

# Is rate of ontogenetic growth constrained by resource supply or tissue growth potential? A comment on West *et al.*'s model

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## Summary

1. West *et al.* (2001) describe a general model of ontogenetic growth in which growth represents the surplus of energy acquisition over maintenance energy requirement, which themselves are allometric (power) functions of body mass with exponents  $3/4$  and 1, respectively. Furthermore, the intercept of the maintenance requirement decreases with the  $-1/4$  power of adult mass.
2. These relationships determine the sigmoid shape of the postnatal growth curve and the  $3/4$  allometric slope of time to complete growth as a function of adult mass.
3. West *et al.*'s growth function is a particular form of the generalized Pütter growth model  $dm/dt = am^y - bm^z$ , which includes other familiar growth functions, such as the logistic and von Bertalanffy equations.
4. Empirical estimates of the allometry of resting metabolism in growing birds are close to  $z = 1$  in some precocial species, but are approximately 50% higher in altricial and semiprecocial birds, which challenges the generality of any single growth function for birds.
5. Rather than growth rate being limited by the difference between energy acquisition and maintenance expenditure, it may also be determined by the growth potential of tissues, which is traded off against functional capacity. Predicted growth curves based on increasing tissue function with age are indistinguishable from the West *et al.* and related equations.
6. Models based on growth rate–functional maturity trade-offs also can produce observed allometric relationships of growth rate to adult mass by incorporating the relative size of the chick at hatching.
7. In contrast to West *et al.*'s model, declining variance in size among individuals as chicks approach adult size implies targeted growth and control of growth rate by feedbacks of body size itself on growth rate.
8. The existence of plausible alternative hypotheses for the control of postnatal growth should stimulate additional experimental studies to elucidate mechanisms of growth rate regulation and to understand the evolutionary diversification of postnatal growth.

*Key-words:* Allometry, growth model, metabolizable energy, postnatal growth

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## Introduction

Geoffrey B. West and his co-authors James H. Brown & Brian J. Enquist (West, Brown & Enquist 2001) recently described a 'general model for ontogenetic growth' that 'provides the basis for deriving allometric relationships for growth rates and the timing of life history events.' Their model raises several issues about

factors that constrain growth and about the generality of any growth model. It also raises a concern about how growth models can be tested. In this paper, I describe general properties of growth models that balance acquisition and utilization of resources and address the way in which growth rate is limited. West *et al.* (2001) suggest that growth rate can be understood in terms of resource provisioning by central supply organs, including the alimentary tract and the circulatory and respiratory systems. Alternatively, I have suggested that growth rate reflects primarily the

potential of peripheral tissues for cell proliferation and growth, which is traded off against functional maturity (Ricklefs 1969, 1979; Ricklefs *et al.* 1998). Models based on both types of premise produce indistinguishable descriptions of growth and fit observed data well, making it difficult to reject any particular model of growth by curve fitting. Beyond the fundamental issue of supply *vs* demand shaping the resource budgets of growing animals, West *et al.* (2001) also assert from theory that the allometric exponents of energy supply and demand are  $3/4$  and 1, respectively. The general validity of these assumptions is challenged by empirical data.

### West *et al.*'s model

West *et al.*'s model is a form of the von Bertalanffy growth function (von Bertalanffy 1938, 1957) in which growth is equal to income minus maintenance expenditure. Specifically, the rate of increase in mass ( $m$ ) is equal to the rate of acquisition of nutrients and energy by the growing individual minus the maintenance requirement of accumulated tissue, with appropriate coefficients for converting inputs to body mass. West *et al.* claimed that their growth model is built on 'basic cellular properties', but the assumptions attributed to cell properties seem no different to me than von Bertalanffy's assumptions about whole organisms, except that cell number replaces organism mass. The additional assumption of a  $3/4$  scaling exponent for energy acquisition with respect to mass is carried over from an independently developed model relating energy metabolism to mass through limitation of energy delivery to tissues (West *et al.* 1997, 2002). A less transparent, and more important, assumption of the West *et al.* model is that growth is supply driven. Thus, growth ( $P$ ) reflects the surplus left over after energy requirements of tissues ( $R$ ) are subtracted from energy acquisition (metabolizable energy,  $ME$ ), which is constrained by the organism system itself. Thus, the West *et al.* model may be characterized as  $P = ME - R$ .

As descriptions of growth, the von Bertalanffy and related equations do not distinguish whether growth rate is determined by the acquisition of resources for growth or by the resource demands of tissues whose growth rate is optimized with respect to other considerations. However, a simple balance equation describing the allocation of energy and nutrients during development becomes a model of growth when the input and output functions are specified as fundamental attributes of the individual or its cells. Von Bertalanffy assumed that tissue maintenance would be proportional to mass but that nutrient provisioning would follow a surface rule and increase with the  $2/3$  power of mass.

