Relationships between Body Size and Some Life History Parameters

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Summary. Patterns in life history phenomena may be demonstrated by examining wide ranges of body weight. Positive relationships exist between adult body size and the clutch size of poikilotherms, litter weight, neonate weight life span, maturation time and, for homeotherms at least, brood or gestation time. The complex of these factors reduces r_{max} in larger animals or, in more physiological terms, r_{max} is set by individual growth rate. Comparison of neonatal production with ingestion and assimilation suggests that larger mammals put proportionately less effort into reproduction. Declining parental investment and longer development times would result if neonatal weight is scaled allometrically to adult weight and neonatal growth rate to neonatal weight. Body size relations represent general ecological theories and therefore hold considerable promise in the development of predictive ecology.

A number of general, if simplistic theories have been advanced which predict various ecological and physiological characteristics from body weight (Rensch, 1959; Stahl, 1962; Bonner, 1965; Schoener, 1968; Farlow, 1976 and others). Such theories give average values which can serve as standards for comparison with specifically interesting sets of data. They can form an empirical foundation for both ecological models and for discussions of ecological generalities, and they allow more objective evaluation of presumed trends. Such relationships are presented as double logarithmic plots described with a power relation of the form $y = a W^b$ where W is body weight and a and b are constants fitted to the data by least squares regression. In this paper, previously published data are used to construct further theories which predict aspects of life history and population growth from animal body weight.

Data were collected from both primary and secondary sources, but no attempt was made to survey the literature exhaustively. When available, species

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Table 1. A comparison of equations from least squares regression analyses of the data presented in the figures. The parameter in column 1 is described as a function of body weight (w, in grams fresh weight) in column 4. The last column (r^2) lists the coefficient of determination which represents the proportion of the variation in y which is explained by the regression (Steele and Torrie 1960)

Parameter	Taxonomic group	Units	Equation	r^2
Fecundity	reptiles	No./clutch	$y = 0.77\ W^{0.48}$	0.78
	salmon and trout	No. in ovaries	$y = 15.3\ W^{0.70}$	0.69
	other fish	No. in ovaries	$y = 408\ W^{0.64}$	0.78
	amphibious and aquatic poikilotherms	No. in ovaries	$y = 347\ W^{0.47}$	0.58
Litter weight	mammals	g/litter	$y = 0.55\ W^{0.82}$	0.97
	birds	g/clutch	$y = 1.24\ W^{0.74}$	0.85
	reptiles	g/clutch	$y = 0.35\ W^{0.88}$	0.96
	poikilotherms	mm^3/clutch	$y = 275\ W^{0.92}$	0.86
Neonate weight	mammals	g/neonate	$y = 0.097\ W^{0.92}$	0.94
	birds	g/egg	$y = 0.26\ W^{0.77}$	0.83
	birds	g/hatchling	$y = 0.28\ W^{0.69}$	0.86
	reptiles	g/egg	$y = 0.41\ W^{0.42}$	0.70
	fish	mm^3/egg	$y = 0.59\ W^{0.43}$	0.26
	Crustacea	mm^3/egg	$y = 0.01\ W^{0.24}$	0.35
	fish and Crustacea	mm^3/egg	$y = 0.06\ W^{0.77}$	0.82
r_{max}	virus to mammals	day^{-1}	$y = 0.025\ W^{-0.26}$	0.90
Defecation	mammals	g/g/day	$y = 0.85\ W^{-0.37}$	0.80
Neonate production	mammals	g/g maternal body wt/day	$y = 0.037\ W^{-0.43}$	0.65
Brood time	birds	days	$y = 9.1\ W^{0.16}$	0.47
Gestation time	mammals	days	$y = 11\ W^{0.26}$	0.72
Average life span	mammals	days	$y = 630\ W^{0.17}$	0.56
Maturation time	virus to mammals	days	$y = 53\ W^{0.27}$	0.96

means were recorded, but if necessary the midpoints of ranges were used. Data were fitted to a power relationship using a pre-programmed analysis provided with a Hewlett-Packard 97 desk-top calculator. This program provided intercept (a), slope (b) and the coefficient of determination, r^2 (Steele and Torrie, 1960).

