SIZE, GROWTH AND REPRODUCTION: THE LOGIC OF ALLOMETRY

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ABSTRACT: During the last twenty years the importance of size on parameters of growth and reproduction has increasingly been realised. Allometric studies have allowed a new synthesis to emerge. Here I formally set out the fundamental assumptions on which our understanding of the scaling of growth and reproduction is based. The evidence for these assumptions is reviewed, and it is shown how these assumptions allow precise quantitative predictions to be made. The result of this procedure is that assumptions are clarified, new predictions are made and tested, and possible areas of future investigation outlined.

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'Ecology is still a branch of science in which it is usually better to rely on the judgement of an experienced practitioner than on the predictions of a theorist. Theory has never played the role that it has in population genetics, perhaps becuase there is nothing in ecology comparable to Mendel's laws in genetics' (Maynard Smith, 1974).

In its most general sense, allometry is any study of size and its consequences. It is found, however, that a great many biological variables are related to body mass as follows:

$$f(M) = \alpha M^{\beta} \tag{1}$$

where M stands for body mass and f(M) for some-sized related measure, such as the length of the organism or its metabolic rate, α and β are constants, and β is referred to as the exponent relating f(M) to M.

During the last twenty years, allometric studies of growth and reproduction have allowed a new synthesis to emerge. Both growth and reproduction depend on an organism's size in ways we now understand. The aim of this paper is to state formally the assumptions on which this synthesis rests, to review the evidence for these assumptions, to test predictions made from the assumptions and to outline new areas for study. It is hoped that the rigorous approach adopted will allow the success of the allometric approach to be judged. Allometry is a powerful tool, and while its role in ecology may never be as central as the role of Mendel's laws in genetics, the basic equations of allometry share with Mendel's laws features of simplicity and generality.

FUNDAMENTAL ASSUMPTIONS

Assumption 1

An individual's energy requirements for everything per unit time except growth and reproduction, E_{req}, are given by

$$E_{req} = k_1 M^{a} \tag{2}$$

where k_1 and a are contants and M is body mass.

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Evidence for Assumption 1

Nagy (1987) provides a useful catalogue of the various terms that have been used to stand for realistic estimates or measurements of the daily energy expenditure of organisms in the field. These include ´average daily metabolic rate´ (ADMR), ´field metabolic rate´ (FMR), ´daily energy budget´ (DEB) and ´daily energy expenditure´ (DEE).

Measurements of a, the exponent in Equation (2), consistently show that it is < 1.0. Most measurements lie between 0.5 and 0.9. This is true for poikilotherms, whether unicellular or multicellular, and for homeotherms, and holds whether measurements are done within a species or across a group of closely related species (Peters, 1093; Reiss, 1985; Bennett and Harvey, 1987). Unlike a, k_i varies considerably between species, being much greater for homeotherms than for poikilotherms, for instance.

Reasons why Assumption 1 holds

The reasons why daily energy requirements are allometrically related to body mass with an exponent of less than 1 are understood (Reiss, 1985, 1989). Basal metabolic rate scales at about $M^{0.67}$ to $M^{0.75}$ for reasons which are fairly well understood, though there is still disagreement about whether it scales closer to $M^{0.67}$ or to $M^{0.75}$ (Maynard Smith, 1968; McMahon, 1973, 1975; Kleiber, 1975; Bartels, 1982; Heusner, 1982; Feldman and McMahon, 1983; McNab, 1988). Of course, basal metabolism is only one component of an organism´s daily energy requirements. Average daily metabolic rate is usually greater than basal metabolic rate by a factor of about 1.5 to 3.0 (Gessaman, 1973; Moen, 1973; King, 1974; Mace, 1979; Nagy and Milton, 1979). In many homeotherms the other major component of average daily metabolic rate is extra-thermoneutral heat production. Theory predicts that this should scale at $M^{0.50}$ to $M^{0.75}$ (Kleiber, 1972; Monteith, 1973; Kendeigh, Dol´nik and Gavrilov, 1977; Reiss, 1985). The daily cost of locomotion is also likely to be allometrically related to body mass with an exponent of less than 1 (Reiss, 1985).

The major components of daily energy expenditure seem therefore to be allometrically related to body mass, and to scale at about $M^{0.5}$ to $M^{0.75}$. As the exponents are similar, one would expect (Laird, 1965) daily energy expenditure itself to scale at about $M^{0.5}$ to $M^{0.75}$, as it does.

Assumption 2

An individual´s energy assimilation per unit time is given by

$$E_{in} = k_a M^b \tag{3}$$

where k_a and b are constants and M is again body mass.

Evidence for Assumption 2

Measurements of b show that its value lies between about 0.6 and 0.9 (Pandian, 1967; Sushchenya and Khmeleva, 1967; Farlow, 1976; Cammen, 1980; Peters, 1983; Reiss, 1985, 1986). As was the case for a, this conclusion is true both for poikilotherms and for homeotherms and holds whether measurements are done within a species or among closely related species.