In most plants, invertebrates and ectothermic vertebrates, growth accounts for a large portion of an individual's nutrient and energy budget and the rate of growth varies flexibly in relation to environmentally

determined resource acquisition (Calow & Townsend 1981; Sibly & Calow 1987; Kooijman 1993). Von Bertalanffy assumed that food acquisition was principally limited by properties of the organism and consequently that growth rate was a feature of organism design. West *et al.* (2001) also adopt this position. In the case of endotherms, particularly precocial birds, growth comprises a relatively small part of the overall food requirement (Ricklefs 1974; Dunn 1980) and while growth rate varies considerably among species it is less variable within species (Ricklefs 1968; Case 1978). Although this implies that growth rate is primarily an intrinsic property of the organism, growth rate may be determined by factors other than the difference between intake and tissue maintenance requirement. For example, Ricklefs (1969, 1979) suggested that individual birds grow at a rate constrained by the functional maturity of their tissues, and that food acquisition is adjusted to meet the demand of the growing tissues. Supply and demand-based models fit relationships between mass and age equally well, and so distinguishing between them, or partitioning their relative influence on growth rate, will probably require alternative, preferably experimental approaches.

In West *et al.*'s model, food acquisition scales to the  $3/4$  power of body mass ( $m$ ) rather than von Bertalanffy's  $2/3$  power, while the cost of maintaining tissue is directly proportional to body mass throughout the growth period. Thus, the rate of change in body mass, that is, the rate of growth, is

$$dm/dt = am^{3/4} - bm. \quad \text{eqn 1}$$

This is West *et al.*'s equation 3. To balance equation 1 above,  $a$  must have units of mass<sup>1/4</sup>/time and  $b$  units of mass<sup>0</sup>/time (1/time). The mass at which income equals expenditure is the asymptotic mass ( $M$ ) of the individual, specifically the mass at which  $aM^{3/4} = bM$ , or  $M = (a/b)^4$ . Because asymptotic mass varies among species,  $a$  and/or  $b$  also must vary. West *et al.* state that  $a$  – the coefficient, or intercept, related to intake – is independent of asymptotic mass, based on empirical evidence. Therefore,  $b$  must scale to the  $-1/4$  power of asymptotic mass. Because  $b$  also is the exponential rate of approach of mass to the asymptote, growth rate scales as the  $-1/4$  power of  $M$  and time taken to complete a particular segment of the growth curve scales as  $M^{1/4}$ .

West *et al.* fitted the sigmoid growth curve corresponding to equation 1 to a variety of species. The fact that the equation fit most growth curves well was offered as support for the generality of the model. To emphasize this generality, the authors constructed a graph having dimensionless mass and time axes, which are the proportion of the asymptote attained and the age scaled by the growth rate  $a$ , on which growth data for all species appear to be superimposed. This device is similar to Brody's (1945) 'physiological time' scale (see Carrel 1931) and Ricklefs's (1967, 1983) 'growth

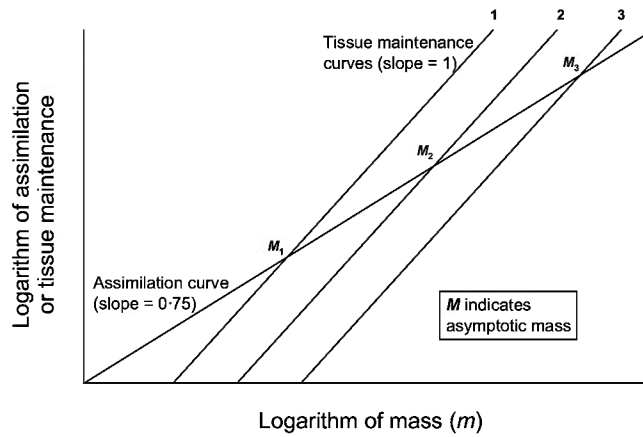


Fig. 1. Predicted asymptotic mass ( $M$ ) when energy acquisition (assimilation, metabolisable energy) increases as the  $3/4$  power of body mass ( $m$ ) during development, which relationship is shared by all species, and tissue maintenance requirements increase in direct proportion to mass but with variation in the intercept among species. In this example, the coefficient ( $b$ ) of the tissue maintenance curve, indicated by the intercept on the vertical axis [ $\log(m) = 0$ ] decreases as the  $-1/4$  power of asymptotic mass between species 1, 2 and 3.

index', previously used to make mass growth curves coincident. West *et al.* did not compare the fits of their growth equation with those of other models. As Banavar *et al.* (2002) point out, and West *et al.* (2002) agree, it is not possible to distinguish among models on the basis of how well they fit data, as many models with different allometric exponents provide adequate empirical description of the data.