Such an approach has several short comings. Because the surveys are not exhaustive, particular groups may exert an undue influence on the relationship. Reliance on secondary sources could introduce biases, both conscious and unconscious, of other scientists. Regression analyses are strictly valid only if the variance in Y is independent of X and is normally distributed about the regression line, but this analysis is usually applied even if these requirements are not met. In keeping with this practice, ordinary predictive regressions in which $b = \Sigma xy / \Sigma x^2$, where $x = X - \bar{X}$ and $y = Y - \bar{Y}$ have been applied here. Ricker (1973) suggests that a functional regression in which slope is $(\Sigma y^2 / \Sigma x^2)^{1/2}$ is preferable for body weight relations, but this statistic has fewer adherents. The slope of the functional regression for the curves presented here can be calculated as b/r (Ricker 1973) using the values listed in Table 1. This increases
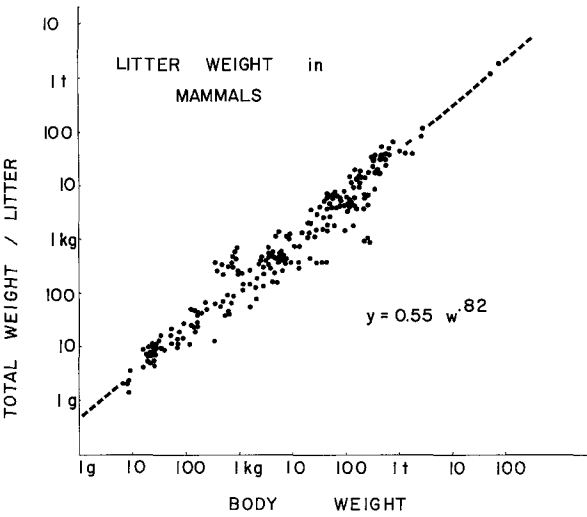
Fig. 1. Mammalian litter weight (y, in g per litter) vs maternal body weight (W, in g). Data from Sacher and Staffeldt (1974) and Leitch et.al. (1959)
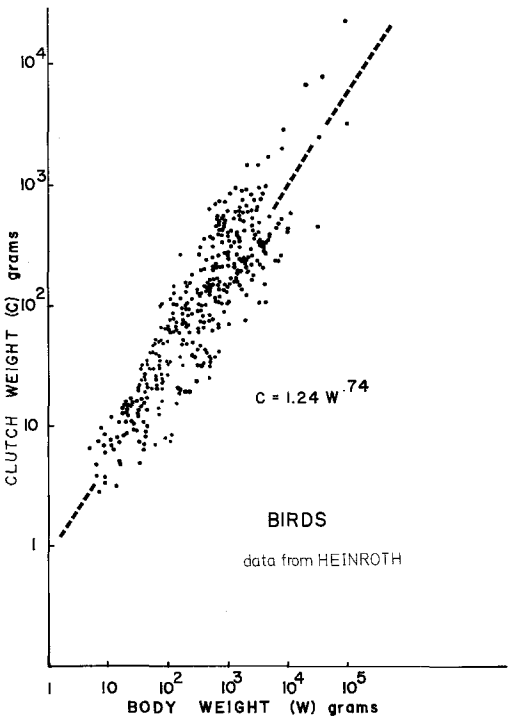

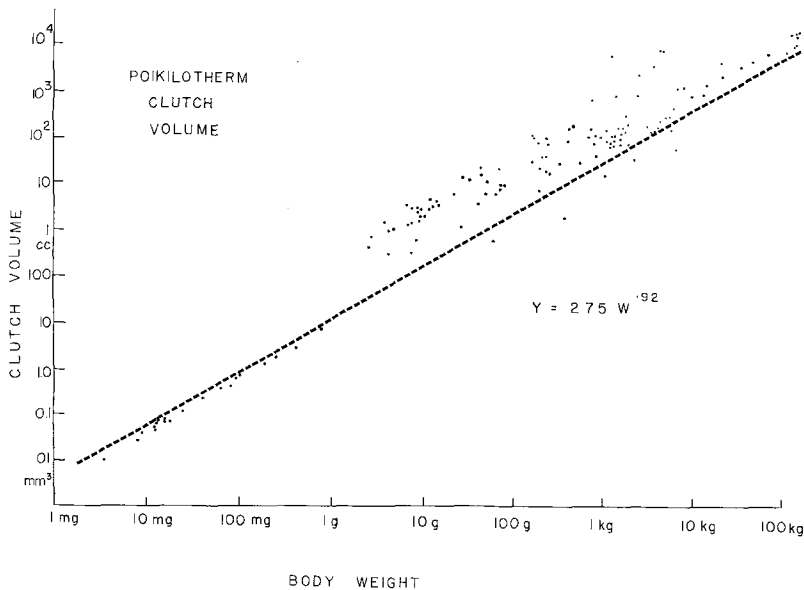**Fig. 2.** Total weight of avian clutch vs maternal body weight

Fig. 3. Clutch volume of poikilotherms (frogs, reptiles, fishes and crustaceans) (y, in mm^3) as a function of maternal body weight (W, in g). A specific gravity of 1 was assumed in order to convert weight to volume for frogs and reptiles. Sources as in Figures 7 and 8 plus Skrzypiec (1964)

the slope but has a pronounced effect only when the scatter in the data is large. In any case, equations with low r^2 values should be viewed with caution.