Reasons why Assumption 2 holds

The scaling of energy assimilation on size is less well understood than is the scaling of metabolic rate on size. However, feeding is fundamentally a surface phenomenon (Gould, 1966). If, for example, energy assimilation is limited by the transfer of nutrients across the gut wall, the exponent of energy assimilation on body mass should lie close to 0.67. It could, though,

be argued that as digestive enzymes operate throughout an animal's gut, b should lie close to 1. It all depends on precisely what is limiting energy assimilation. In hummingbirds, for instance, it is not yet clear whether energy assimilation is limited by the rate at which flowers can be visited, the rate at which flowers replenish their nectar reserves or the rate at which the nutrients can be absorbed (Hainsworth, 1973; Brown, Calder and Kodric-Brown, 1978; Karasov, 1986).

Prediction 1

Interspecific plots should show that the energy females can invest in their offspring per unit time is allometrically related to their body mass with an exponent of between about 0.5 and 0.9.

Reasons for Prediction 1

This follows from Assumptions 1 and 2.

Let E_{rep} be the energy an adult female can devote to reproduction per unit time. Then as E_{req} stands for her energy requirements for everything except growth and reproduction per unit time and E_{in} for energy assimilation per unit time, we have

$$E_{rep} = E_{in} - E_{req} \tag{4}$$

as proposed by Ware (1980), Roff (1983) and others. We can now substitute for E_{in} and E_{req} from Equations (2) and (3) into Equation (4), resulting in

$$E_{rep} = k_2 M^b - k_1 M^a \tag{5}$$

It is clear from Equation (5) that the exponent for an interspecific plot of E_{rep} as a function of M should lie between about 0.5 and 0.9 (Reiss, 1985), as these are the exponents that interspecifically relate non-reproductive energy requirements and energy assimilation to body mass.

Evidence bearing on Predictions 1

The energy females invest in their offspring is often difficult to measure (Hirshfield and Tinkle, 1975; Dittus, 1979) and various indices of reproductive effort have been used to quantify parental investment (Calow, 1979; Tuomi, Hakala and Haukioja, 1983). Measurements of the interspecific scalings of E_{rep} on M are listed in Table 1 (Reiss, in press). Despite the variety of methods used to estimate E_{rep}, the relationship of E_{rep} to M is well described by the allometric equation and, as predicted, the exponent relating E_{rep} to M lies between about 0.5 and 0.9, so that larger species do invest relatively less in their offspring per unit time (Reiss, 1985).

It may be that different groups of species have different interspecific values of the exponents relating non-reproductive energy requirements and energy assimilation to size. If this is the case, then some of the variation in the exponents relating E_{rep} to M listed in Table 1 may be explainable. For instance, it is possible that the energetic costs of hovering scale on body mass with an exponent of close to 1.0, although this is not known for certain (Hainsworth and Wolf, 1972; Casey, 1981). If this is the case, it might be that in organisms such as hummingbirds and hoverflies, which spend a lot of time hovering and in which hovering is a major component of energy expenditure, a is close to 1.0. It is tempting to see confirmation of this in the observation that the largest exponent in Table 1 is indeed for hoverflies. However, it might be that larger species of hoverflies hover for less time each day, which would reduce the interspecific value of a. In birds, larger species spend a significantly smaller percentage of the active day in powered flight than do smaller species (Walsberg, 1983).

Table 1. Interspecific exponents for E_{rep}, the energy females invest in reproduction, on M, female body mass. Standard errors of the exponents are given where possible.

Taxon	Measurement of E_{rep}	Exponent	±1SE	Source
Spiders	Clutch number	0.84		(1)
Aphids	Clutch number	0.51-0.69		(2)
Hoverflies	Clutch volume	0.95	0.10	(3)
Poikilotherms	Clutch volume	0.92		(4)
Salamanders	Clutch volume	0.64		(5)
Frogs	Clutch volume	0.90		(6)
Reptiles	Litter weight	0.88		(4)
Birds	Clutch weight	0.52-0.74	0.13-0.18	(7-9)
Mammals	Litter weight	0.77-0.83	0.01	(10, 11)
Mammals	Litter weaning weight	0.70-0.73	0.02	(12, 13)
Mammals	Milk yield (kcal/day)	0.69	0.04	(14)

Sources: (1) Petersen, 1950; (2) Llewellyn and Brown, 1985; (3) Gilbert, 1982; (4) Blueweiss et al., 1978; (5) Kaplan and Salthe, 1979; (6) Crump, 1974; (7) Lack, 1968; (8) Rahan, Paganelli and Ar, 1975; (9) Heinroth, 1922; (10) Leitch, Hytten and Billewicz, 1959; (11) Millar, 1981; (12) Millar, 1977; (13) Russell, 1982; (14) Hanwell and Peaker, 1977.
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Prediction 2

   For species in which individual females change little in body size during the course of their reproductive lifespans, an intraspecific plot of log energy invested in reproduction per unit time on log body mass should reveal a straight line with slope of about 0.5 to 0.9.

Prediction 3

   For species in which individual females continue to grow during the course of their reproductive lifespans, an intraspecific plot of log energy invested in reproduction per unit time on log body mass should have a slope greater than that expected for species in which individual females change little in body size during the course of their reproductive lifespans, though there is no certainty that the relationship will be linear.