West *et al.* provide insights into several important issues concerned with growth rates, including the distinction between determinate and indeterminate growth and the allocation of resources between growth and reproduction in the case of indeterminate growth. However, their analysis also raises a number of issues that were not discussed by the authors but bear critically on one's concept of growth and, indeed, most physiological function. It is important to determine what result would falsify West *et al.*'s model as a general description of the growth process applicable to all types of animals. For example, if the  $3/4$  scaling exponent were not universally applicable, would this mean that certain assumptions or empirically determined constants need modification, or that the model should be rejected outright? How does the West *et al.* model compare with other models for growth, and how can one distinguish between them? How can one assess the assumptions of West *et al.*'s model directly? I cannot answer these questions definitively here. However, a closer consideration of postnatal growth in birds – the only group with which I have worked – brings these questions into focus and emphasizes the important role that postnatal growth can play in understanding the evolutionary diversification of organism performance more generally.

### The $3/4$ scaling exponent

West *et al.*'s model has two aspects, which can be treated independently. The first is the general property

that growth is determined by the difference between resource supply and maintenance resource requirement, hence that growth rate is constrained by delivery of resources to the tissues. This is the more important issue, but I shall defer it until after considering the second point, which concerns the particular allometric relationships between acquisition, requirement and mass, both ontogenetically within species and phylogenetically among species. West *et al.* assumed a  $3/4$  power relationship between resource acquisition and mass within species, based primarily on theoretical considerations and supported by empirical observations across species (Dawson 2001; but see Hayssen & Lacy 1985; Kozłowski & Weiner 1997; West *et al.* 1997). They also assumed a direct proportionality (power of 1) between tissue maintenance requirement and mass. As mentioned earlier, the intercepts of these relationships are assumed to be independent of adult body mass among species in the case of resource supply ( $a$ ), and to vary as the  $-1/4$  power of adult body mass in the case of tissue maintenance ( $b$ ). These relationships are illustrated in Fig. 1, in which three species share a common provisioning line but have displaced tissue maintenance lines. This results in different asymptotic masses, that is, the masses at which requirements equal intake.

Growth and maintenance metabolism cannot be separated easily in growing animals because a part of the measured energy expenditure is the cost of biosynthesis, which properly belongs with growth (Ricklefs 1974; Blaxter 1989). The metabolic cost of tissue maintenance can be estimated by subtracting from RMR the cost of biosynthesis, which Ricklefs (1974) estimated from studies on animal production to be about one-third the energy accumulated in growing tissues (see also, Konarzewski 1995; Ricklefs *et al.* 1998). When this is done, the ontogenetic relationship between tissue maintenance requirement and mass varies among birds, having an allometric constant

**Table 1.** The allometric scaling exponent for the relationship of maintenance metabolism to body mass when the cost of biosynthesis is assumed to be 0.2, 0.3, or 0.4 times the energy accumulated in tissues. Analyses are provided for sparrows, terns (data courtesy of M. Klaassen) and galliforms (data courtesy of M. Dietz)

	Mode of development	Cost of biosynthesis		
		0.2	0.3	0.4
Sparrows <sup>a</sup>	Altricial	1.41 ± 0.04	1.51 ± 0.05	1.63 ± 0.07
Terns ( <i>Sterna</i> spp.) <sup>b</sup>	Semiprecocial	1.44 ± 0.04	1.53 ± 0.05	1.65 ± 0.06
Turkey and Guinea Fowl <sup>c</sup>	Precocial	0.92 ± 0.03	0.97 ± 0.05	1.06 ± 0.08

<sup>a</sup>Based on data from the Chipping Sparrow (*Spizella passerina*) for metabolism (Dawson & Evans 1957) and the Rufous-Winged Sparrow (*Aimophila carpalis*) for growth (Austin & Ricklefs 1977).

<sup>b</sup>Combined data for the Common, Arctic and Antarctic Terns (*Sterna hirundo*, *S. paradisea* and *S. vittata*). Maintenance metabolism estimated for 68 chicks weighing less than 100 g (species asymptotes 107, 114 and 133 g), using average growth data and increase in energy density of tissues with age (Klaassen 1994). Allometric constants for the three species did not differ by analysis of covariance.