The first Figures (1–3) show that litter weight is tightly correlated with maternal weight (Sacher and Staffeldt, 1974; Millar, 1977) for all groups examined. Good relations also exist between the weight of individual offspring and maternal weight (Figs. 4–8). Poikilotherms increase fecundity per clutch as adult body size increases (Figs. 9 and 10). Certain anecdotal information (Southwood et al., 1974) suggests that this may also hold for homeotherms, but neither birds (data from Heinroth, 1922) nor mammals (data from Leitch et al., 1959; Sacher and Staffeldt, 1974) showed a relationship between the number of offspring per litter and adult body weight. Millar (1977) previously observed this lack of relation in small mammals. The average clutch size of birds in Heinroth's (1922) data is 4.85 (standard deviation = 3.04) and, for mammals, the mean number per litter (Leitch et al., 1959; Sacher and Staffeldt, 1974) was 2.71 (S.D. = 2.19).

Comparison among these regression lines (Fig. 11) shows that the litter weight of most animals is a strikingly similar function of adult body weight. Homeotherms of similar adult body size also produce offspring of similar size, but individual egg size for reptiles increases less rapidly with adult body size reflecting the poikilothermic tendency to increased clutch size in larger animals. Fish and Crustacea clearly produce more young per unit of litter weight, even though the scatter in Figure 9 is quite high. Figure 11 shows that smaller organ-
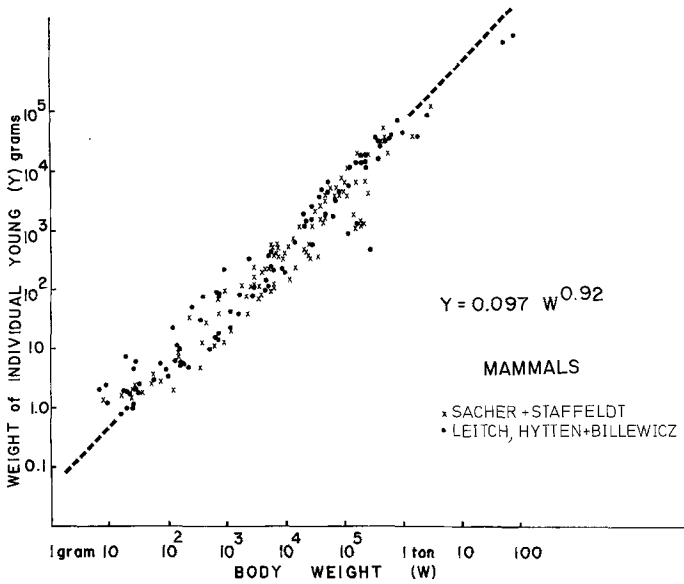
Fig. 4. Weight of individual neonate (y, in g) vs maternal body weight (w, in g) for mammals
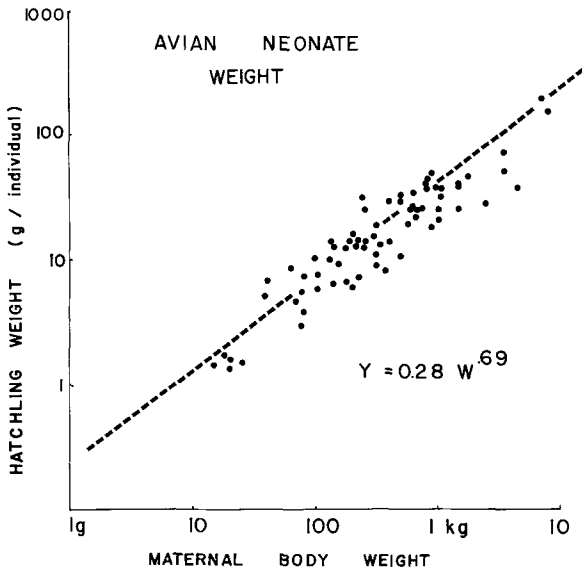