Reasons for Predictions 2 and 3

   Consider, first, species in which individual females do not change much in mass during the reproductive phase of their lives. In this case, Equation (5)

$$E_{rep} = k_2 M^b - k_1 M^a$$

is still valid, and the intraspecific prediction for the dependence of E_{rep} on M is the same as the interspecific prediction: E_{rep} is expected to scale on M with an exponent of between 0.5 and 0.9.
   For species, however, where each female reproduces over a wide range of body masses, Equation (4) needs to be replaced by

$$E_{gro+rep} = k_2 M^b - k_1 M^a \tag{6}$$

where $E_{gro+rep}$ is the energy available for growth and reproduction per unit time. In such species there is no particular reason to expect E_{rep} to be related to M by Equation (1). However, a plot of $\log E_{rep}$ on $\log M$ should have a slope greater than that for species where individual females do not continue to grow during the reproductive phase of their lives. This is because data from the lower body masses are likely to come from individuals apportioning only some of their available energy for growth and reproduction to reproduction, and the rest to growth (Reiss, 1987). Larger females are likely to apportion a smaller proportion of their available energy for growth and reproduction to growth than are smaller females.

Evidence bearing on Predictions 2 and 3

Table 2 (Reiss, in press) reviews data on the intraspecific scaling of E_{rep}. The best data for organisms that change considerably in mass during the reproductive phase of their lives come from fishes (Wootton, 1979). Isopods and aphids are organisms in which individuals vary little in mass during the reproductive phase of their lives (Steel, 1961; Anderson, 1969; Ellis, 1971). As predicted, isopods and aphids have exponents relationg E_{rep} to M of about 0.5 to 0.9, while fish have exponents greater than this. Of course, data from a variety of other taxa will be needed before the predictions outlined here can be thought to hold generally.
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Table 2. Intraspecific exponents for E_{rep}, the energy females invest in reproduction, on M, female body mass. Standard errors of the exponents are given where possible.

Taxon	Measurement of E_{rep}	Exponent	±1SE	Source
5 species of isopods	Fecundity	0.77	0.04	(1)
1 species of aphid	Fecundity	0.47-0.62	0.04	(2)
62 species of fish	Fecundity	1.11	0.03	(3)
14 species of fish	Weight of gonads	1.0-1.9		(4)

Sources: (1) Ridley and Thompson, 1979; (2) Kempton, Lowe and Bintcliffe, 1980; Reiss, 1989; (3) Wootton, 1979; Reiss, 1987; (4) Roff, 1983.
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Of fish, isopods and aphids, it appears that fish show the greatest range in exponents relating fecundity intraspecifically to body mass (from 0.33 to 2.33 (Wootton, 1979). This may simply be because data are available from more species of fish than from isopods and aphids. However, Wootton (1979) noted that short-lived species or those with poor post-spawning survival tend to have lower exponents than do long-lived species with good post-spawning survival. This is as one would expect from Equation (6). In species that are long-lived and have good post-spawning survival, it will be to a female's advantage to devote a high proportion of her energy requirements to growth when she is young and relatively small. There is a trade-off between growth and reproduction (Sibly & Calow, 1986). Whether natural selection favours semelparity or iteroparity depends on the ecology of the population (Schaffer & Schaffer, 1977).

Prediction 4

During growth we would expect

$$dM/dt \propto k_2 M^b - k_1 M^a \qquad\qquad (7)$$

to give a better fit to data than conventional growth equations such as the von Bertalanffy equation

$$dM/dt = AM^m - BM$$

the Gompertz equation

$$dM/dt = AM(\log_e M)$$

or the Logistic equation

$$dM/dt = AM - BM^2$$

where A, B and m are constants and t is time.

Reasons for Prediction 4

During growth and before reproduction, Equation (6) reduces to

$$E_{gro} = k_2 M^b - k_1 M^a \qquad\qquad (8)$$

Evidence bearing on Prediction 4

Ursin (1967, 1979) has estimated the values of the exponents a and b in Equation (7) for 81 fish species from a detailed review of their growth curves. He concludes that a = 0.83, b = 0.59 (with 95% confidence limits equal to ±0.06 and ±0.02 respectively) gives a significantly better fit than a = 1, b = 2/3, as required by the most frequently used form of the von Bertalanffy growth equation. Equally, these values of a and b obviously give a better fit than a = 2, b = 1, required by the Logistic growth equation.

Prediction 5

Growth rates should scale at about $M^{0.7}$, both for an individual as it grows and across species of different adult sizes.

Reasons for Prediction 5

Prediction 6 follows from Equation (7), given that both a and b are approximately equal to 0.7.