<sup>c</sup>Combined data for Domestic Turkey (*Meleagris gallopavo*) and Guinea Fowl (*Numida meleagris*), based on 15 increments in measured tissue energy contents between age classes and averaged measurements of RMR for those age classes (Dietz 1995). Allometric constants did not differ between the two species.

close to 1 (the value assumed by West *et al.*) in species with precocial development but a higher value in species with semiprecocial and altricial development (Table 1). At least in the case of birds, the evidence for a single allometric scaling exponent of either energy acquisition or maintenance metabolism with body mass during ontogeny is not compelling.

West *et al.* (2001) drew empirical data on resting metabolic rates (RMR) of birds from Weathers & Siegel's (1995) compilation of allometric constants relating RMR (comprising tissue maintenance plus an undetermined portion of tissue growth) to body mass during development. West *et al.* recognized that the allometric constants varied, for example averaging  $1.10 \pm 0.36$  SD for species with altricial development ( $n = 10$ ), and argued that the relatively high allometric slope is related to the increasing functional maturity – the 'proportion of metabolically active mass' – of the individual during the growth period, which is accompanied by an increase in the dry fraction of tissues (Ricklefs 1974; Visser & Ricklefs 1993). When Weathers & Siegel (1995) compared RMR to dry mass in the Yellow-Eyed Junco (*Junco phaeonotus*), the scaling exponent for this species changed from 1.67, based on wet mass, to  $0.71 \pm 0.11$ . The latter value did not differ significantly from  $3/4$ . Nonetheless, if one accepts this 'correction' for tissue water content, one should also describe growth based on dry rather than wet mass. Moreover, the same correction should apply to other species, which among altricial birds had scaling exponents relating RMR to wet mass varying between 1.67 and 0.91. Clearly these relationships are complex and a single growth function is unlikely to capture the observable variation in growth patterns.

#### A SPECTRUM OF GROWTH MODELS

The fit of a particular growth model to data does not confirm the underlying processes embedded in the model. Nor do deviations from a model necessarily

invalidate it. Irrespective of the mechanisms of growth, however, we may ask whether a particular equation, such as that of West *et al.* provides a good empirical description of growth. Ricklefs (1968) used three different functions to fit the growth curves of species of birds: the logistic, Gompertz and von Bertalanffy. The latter, like the function of West *et al.* is a form of the Pütter equation (Pütter 1920). Variations in the Pütter equation are summarized in Table 2, which also lists the asymptote ( $M$ ) and the inflection point ( $I$ , size at maximum growth rate) for each equation.

The growth curves of most species of bird are fitted best by the logistic equation ( $y = 1$ ,  $z = 2$ ), although many precocial species conform more closely to the Gompertz function ( $y, z \rightarrow 1$ ), and a small number of species, primarily slowly growing pelagic seabirds and raptorial birds, more closely resemble the von Bertalanffy function ( $y = 2/3$ ,  $z = 1$ ; Ricklefs 1968). West *et al.*'s equation lies between the Gompertz and von Bertalanffy models. Most growth curves of mammals are fitted best by either logistic or von Bertalanffy equations, suggesting a bimodal distribution of growth curve shapes (Zullinger *et al.* 1984). The different functions that apply to the growth curves of different species are consistent with variation among species in the scaling exponents for resource provisioning and tissue maintenance (see Table 1). Part of this variation may result from different proportions of metabolically active tissue and different types of tissue accumulated during development, particularly the amount of lipid stored. Evaluating and interpreting the scaling exponents of the Pütter equation adequately will require direct measurements of these variables.

#### ALLOMETRIC SCALING OF GROWTH RATE

Consistent with the variation in the scaling exponents for metabolism, the allometric relationship between growth rate and asymptotic body mass varies widely among taxonomic groups, although the functional

**Table 2.** Coefficients of the Pütter equation define the shape of the growth curve, indicated by the inflection point as a fraction of the asymptote