Fig. 5. Individual hatchling weight (y, in g) vs maternal body weight (w, in g) for birds. Data from Heinroth (1922)
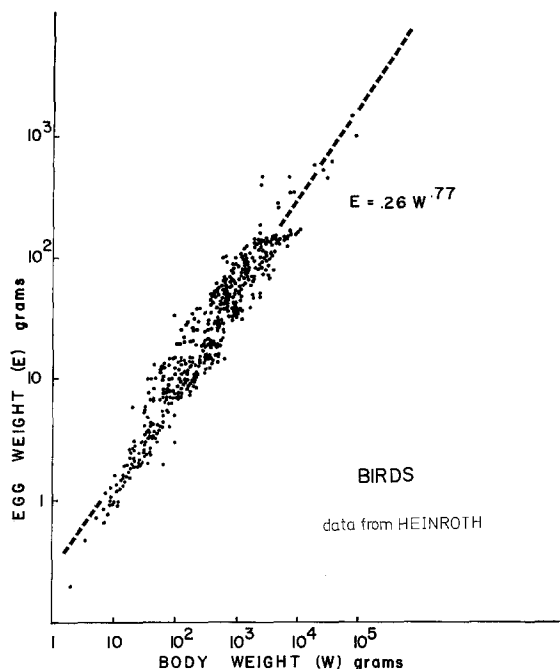
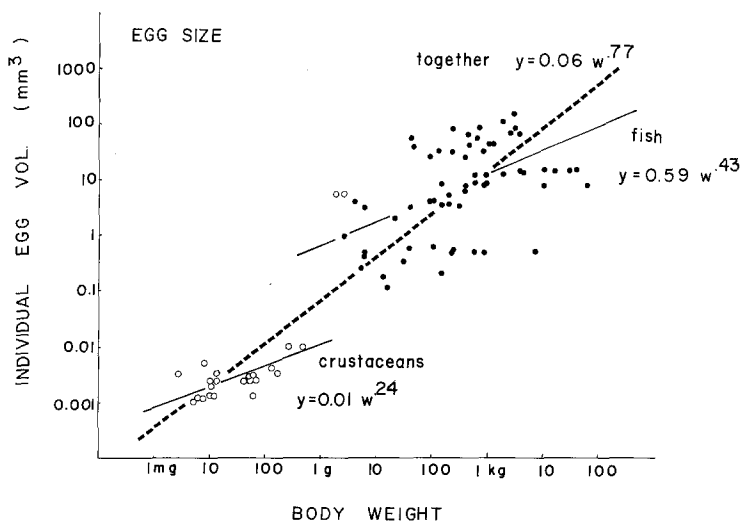**Fig. 6.** Egg weight (E, in g) vs maternal body weight for birds

Fig. 7. Individual egg volume (y, in mm^3) vs maternal body weight (w, in g) for fish, crustaceans and for both. Data from Scott and Crossman (1973), Carlander (1950), Colette and Earle (1922), Juszcyx (1971), Kozlowska (1971). Abrahamsson and Goldman (1970), Apollonio (1969), Mauchline and Fisher (1969)
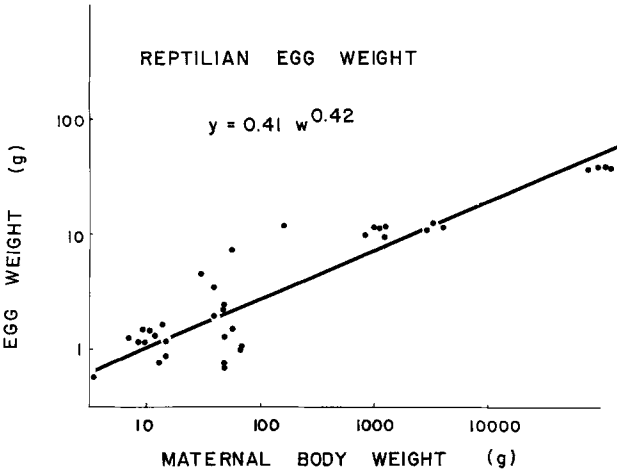
Fig. 8. Individual egg weight (y, in g) vs maternal body weight (w, in g) for reptiles. Data from Bustard (1971), Goldberg (1971), Parker (1973), Vitt and Ohmart (1974), Parker and Pianka (1973), Tanner and Krogh (1974), Vitt (1975), Clark (1974), Limpus (1973), Graham (1971), White and Murphy (1973), Yntema (1970), Cagle (1950, 1952)
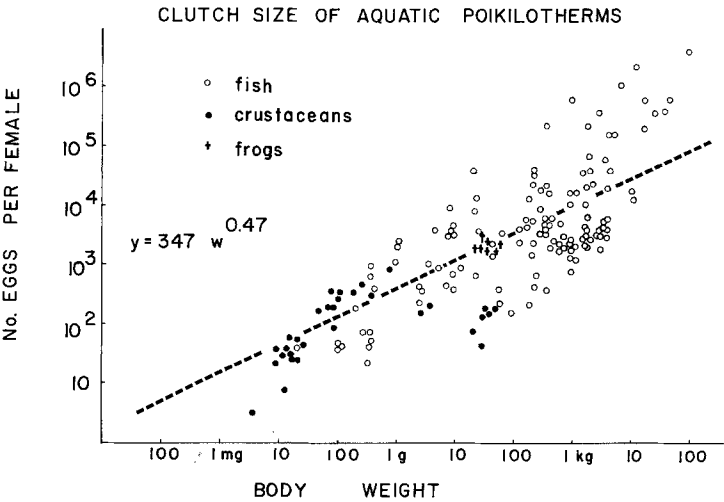

