more than the K-strategist, but the latter

must continue to invest heavily in order to produce surviving offspring while the former incurs low or no additional cost (May and Rubenstein 1984, Wilson 1975). Differences in the cost of reproduction between ectotherms and endotherms up to the time of release of offspring may reflect differences in reproductive strategies consisting in different allocation of reproductive energy to the prenatal and postnatal period. It would be interesting to assess the relative pre- and postnatal costs of reproduction in typical K-strategist ectotherms like brood-caring solitary Hymenopterans. The proportion of total lifetime devoted to reproduction by ectotherms and endotherms should also be taken into account for a more comprehensive comparison of their costs of reproduction. Rather than emancipating themselves from the cost of reproduction, mammals and birds have to invest a high percentage of ADMR in raising offspring. These percentages appear comparable to or higher than those Wieser (1985) gives for ectotherms.

His equation (from Rahn 1982) for total daily energy consumption expressed in terms of litter mass (Kg) is

$$\dot{E}_{\text{tot}} = 2,190 M_{\text{lit}} \quad (\text{KJ/day}) \quad (1)$$

Using Millar’s (1981) allometric equation which relates litter mass to adult mass (Millar 1981), i.e.

$$M_{\text{lit}} = 0.122 M_{\text{ad}}^{0.767} \quad (\text{Kg}) \quad (2)$$

we obtain

$$\dot{E}_{\text{tot}} = 267 M_{\text{ad}}^{0.767} \quad (\text{KJ/day}) \quad (3)$$

Hanwell and Peaker (1977) have given an allometric expression which relates the daily cost of lactation to adult mass (kg):

$$\dot{E}_{\text{lact}} = 532 M_{\text{ad}}^{0.694} \quad (\text{KJ/day}) \quad (4)$$

Dividing (4) by (3) we get

$$\dot{E}_{\text{lact}}/\dot{E}_{\text{tot}} = 532/267 M_{\text{ad}}^{-0.073} \approx 2.0$$

The exponent in this equation appears insignificantly different from zero. Therefore we can suggest that mammals increase their daily energy consumption by 100% during lactation. A review of lactation cost measurements in a few mammals supports this conclusion (Table 1). Measurements of the cost of gestation are also slightly higher than estimates derived from allometric equations (Rahn 1982). Randolph et al. (1977, Table 3) list the additional cost of pregnancy for 9 species and find that the average increase

Table 1. Daily energy consumption of a few mammalian species during pregnancy and lactation. In brackets: percentage increase over energy consumption of non-reproductive animals

Species	Adult female weight (kg)	\dot{E}_{gest} (KJ/d)	\dot{E}_{lact} (KJ/d)	Source
Cotton rat	0.084	24 (+16%)	118 (+82%)	Randolph et al. 1977
European common vole	0.025	16 (+32%)	73 (+133%)	Migula 1969
Bank vole	0.023	20 (+24%)	76 (+92%)	Kaczmarek 1966
Grey seal	170	–	71,200 (+131%)	Fedak and Anderson 1982
Elephant seal	700	–	90,400 (+147%)	Ortiz et al. 1984, Costa et al. 1986

Table 2. Daily energy consumption of free-living birds feeding chicks. ADMR = Average Daily Metabolic Rate

Species	Adult female weight (g)	\dot{E}_{tot}^a (KJ/day)	ADMR while feeding chicks (KJ/day)	Source
Starling	74.1	177	333 (+88%)	Ricklefs and Williams 1984
House martin	18.5	76	103 (+36%)	Westertorp and Bryant 1984
Sand martin	13.0	62	90 (+45%)	Westertorp and Bryant 1984
Swallow	19.2	78	109 (+40%)	Westertorp and Bryant 1984
Blue tit	10.6	55	69 (+25%)	Westertorp and Drent (unpublished work)
Great tit	19.0	78	80 (+3%)	Westertorp and Drent (unpublished work)
Kingfisher	77.0	181	323 (+78%)	Reyer 1984
Gentoo penguin	6,200	2,575	4,878 (+89%)	Davis et al. 1983

^a ADMR of non-reproductive birds calculated from Walsberg's (1983) Eq. (8):

$$\dot{E} = 13.05 \times M_{\text{ad}}^{0.6052} \quad (\text{KJ/day}, M = \text{mass in g})$$

in dietary energy intake is 36%. Their corresponding Fig. for lactation is 114% (excluding the value for humans).

Peak daily energy expenditure on the production of birds' eggs have been estimated by Walsberg (1983). His Table IV data give an average peak rate of energy expenditure of $46 \pm 12\%$ of basal metabolic rate (BMR) for birds with altricial young ($n=6$) and of $123 \pm 53\%$ of BMR for those with precocial young ($n=11$). Excluding the exceptional rate of the Kiwi (229% of BMR) reduces the latter

average to $113 \pm 42\%$ of BMR. Thus egg production may cause a real short-term energetic bottleneck. The period of care for dependent young is also a bottleneck in the reproductive cycle (Drent and Daan 1980). Available data, some of which are listed in Table 2, generally support this idea. ADMR during feeding of nestlings averages 50.5% higher than that calculated from Walsberg's (1983) allometric equation for energy consumption of a non-reproductive bird.

Wieser's (1985) statement that "by increasing total metabolic power more than ten-fold, but keeping the energy cost of reproduction constant, emancipation from the burden of reproduction has been achieved" by endotherms appears unwarranted if the cost of reproduction is defined as total costs incurred until the offspring become independent.

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