

## Short communication

# The relationship between fecundity and adult body weight in Homeotherms

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**Summary.** Although most life history traits in birds and mammals show an allometric relationship with body weight (Brody 1945; Lack 1968; Peters 1983; Calder 1984), such studies have failed to show a clear relationship for the components of fecundity: litter size and number of litters per year. By using a functional definition of the fecundity as the product of the number of litters per year with litter size, however we find an allometric relationship with allometric exponents of  $-0.15$  in birds and  $-0.22$  in mammals. The observed value of the allometric exponent for each order is discussed with regard to the theoretical value expected for variables dependent on time according to Lindstedt and Calder (Lindstedt and Calder 1981; Lindstedt et al. 1986). This has direct implications for investigation of demographic strategies.

**Key words:** Body Size – Fecundity – Homeotherms

Most life history traits show a strong allometric relationship with adult body weight. This relationship is described by the allometry equation:

$$Y = aM^b \Rightarrow \ln Y = \ln a + b \ln M$$

where  $M$  is adult body weight,  $Y$  the life history trait,  $a$  the allometric coefficient and  $b$  the allometric exponent (Brody 1945; Lack 1968; Millar 1977, 1984; Western 1979; Martin 1981; Calder 1983; Harvey and Bennett 1983; Peters 1983; Stearns 1983; Calder 1984). Among the variables characterizing reproduction, the logarithm of gestation (relative to incubation) time and lactation (relative to dependent period) increases linearly with the logarithm of adult body weight (Sacher and Staffeldt 1974; Millar 1977 but see Clutton-Brock and Harvey 1984; Millar 1984; Western and Ssemakula 1982). On the contrary, litter size (relative to clutch size) does not seem to follow such a relationship (Millar 1984; Harvey and Clutton-Brock 1985). Tuomi (1980) describes three main phases in the allometric relationships between body weight and litter size: litter size increases with adult body weight up to one kilogram and decreases thereafter to stabilize at one young per litter. This result can be easily interpreted as a consequence of strong constraints (Stearns 1976, 1977). For example, in small mammals, viability (i.e. thermoregulation maintenance for neonate) and the energy requirement of

lactation enforce a minimum weight at birth. As a consequence an adult female is unable to give birth in a single litter to a large number of young. In large eutherian mammals, the high weight at birth implies a long gestation period. Together with long parental care, it makes a large litter size difficult and numerous litters per reproductive season impossible. Moreover, physiological differences between small and large mammals influence the rhythm of reproduction (Weir and Rowlands 1973): in small mammals the gestation and lactation periods do not exceed a few months with sometimes a post-partum oestrus; large mammals are characterized by a gestation time which sometimes exceed one year and often by a long period of parental care. This suggests that litter size cannot be taken as a good measure of the reproductive potential without considering the number of litters per year. Similar arguments can be developed about birds (e.g. Passerines versus large sea birds, Lebreton et al. 1987).

Therefore fecundity should be measured as the product of litter (relative to clutch) size with the mean number of litters (relative to clutches) per year, i.e. the mean number of neonates (relative to eggs) produced per year and per breeding female as already used in a different context by Padley (1985) and Thompson (1987). As expected the correlations between the logarithm of litter (relative to clutch) size and the logarithm of adult body weight are lower than the correlations between the logarithm of fecundity and the logarithm of adult body weight:  $-0.20$  versus  $-0.38$  in birds,  $-0.51$  versus  $-0.61$  in mammals. The regression slopes for the linear relationship between the logarithm of fecundity and the logarithm of adult body weight for 282 bird species (15 orders) and 259 mammal species (10 orders) are  $-0.17$  and  $-0.21$  respectively (Fig. 1). Previous work (Western 1979; Stearns 1983; Martin and Harvey 1985), suggest that this allometric relationship is the resultant of several order-specific relationships. Although regression slopes differ significantly between orders, their heterogeneity is moderate (Table 1). Within-orders heterogeneity, sometimes obvious at the between family level (Pelecaniformes, Lebreton et al. 1987) but not restricted at this level, probably explains a large part of the difference between slopes. This difference is moderate enough to allow a comparison of intercepts which will at least be indicative: difference between orders is large (Table 1). In this case, a better estimation of the allometric exponent between fecundity and body weight is to average the slopes estimated at the order level:  $-0.15$  in birds and  $-0.22$  in mammals.