Fig. 9. The influence of maternal body weight (W, in g) on the number of eggs in the ovaries or in the clutches of aquatic and amphibious poiklilotherms. Sources as in Figure 7 plus Skrzypiec (1964)

isms invest more in reproduction, relative to their body weight, and that, for animals of a given size, this investment is roughly a constant fraction of their weight. Conversely, neonates of smaller animals are closer to the adult body size; the difference between adult and neonate size is more pronounced in poikilotherms, especially large poikilotherms. Among mammals, the ratio of
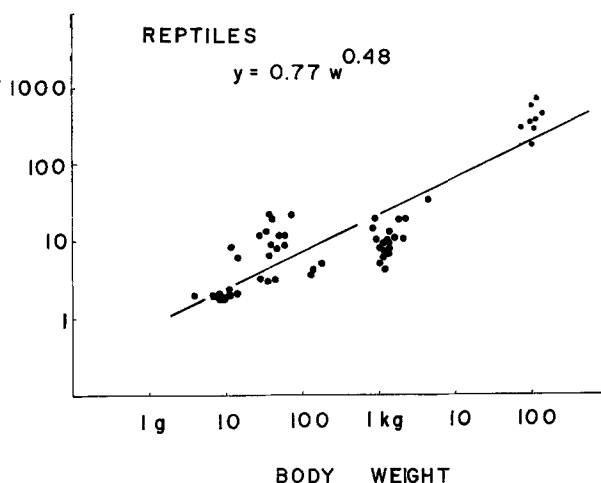
Fig. 10. The influence of maternal body weight (W, in g) on the number of eggs per clutch in reptiles. Sources as in Figure 8
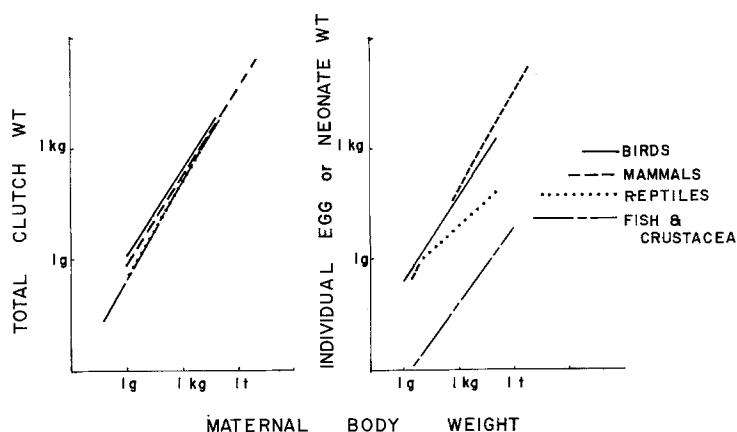

Fig. 11. Comparison of regression lines of clutch weight vs maternal body weight and of egg or neonate size vs maternal body weight for birds, mammals, reptiles and fish and Crustacea

neonate weight to maternal weight changes less rapidly with changes in maternal weight.

Rates of reproduction are also related to body size, although less variance is explained in these cases (Table 1). Figure 12 summarizes the relationship between mammalian gestation time and body size; Fig. 13 gives data regarding the length of brood time in birds. While it is hardly surprising that the larger neonates of larger animals require longer developmental times, the exponents in these relationships suggest that the amount of resources available to the neonate is set by adult body size and that the rate of utilization of these resources is determined by neonate size (see below).
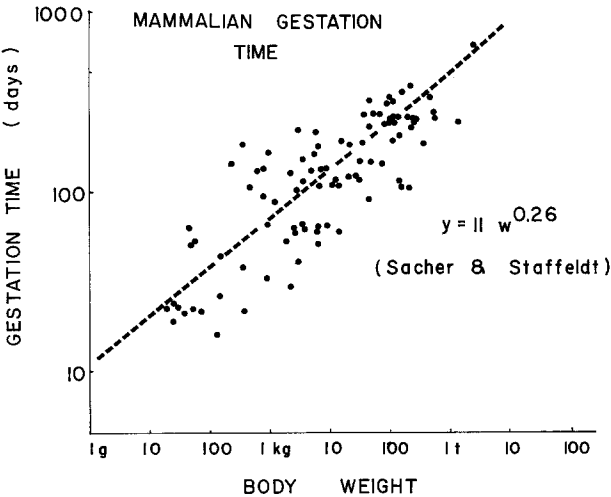
Fig. 12. Mammalian gestation time (y, in days) as a function of maternal body weight (w, in g)
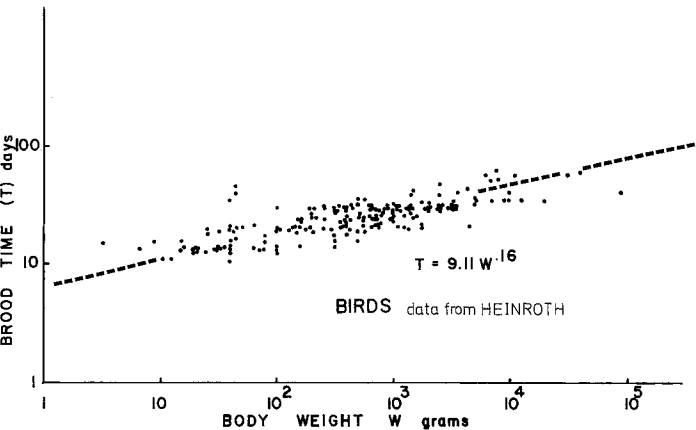