Evidence bearing on Prediction 5

Interspecifically, growth rates scale as $M^{0.61}$ in fish (Case, 1978), as $M^{0.67}$ in reptiles, as $M^{0.66}$ in birds (Ricklefs, 1979) and as $M^{0.72}$ in mammals (Case, 1978). A reason for this interspecific scaling of growth rate on size seems to have been lacking. A number of authors have merely assumed that growth rates and metabolic rates should both depend on body size in the same way. However, this is to ignore the importance of the scaling of energy intake on body size. As Case (1978) writes ´Why, in fact, should growth rate and metabolic rate vary with body size at roughly the same rate? The answer is not at all obvious.´

The most pertinent data for the dependence of growth rate on size for individuals as they grow come from analyses of the scaling of relative growth rates. Relative growth rate is the percentage mass gained per day. In fish, intraspecific plots of log relative growth rate on log body mass give straight lines with slopes that vary from -0.49 to -0.28 (Brett and Shelbourn, 1975; Brett, 1979). This means that as fish grow larger, each day their mass, though still increasing, increases by a smaller percentage of their current body mass.

This follows from Equation (7). As a $\approx$ b $\approx$ 0.7,

$$dM/dt \propto M^{0.7}$$

and so

$$(1/M)(dM/dt) \propto M^{-0.3} \tag{9}$$

(Reiss, 1989).

The intraspecific dependence of relative growth rates, $(1/M)(dM/dt)$, also seems previously to have lacked explanation, Ricklefs has repeatedly emphasized (Ricklefs, 1968, 1973, 1974, 1979) that 'the general decrease in growth rate, expressed as a percentage of adult weight, with increasing adult body weight still defies explanation' (quote from Ricklefs, 1974).

Prediction 6

Age at maturity and generation time should each scale interspecifically at about $M^{0.3}$.

Reasons for Prediction 6

As growth rates scale, as predicted, at about $M^{0.7}$, age at maturity will be expected to scale interspecifically as

$$M/M^{0.7} = M^{0.3}$$

Generation time is similarly predicted to scale interspecifically as $M^{0.3}$ on the implicit assumption that the gap in time between an organism reaching adult mass and reproducing is either negligible or scales on body mass with an exponent of about 0.3, as appears to be the case (Taylor, 1965, 1968).

Evidence bearing on Prediction 6

From viruses to giant sequoia trees, generation time and age at maturity scale interspecifically from $M^{0.21}$ to $M^{0.39}$ (Bonner, 1965; Taylor, 1968; Fenchel, 1974; Finlay, 1977; Blueweiss et al., 1978; Western, 1979; Baldcock, Baker and Sleigh, 1980; Taylor and Shuter, 1981).

Prediction 7

The proportion of its energy budget that an individual devotes to growth as it grows, E_{gro}/E_{in}, is related to its size as

$$E_{gro}/E_{in} = 1 - (k_1/k_2)M^{a-b} \tag{10}$$

Reasons for Prediction 7

Paloheimo & Dickie (1966), Ursin (1967) and Staples and Nomura (1976) point out that the proportion of the energy budget that is devoted to growth will decrease as an individual grows if metabolic requirements scale more steeply on body weight than does food intake. Over a small unit of time, δt, we have from Equations (2), (3) and (8)

$$E_{gro} = (k_2 M^b - k_1 M^a)\delta t$$

and

$$E_{in} = k_2 M^b$$

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so that we may write

$$E_{gro}/E_{in} = \{(k_a M^b - k_i M^a)\delta t\}/k_a M^b$$

which reduces to Equation (10).

Evidence bearing on Prediction 7

Growth efficiencies usually decrease as an individual grows (Waldbauer, 1968; Calow, 1977; Reiss, 1989). Data for four species with good datasets are plotted in Figures 1(a) - 1(d), Analysis (Table 3) of the data in these Figures shows that there is a good correlation between $\log (1 - E_{gro}/E_{in})$ and $\log M$, and that, as predicted by Equation (10), this correlation is slightly greater than the correlation between $(1 - E_{gro}/E_{in})$ and M.
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Table 3. Analysis of Figures 1(a) - 1(d)

Species	Regression of $\log(1 - E_{gro}/E_{in})$ on $\log M$			Regression of $(1 - E_{gro}/E_{in})$ on M
	a − b	95% confidence limits of a − b	r	r
Jersey cattle	0.171	± 0.025	0.958	0.900
Megalops cyprinoides, fish	0.072	± 0.036	0.779	0.712
Ophiocephalus striatus, fish	0.087	± 0.016	0.959	0.844
Oceanodoma leucorhoa, bird	0.329	± 0.042	0.997	0.995

Sources: Jersey cattle - Brody, 1945; fish - Pandian, 1967; bird - Ricklefs et al., 1980.
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If there are species in which the proportion of the energy budget devoted to growth remains constant or even increases as the animal grows, then such species presumably show indeterminate growth.

Prediction 8

Across species, productivity/assimilation ratios should be independent of the mean sizes of species.