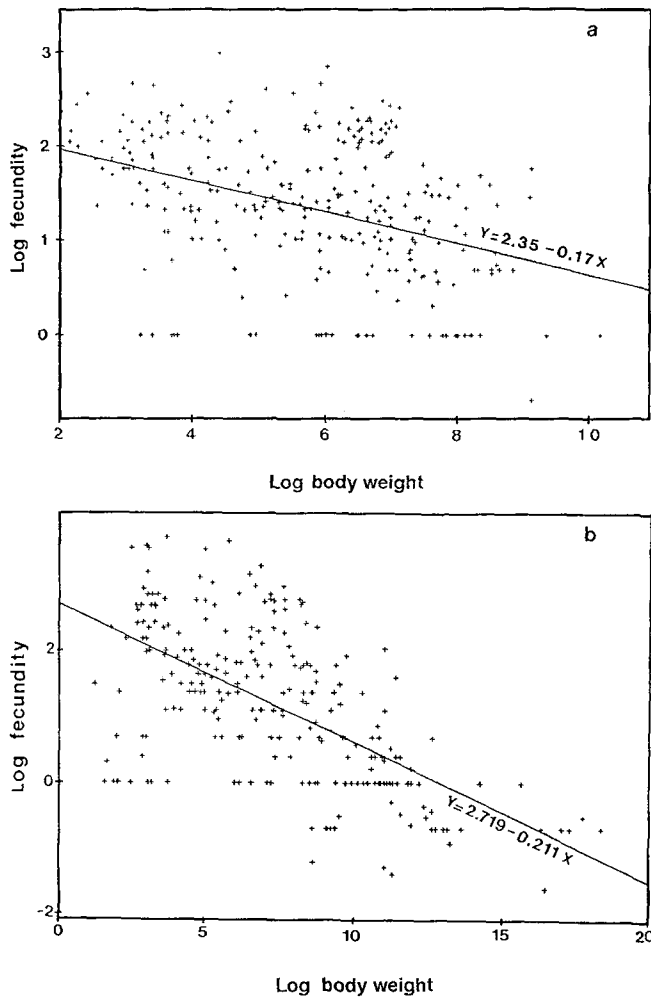


Fig. 1a, b. Allometric relationships between fecundity and body weights for 282 bird species a and 259 mammal species b

In this definition ((number of young produced) / (number of reproductive females  $\times$  number of years)), fecundity can be viewed as a frequency with dimension:  $[N] / ([M] \times [T]) = [T]^{-1}$ . According to Lindstedt and Calder 1981 and Lindstedt et al. 1986, time variables are related to body weight with an allometric coefficient of 0.25. The allometric exponent expected in this case is  $-0.25$ . Though this theoretical coefficient is empirical, all studies based on samples where a wide variability of body weight is considered provide allometric coefficients comparable to the theoretical ones (Saether 1987 for reproductive variables in birds, Sacher and Staffeldt 1974 and Stearns 1983 for mammals; Calder 1983 for mammals and birds; Peters 1983 for a review). A deviation from the theoretical values is found either when the analysis of the allometric relationship takes into account characteristics related to selective pressures (e.g. Martin and MacLarnon 1985 establish an allometric relationship with gestation length on two groups of mammals precocial and altricial), or when it is applied to a single phylogenetic group (e.g. Primates in Harvey and Clutton-Brock 1985). For us the theoretical coefficient is the expression of the *scaling principle* defined by Martin and Harvey (1985).