Fig. 13. Avian brood time (y, in days) as a function of maternal body weight (w, in g)

Growth and development are also functions of adult body size. Over a very wide range of organisms (i.e. from virus to whales), the time to sexual maturity is a function of body size (Fig. 14). Bonner (1965) took this parameter to be an estimate of generation time as well. The maximum life span also increases with body size (Rensch, 1959) in a miscellaneous group of animals (*Daphnia* to elephants, Fig. 15), as does the average life span in mammals (Fig. 16). Since the inverse of life span approximates the death rate in the absence of predation and disease, these figures may show that physiological death rate increases as body size decreases.
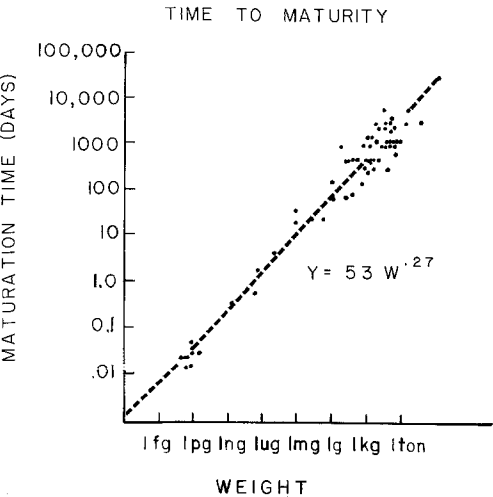
TIME TO MATURITY

Fig. 14. Maturation time (*y*, in days) as a function of adult body weight (*w*, in g) for a broad range of animals. Data from Yarwood (1956), Altman and Dittmer (1962), Bonner (1965), Chapman (1928), De witt (1954), Reay (1970), Demir (165), McCullough and Inglis (1961), Belynina (1969), Burton (1962), Raitt (1968), Meuller et al. (1976), Kirkpatrick (1944), Blacker (1971), Keith (1960), Johnsgard (1973), Weller (1965), Elder (1946), Schreiber (1976), Rue (1969), Stonehouse (1975), Williams (1963), Rutter (1962), Rutter and Pimlott (1968), Perry (1970), Cowie (1966), Warmer (1966), Caldwell and Caldwell (1972) and Batchelor (1963)
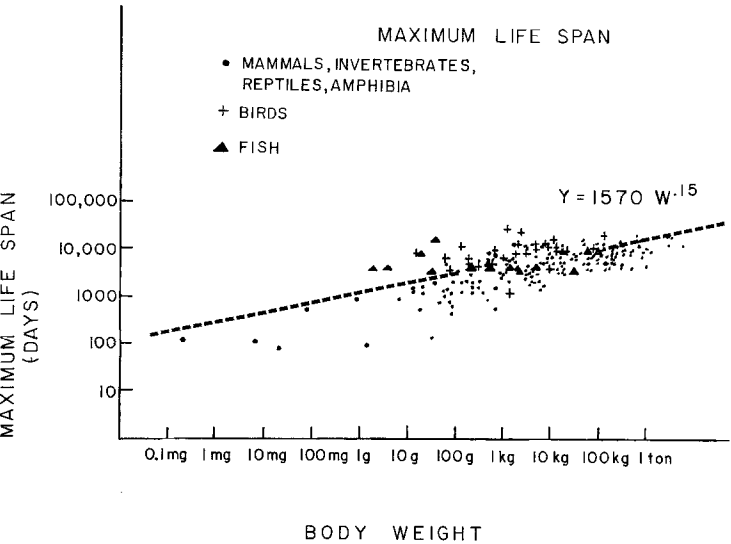