Reasons for Prediction 8

Production refers to the manufacture of new biological materials. It therefore includes growth and reproduction. As both growth and reproduction scale interspecifically per unit time on body mass with exponents of close to 0.7, productivity does too. Assimilation per unit time scales interspecifically at about $M^{0.7}$, as discussed above. Consequently we predict that productivity/assimilation ratios will scale interspecifically as
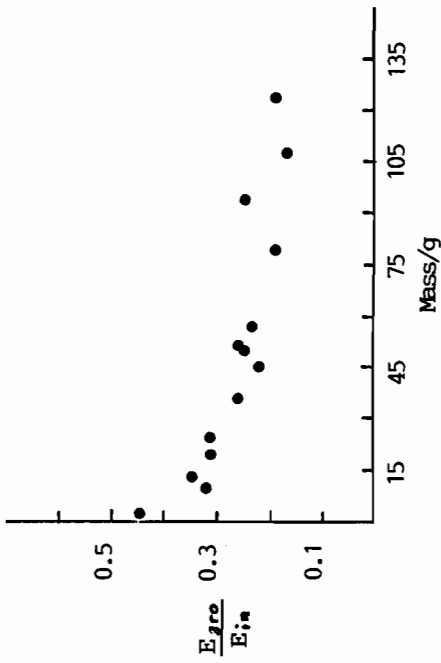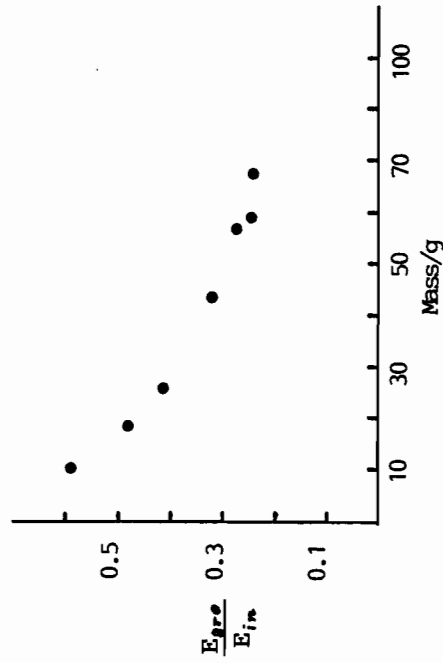
$$M^{0.7}/M^{0.7} = M^{0}$$

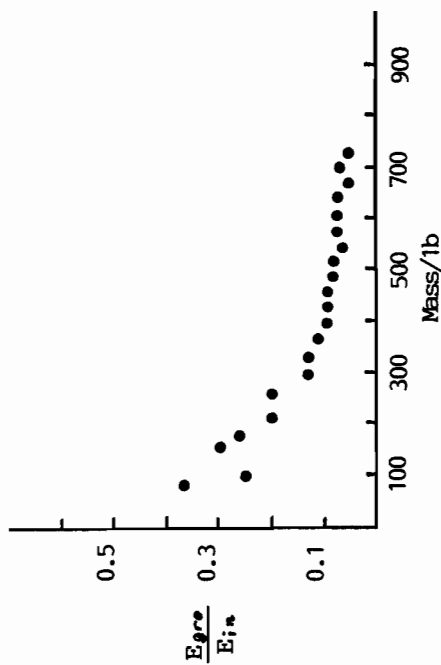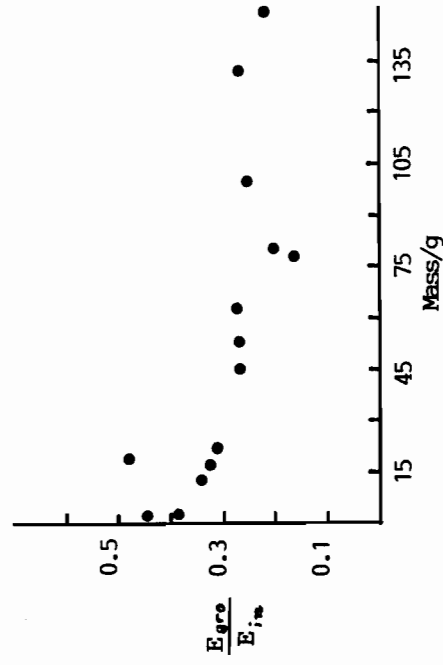**Figure 1** Growth efficiency, E_{gro}/E_{in}, as a function of size within four species: (a) Jersey cattle – data from Brody (1945); (b) Megalops cyprinoides, fish – data from Pandian (1967); Ophiocephalus striatus, fish – data from Pandian (1967); (d) Oceanodroma leucorhoa, Leach's storm-pertel – data from Ricklefs et al., (1980).

Evidence bearing on Prediction 8

Humphreys (1979), in an analysis of 235 energy budgets, showed that the ratio of production to assimilation is indeed independent of mass in interspecific comparisons. Assimilation equals production plus respiration. The slope of the least squares common regression of log production on log respiration equalled 0.96, with 95% confidence limits equal to ± 0.04, $r = 0.94$.

There do not appear to have been any previous explanations for why the ratio of production to assimilation is interspecifically independent of species size. Koller and Leonard (1981) thought that the ratio should be smaller in smaller species on the grounds that metabolic rate and body size are inversely related.

Prediction 9

Across species, productivity/biomass ratios should scale at about $M^{-0.3}$.