The slope differs significantly from the theoretical value of  $-0.25$  for three orders in birds (Charadriiformes, Procellariiformes and Passeriformes) and for one in mammals

**Table 1.** The correlation and regression of fecundity on adult body weight. Both variables were transformed with natural logarithms prior to this analysis. When observed values are mentioned in brackets, the correlation coefficient is not statistically different from zero. The star indicates that the theoretical value of  $-0.25$  (Lindstedt & Calder 1981, Lindstedt & al. 1986) belongs to the confidence interval of the observed slope value. *Slope comparison*:  $F(14,252) = 3.17$ ,  $p < 0.05$  in birds,  $F(8,229) = 3.22$ ,  $P < 0.05$  in mammals. *Intercept comparison*:  $F(14,266) = 57.6$ ,  $P < 0.01$  in birds,  $F(8,237) = 29.21$ ,  $p < 0.01$  in mammals

Order	N	r	slope	intercept
Sphenisciformes	7	$-0.78$	$-0.25^*$	2.63
Procellariiformes	22	$-0.34$	$-0.03$	0.14
Pelecaniformes	14	(0.33)	(0.23)	( $-1.1$ )
Ciconiiformes	15	( $-0.31$ )	( $-0.15$ )	(2.29)
Anseriformes	39	$-0.71$	$-0.28^*$	3.99
Accipitriformes	28	$-0.70$	$-0.25^*$	2.75
Galliformes	13	$-0.56$	$-0.24^*$	3.81
Gruiformes	9	$-0.88$	$-0.45^*$	4.62
Charadriiformes	47	$-0.30$	$-0.12$	1.58
Columbiformes	7	( $-0.37$ )	( $-0.13$ )	(2.33)
Strigiformes	13	( $-0.42$ )	( $-0.15$ )	(2.33)
Apodiformes	6	( $-0.80$ )	( $-0.50$ )	(3.22)
Coraciiformes	6	( $-0.62$ )	( $-0.34$ )	(3.34)
Passeriformes	50	$-0.29$	$-0.12$	2.38
Piciformes	6	( $-0.28$ )	( $-0.14$ )	(2.37)
Primates	22	$-0.85$	$-0.37$	2.82
Carnivora	48	$-0.78$	$-0.30^*$	3.54
Artiodactyla	48	$-0.37$	$-0.17^*$	2.03
Cetacea	7	( $-0.13$ )	( $-0.06$ )	(0.40)
Marsupialia	13	$-0.85$	$-0.36^*$	3.97
Insectivora	16	( $-0.28$ )	( $-0.13$ )	(2.56)
Xenarthrans	7	(0.03)	(0.01)	(0.26)
Lagomorpha	20	( $-0.10$ )	( $-0.06$ )	(3.05)
Chiroptera	12	( $-0.27$ )	( $-0.05$ )	(0.34)
Rodentia	66	$-0.35$	$-0.15^*$	2.83

(Primates) (Table 1). Some particular phylogenetic constraints (increase in developmental time in Procellariiformes Jouventin and Mougin 1981 and Primates Western 1979), taxonomic heterogeneity (Charadriiformes) or the wide ecological diversification together with a narrow variation in body weight in Passeriformes might explain such deviation from the model. This may also suggest that for many species with one young per litter, the average reproduction periodicity is not adequately known (Procellariiformes). Although this does not validate Lindstedt and Calder's model, orders with enough homogeneity (Sphenisciformes, Anseriformes, Accipitriformes) show a good agreement with the predicted allometric exponent.

As a conclusion, when defined as the number of young per breeding female per year, fecundity is a functional measure which correctly describes the process of production of young. Defined in this way, fecundity shows a meaningful allometric relationship with adult body weight, which is not observed when its components, litter size (Tuomi 1980) or number of litters per year (Stearns 1983), are analysed separately. Consequently, this measurement of fecundity should be more appropriate than litter size in further analyses of demographic strategies in homeotherms particularly when reproductive tactics are under consideration.

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