Fig. 15. Maximum life span (*y*, in days) for a broad range of animals vs adult body weight (*w*, in g). Data from Grzimek (1974), Walker (1975), and Altman and Dittmer (1962, 1973)
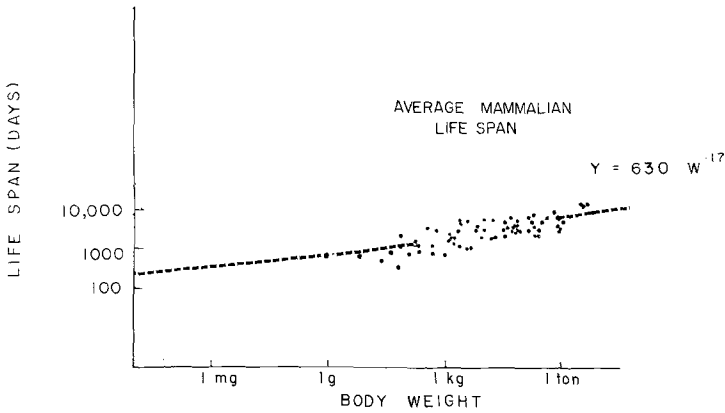
Fig. 16. Average life span (y, in days) of mammals vs adult body weight sources as in Figure 17
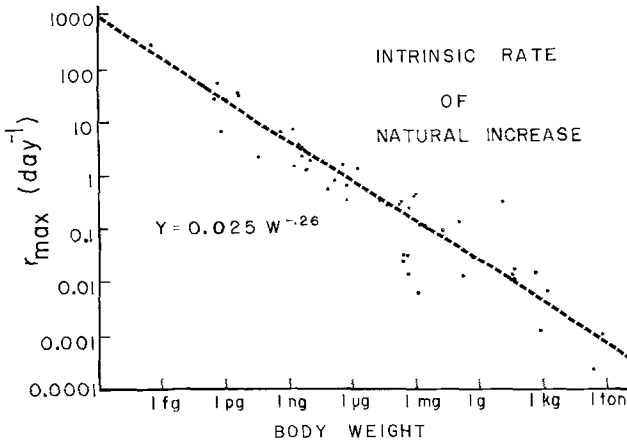

Fig. 17. The intrinsic rate of population growth, r_{max} (y, in day^{-1}) vs adult body size (w, in g) for a broad range of organisms. Data from Fenchel (1974), Nagel and Pimentel (1964), Clarke and Sardesi (1959), David and Fouillet (1971), Frazer (1972), Wrensch and Young (1974), Lauglin (1965), Murphy (1967), French and Kaaz (1968), Watson (1970) and Lowe (1969)

Smith (1954) and Fenchel (1974) have shown that the intrinsic rate of population growth, r_{max}, decreases with adult body size. Fenchel (1974) interpreted his data as three parallel curves corresponding to the r_{max} of unicells, poikilotherms and homeotherms. However, reanalysis of his data showed that all points could be treated with a single curve (Fig. 17). The product of r_{max} and adult weight is an estimate of the maximum possible rate of production. Figure 18 compares this transformation with the observed rates of individual growth reported in a range of ecological studies (Ecology 1961 to 1975, J. Anim. Ecol. 1968 to 1975; Peters, 1978). The close similarity between the curve and the data points suggests that differences between r_{max} and observed rates of population growth may reflect increased predation rates rather than decreased rates
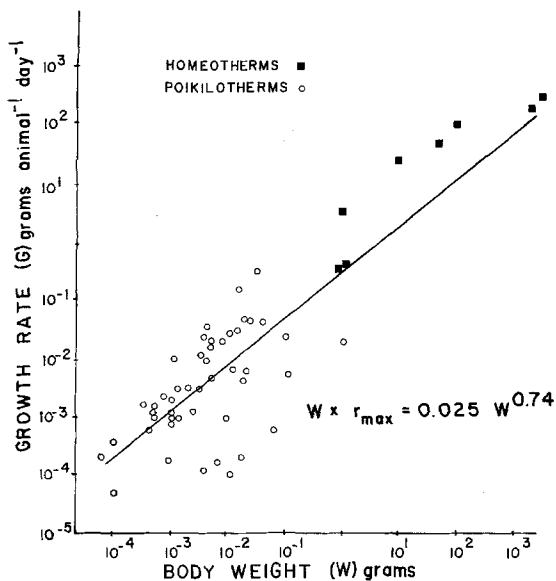
Fig. 18. A comparison of maximum rate of population growth in grams individual^{-1} day^{-1} calculated as $r_{max} \times$ adult body weight (curve and equation) and measurements of individual growth rates as reported in Ecology 1961 to 1975 and J. Anim. Ecol. 1968 to 1975 (data points for homeotherms and poikilotherms)

Fig. 19. Comparison of energy available from ingestion or assimilation and the rate of production of neonates (y, g of neonate/g of maternal weight/day) over a range of maternal weights (w, in g). Data from Sacher and Staffeldt (1974)

of birth and individual growth. However, much of the data regarding individual growth rates was obtained in the laboratory and might over-estimate natural rates.