Reasons for Prediction 9

Productivity equals the number of individuals sampled, N, multiplied by each individual's productivity. Biomass equals N multiplied by the mass of each individual.
Consequently we have

$$\text{Productivity/biomass} \propto NM^{0.7}/NM$$

and therefore

$$\text{Productivity/biomass} \propto M^{-0.3} \tag{11}$$

Evidence bearing on Prediction 9

In invertebrates, productivity/biomass ratios scale interspecifically as $M^{-0.37}$, with 95% confidence limits of the exponent equal to ± 0.07 (Banse and Mosher, 1980). In fish, productivity/biomass ratios scale interspecifically as $M^{-0.26}$, with 95% confidence limits of the exponent equal to ± 0.16 (Banse and Mosher, 1980). In mammals, productivity/biomass ratios scale interspecifically as $M^{-0.27}$, with 95% confidence limits of the exponent equal to ± 0.03 (Farlow, 1976).

With the exception of Peters (1983), who pointed out that we would expect productivity/biomass ratios to scale at about $M^{-0.25}$ on the grounds that its unit is the reciprocal of time, there do not appear to have been any previous attempts to explain the dependence of productivity/biomass ratios on size.

Assumption 3

Adult female body mass has evolved so as intraspecifically to maximize E_{rep}.

Assumption 4

Within a species, k_1/k_2 has the same value for males and females.

Evidence for Assumptions 3 and 4

Figure 2 shows how $k_1 M^a$ and $k_2 M^b$ depend intraspecifically on body mass. It is assumed that a exceeds b, as discussed above. If a does not exceed b, then the two curves diverge. It seems reasonable to suppose that female body mass might be constrained so as to maximize the energy that can be invested in reproduction per unit time. For the females of many species the energy

available for reproduction is limiting (McNab, 1963; Klein, 1964; Watson, 1970; Sadleir, Casperson and Harling, 1973; Randolph et al., 1977; Sinclair, 1977; Mitchell, Staines and Welch, 1977; Belovsky, 1978). In particular, Belovsky (1978) on moose, Alces alces, and Searcy (1979) on red-winged blackbirds, Agelaius phoeniceus, suggest that the energy available for reproduction is size-dependent and that female body weight has evolved so as to maximize it.
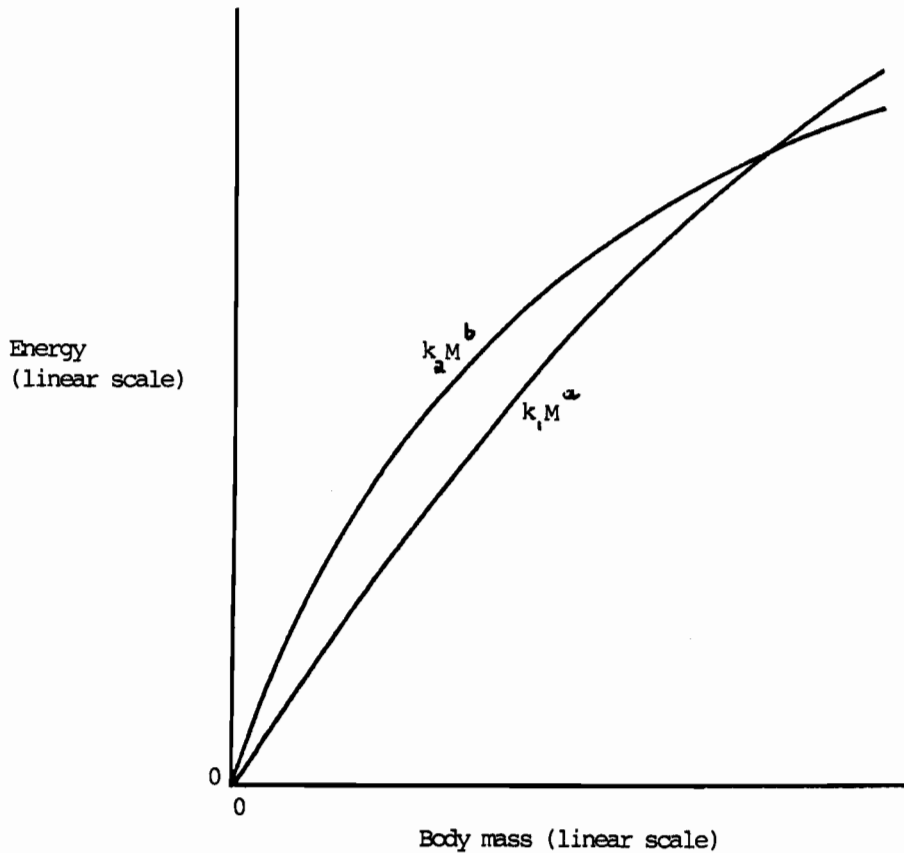***

Figure 2 The intraspecific dependence of $k_1 M^a$ and $k_a M^b$ on body mass. $k_1 M^a$ is an individual's energy requirements for everything except growth and reproduction per unit time, where k_1 and a are constants and M is body mass. $k_a M^b$ is an individual's energy assimilation per unit time, where k_a and b are constants and M is again body mass.
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Sex-specific differences in k_1 / k_a are almost bound to exist. What is as yet unknown is the precise magnitude of these differences. Moors (1977) looked for a significant difference in k_1 between male and female weasels, Mustela nivalis, but failed to find one. An indication, however, that sex-specific differences in k_1 / k_a may exist comes from the observation that in many dimorphic species males and females differ in growth rates (e.g. Blaxter et al., 1974; Trivers, 1976; Tanner, 1978; Van Devender, 1978).

Prediction 10

The ratio of male to female body mass, M_m/M_f, within a species lies within limits given by

$$0 \leqslant M_m/M_f \leqslant (a/b)^{1/(a-b)} \tag{12}$$

Reasons for Prediction 10

From Assumption 3 we have

$$\frac{d}{dM}(k_2 M^b - k_1 M^a) = 0$$

and

$$\left.\frac{d^2}{dM^2}(k_2 M^b - k_1 M^a)\right|_{M_f} < 0$$

So

$$M_f^{a-b} = k_2 b / k_1 a \qquad\qquad (13)$$

(Sebens, 1979), and

$$a > b$$

Although it may be fair to assume that adult female body mass has evolved so as intraspecifically to maximize the energy females can invest in reproduction, this may not necessarily be the case for males. For instance, in some species of snakes (Shine, 1978) and turtles (Berry & Shine, 1980), large male size has evolved, relative to female size, because of the advantage it gives males in intrasexual combat. In such a situation there is no reason to suppose that male body size has evolved so as intraspecifically to maximize the energy males can invest in reproduction. Indeed, it seems likely that in such species males have less energy available for reproduction than do females. There is a balance between the advantage that large male size gives in combat, and the disadvantage it carries of reducing the amount of energy available for full grown males to devote to reproduction.

Males must have some energy to devote to reproduction. Within a species, the energy available for reproduction as a function of size is shown in Figure 3. The energy males can invest in reproduction will equal zero when $E_{in} = E_{req}$, i.e.

$$k_2 M_m^b = k_1 M_m^a \qquad\qquad (14)$$

There are two solutions to Equation (14). Either

$$M_m = 0 \qquad\qquad (15)$$

or

$$M_m^{a-b} = k_2 / k_1 \qquad\qquad (16)$$

Given Assumption 4, that k_1/k_2 has the same value for males and females, we can combine Equations (13), (15) and (16) to find two extreme values of M_m/M_f. Either

$$M_m/M_f = 0$$

or

$$(M_m/M_f)^{a-b} = (k_2/k_1) \cdot (k_1 a/k_2 b) = a/b$$

Consequently, for any species we have the inequality

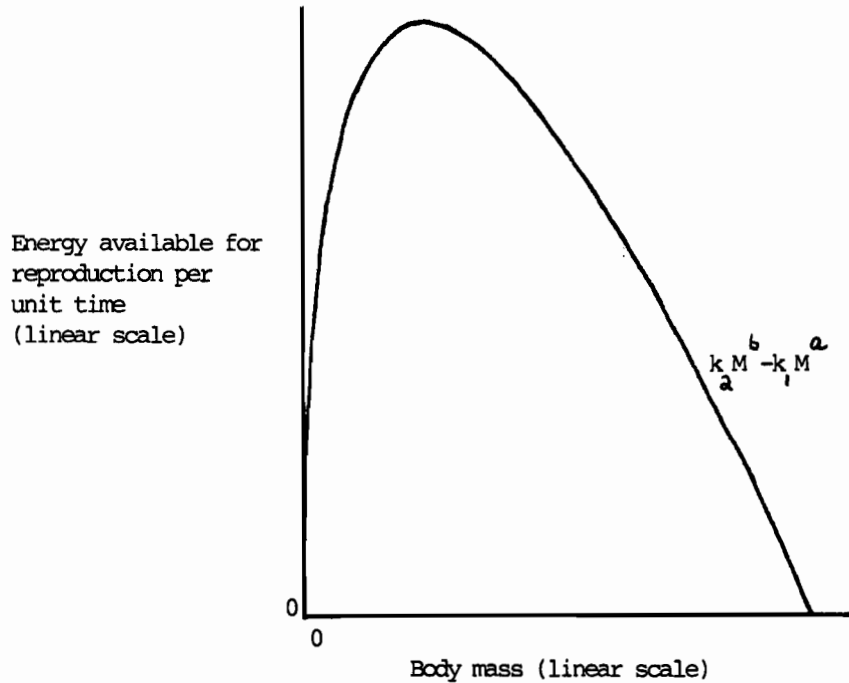$$0 \leqslant M_m/M_f \leqslant (a/b)^{1/(a-b)}$$

(Reiss, 1982).