For many organisms, metabolic rate per animal varies as $W^{0.75}$ (Hemmingsen, 1960). This implies that metabolic rate per gram varies as $W^{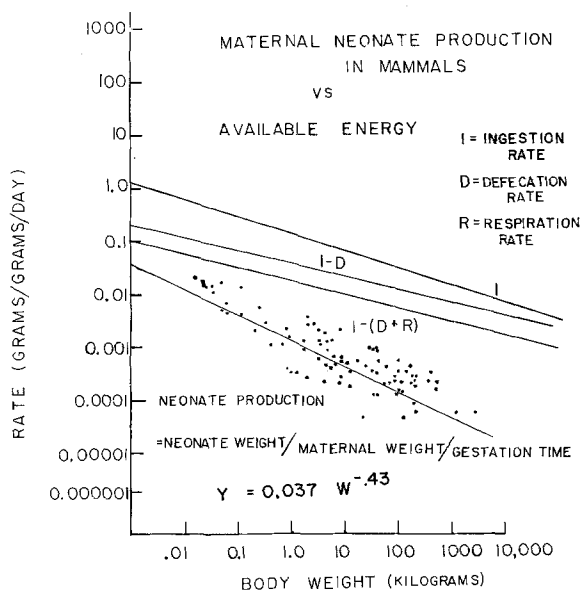-0.25}$ and that the time required for a unit of metabolic work varies as $W^{0.25}$ (Stahl 1962). Table 1 shows that exponents from equations describing growth and reproduction are frequently similar. Some of the departures from these exponents probably reflect only scatter in the data, but others may be real.

Among the most interesting of the apparent departures is neonatal production, defined as litter weight/(maternal weight × gestation time). Figure 19 compares these data with the energy available per gram from ingestion (from Farlow, 1976) or assimilation defined as ingestion − defecation and as ingestion − (defecation + basal metabolic rate) (Hemmingsen, 1960). Apparently larger mammals put less effort into reproduction than do small relative to available energy. Millar (1977) reached a similar conclusion based on the metabolic demands of the litter just prior to weaning. His calculations show that the effort of the mother declines as $W^{-0.42}$, a value very close to that in Figure 19, $W^{-0.43}$. Pearson (1968) observed that small sea birds spend a larger proportion of their time finding food for their young than do larger sea birds; this may be a specific example of the increased cost of reproduction in smaller homeotherms.

The exponent, −0.43, can be rationalized if the rate of neonate production is considered a function of neonate body weight, W_n, rather than maternal body weight, W. Since

$$W_n = 0.097 \ W^{0.92} \tag{1}$$

and production, P_n in g/g of neonate/day is approximated (Fig. 17) by

$$P_n = 0.025 \ W_n^{-0.26} \tag{2}$$

the average rate of production of neonates, P in g/g of maternal weight/day, can be determined by substituting Equation 1 for W_n in Equation 2 to give P_n as a function of maternal weight, and then multiplying by (total litter weight/maternal weight)

$$P = P_n \times 0.55 \ W^{0.82}/W = 0.025 \ W^{-0.42} \tag{3}$$

A parallel argument can be applied to gestation time (G) and brood time (B). Since G is the time required to produce a neonate, then G can be calculated as neonate weight divided by foetal growth rate; substituting Equation 1 for W_n gives G as a function of maternal weight, W

$$G = W_n/0.025 \ W_n^{0.74} = 26 \ W^{0.21} \tag{4}$$

and B can be predicted from hatchling weight, W_H

$$B = W_H/0.025 \ W_H^{0.74} = 29 \ W^{0.18} \tag{5}$$

The exponents predicted by assuming that foetal growth rate is a function of neonate size and that neonate size is a function of maternal weight are quite close to those observed when the scatter in the data and the approximation involved in substituting neonate weight for some average foetal weight are considered. The elevations in Equations 3 to 5 are higher than those observed (Table 1) which suggest that actual embryonic growth rates are two to three times faster than those predicted from population growth rates (Eq. 2). It is a commonplace that individual growth rate decreases with age (Brody, 1945; Millar, 1977) if the rate is expressed per unit weight.

Each of the curves presented in this overview of the life history and reproductive processes is a general biological theory (Wilkie, 1977). Each predicts some general characteristic which is difficult to measure, from a simple, easily measured, independent variable, body weight (Peters, 1977). By comparing curves, we can identify ecological constants like total investment/clutch (Fig. 11) and regular shifts such as the demands of reproduction relative to available energy (Fig. 19). The most likely applications of such theories are in treatments of community production (Sheldon et al. 1977), succession, material flow (Peters, 1978) or other properties of multi-specific animal assemblages. However even a confirmed autecologist will find these curves more suitable standards of comparison than data from individual species. Lastly, these relationships illustrate both the strengths and weaknesses of biological trends which many of us presume but frequently cannot adequately demonstrate.

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