Figure 3 The intraspecific dependence on size of the energy available for reproduction per unit time. The energy available for reproduction is equal to $k_2 M^b - k_1 M^a$, the difference between energy assimilation per unit time and energy requirements for growth and reproduction per unit time.
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Evidence bearing on Prediction 10

The values of $(a/b)^{1/(a-b)}$ for some values of a and b are given in Table 4. As $b \to a$, $(a/b)^{1/(a-b)} \to e^{1/a}$, where $e = 2.71828 \ldots$. We therefore expect that, within a species, sexual dimorphism in body mass, M_m/M_f should lie between 0 and about 10.
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Table 4. Predicted maximal values of the degree of sexual dimorphism in body mass M_m/M_f, in species where males are heavier than females, as functions of a, the intraspecific slope of log average daily metabolic rate on log body mass, and b, the intaspecific slope of log energy assimilation on log body mass.

		a		
		0.5	0.75	1.0
	0.333	11.40	7.01	5.20
b	0.667	–	4.11	3.37

Note: These values of the maximal degree of sexual dimorphism in body mass, in species where males are heavier than females, are calculated from Equation (12).
****
As predicted, the most dimorphic species known are those in which females

far outweigh males, so that M_m/M_f lies close to 0. Species of <u>Bonellia</u> in the phylum Echiura have extremely low values of M_m/M_f. In <u>B. viridis</u> females are hundreds of times larger than males (up to 1 m for females, up to 3 mm for males (Barnes, 1974) and therefore possibly millions of times heavier. Very low values of of M_m/M_f also occur in some solitary haplodiploids (Hamilton, 1967), in ceratioid anglerfish (Pietsch, 1975, 1979), in several molluscs (Morton, 1981) and in many social insects.

Sexual dimorphism in body mass, as predicted, is less extreme when males outweigh females. The greatest value of M_m/M_f seems to be about 8 in the southern elephant seal, <u>Mirounga leonina</u>, (Bryden, 1969). In birds the greatest values of M_m/M_f lie between 2 and 3 (Selander, 1972; Ralls, 1976).

Factors which influence the precise degree of sexual dimorphism in body weight are considered quantitatively by Reiss (1989).

DISCUSSION

Equations (2) and (3) are, like nearly all biological laws, only approximations. Nevertheless, the available data show that they may be close approximations. Indeed, very many anatomical and ecological measures are allometrically related to body weight, for reasons understood at least to some extent (Brody, 1945; Calder, 1974, 1984; Apple and Korostyshevskiy, 1980).

Occasionally energy requirements or energy assimilation are represented as depending on body mass by some other equation than the allometric one - Equation (1) - (e.g. Daborn, 1975). Such equations have the disadvantage that they lack any functional explanation. Additionally, there is no evidence that they fit the data better (<u>pace</u> Smith, 1980).

One advantage in setting out assumptions and predictions as rigorously, some would say as pedantically, as above, is that it helps one to notice implicit assumptions. Assumption 3 was that adult female body weight has evolved so as to maximize E_{rep} intraspecifically. E_{rep} is the energy females invest in reproduction per unit time. If lifetime reproductive success is more important for natural selection (Clutton-Brock, 1988), then Assumption 3 makes the implicit assumption that lifespan is independent of female size intraspecifically. Of course, if lifespan is related to body size intraspecifically (Partridge and Farquhar, 1981), then models can be produced (Reiss, 1989) to take this into account.

Interspecifically we can be more confident about the relationship between size and lifespan. Lifespan is allometrically related to body mass with an exponent of about 0.15 to 0.3 (Stahl, 1962; Blueweiss et al., 1978; Prinzinger, in press). Combining this relationship with the data in Table 1, it is evident that over the course of their lives, the energy females devote to reproduction scales interspecifically on body mass with an exponent close to 1.0 (Gordon, 1989; Reiss, 1989). One might expect this as lifetime energy intake and lifetime energy expenditure also scale on body mass with exponents of approximately 1.0 (Reiss, 1989; Jürgens and Prothero, in prep.).

In this paper I have mainly concentrated on allometric generalisations which apply to all species. Most of the predictions are independent of the phylogeny, ecology or taxonomic level of the taxa concerned. One exception to this is Prediction 3, which, within a species, relates the scaling in females of reproductive effort on size to the pattern of growth within females of the species. Another exception is the suggestion, just before Prediction 2, that in taxa which spend a lot of time hovering, the interspecific exponent relating the energy females invest in reproduction per unit time to their body mass should be steeper than in taxa where the constituent organisms do not hover. Some people find general allometric trends rather boring and prefer to investigate departures from these trends; others like the uniform trends, and enjoy extracting regularity from the scattered data obtained from a large number of species. Whichever one prefers, the general trends need to be established before the departures from the trends can be investigated.

It is worth stressing that the analogy between allometric rules and

Mendel's laws can be pushed too far. To some extent it is the case that while Mendel's laws define purely causal relationships, the rules of allometry are largely descriptive. Nevertheless, as argued above, allometry is becoming increasingly powerful as a tool capable of making precise and testable predictions. Furthermore, we do understand the reasons, again, as discussed above, for some of the fundamental allometrical relationships that are observed in nature. It should be remembered that at the time Mendel formulated his two laws, neither he nor anyone else had the slightest understanding of why they held. It may be that as our knowledge increases, the comparison of Mendel's laws and the rules of allometry will be seen to be a close and fair one.

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