Model	$dm/dt$	Asymptote ( $M$ )	Inflection ( $I/M$ )	Maximum ( $dm/dt/M$ )
Pütter	$am^y - bm^z$	$(alb)^{1/(z-y)}$	$(y/z)^{1/(z-y)}$	$aI^y - bI^z$
	$am - bm^4$	$(alb)^{1/3}$	$(1/4)^{1/3} = 0.630$	$0.473a$
	$am - bm^3$	$(alb)^{1/2}$	$(1/3)^{1/2} = 0.577$	$0.385a$
Logistic	$am - bm^2$	$alb$	$(1/2)^1 = 0.500$	$0.250a$
	$am - bm^{3/2}$	$(alb)^2$	$(2/3)^2 = 0.444$	$0.148a$
	$am - bm^{4/3}$	$(alb)^3$	$(3/4)^3 = 0.422$	$0.106a$
Gompertz ( $y, z \rightarrow 1$ )	$am - bm \ln(m)$	$\exp(alb)$	$1/e = 0.368$	$0.368b \exp(alb)$
West <i>et al.</i>	$am^{3/4} - bm$	$(alb)^4$	$(3/4)^4 = 0.316$	$0.106b$
Von Bertalanffy	$am^{2/3} - bm$	$(alb)^3$	$(2/3)^3 = 0.296$	$0.148b$
	$am^{1/2} - bm$	$(alb)^2$	$(1/2)^2 = 0.250$	$0.250b$
	$am^{1/3} - bm$	$(alb)^{3/2}$	$(1/3)^{3/2} = 0.193$	$0.385b$
	$am^{1/4} - bm$	$(alb)^{4/3}$	$(1/4)^{4/3} = 0.158$	$0.473b$

relationship between the two has not been firmly established. Starck & Ricklefs (1998b) analysed growth rates for 557 species of birds representing all the major orders. Growth rate constants were obtained from fits of logistic equations, or of Gompertz equations with a suitable conversion factor determined in relation to the maximum growth rate (Table 2; see Ricklefs 1968). The value of the allometric constant for all species depends on the way in which phylogenetic relationships among species are handled (Felsenstein 1985; Harvey & Pagel 1991). When species values are used without regard to phylogenetic relationship, the logarithmic regression of growth rate on body mass has an allometric constant of  $-0.32 (\pm 0.01 \text{ SE})$ . Non-standardized phylogenetic independent contrasts (PICs) (Garland *et al.* 1992, 1999) yield a slope of  $-0.25 (0.02)$ ; standardization by branch lengths reduces this slightly to  $-0.22 (0.03)$ . Thus, contrasts conform well to the prediction of West *et al.* of a  $-1/4$  allometric relationship between growth rate and body mass.

A hierarchical analysis of variance (Derrickson & Ricklefs 1988; Bell 1989; Ricklefs & Nealen 1998) of growth rates in birds based on taxonomic categories of Sibley & Ahlquist (1990) shows that the  $-1/4$  allometric constant applies to variation close to the tips of the phylogenetic tree (i.e. species within genera  $[-0.25]$ , and genera within families  $[-0.25]$ ), but that the slope of families is shallower ( $-0.18$ ) and the slope among orders is much steeper ( $-0.39$ ) (Starck & Ricklefs 1998b). The between-order relationship reflects the early diversification of modern birds, during which shifts in body mass were probably associated with major changes in ecological relationships and life histories, accompanied by changes in the mode of development. Indeed, most of the variation in mode of development (i.e. altricial *vs* precocial) resides at a high taxonomic (ordinal) level in birds (Starck & Ricklefs 1998a). Within-family variation in growth rate reflects variation in body mass without significant modification of the relationship between growth and development. This variation conforms closely to the allometric relationships expected from the West *et al.* assumption of  $3/4$  scaling.

Allometric slopes within orders of birds vary considerably, however, with songbirds (Passeriformes, slope =  $-0.16$ ), swifts (Apodiformes,  $-0.16$ ), parrots (Psittaciformes,  $-0.18$ ), shorebirds (Charadriiformes,  $-0.12$ ) and ducks (Anseriformes,  $-0.16$ ) having low values, and penguins (Sphenisciformes,  $-0.32$ ) and hawks (Falconiformes,  $-0.44$ ) exhibiting high values. As yet, we do not know how these allometric slopes are related to the allometries of tissue maintenance and energy provisioning, or whether they are influenced by subtle variation in the pattern of development.

**Growth rate: limitation by resource supply or tissue growth potential?**

A more fundamental issue raised by the model of West *et al.* is whether the energy allocated to growth ( $P$ ) is limited by the provisioning of resources to the tissues (acquisition, or supply) or by constraints inherent to the tissues themselves and related to their performance (growth potential). From the first perspective,  $P = \text{metabolizable energy (ME)} - \text{maintenance (R)}$ , and  $ME$  is constrained by design limits of the organism. In this case,  $R$  and  $P$  would be negatively related. Alternatively,  $ME$  is the sum of growth and requirements, which are unconstrained with respect to each other. Thus,  $ME = R + P$ , and the relationship between  $R$  and  $P$  could be positive or negative, but would not reflect a direct trade-off caused by allocation of limited resources. To the extent that the biosynthetic requirements of growth and the metabolic requirements of tissues needed to support growth contribute to metabolizable energy,  $R$  and  $P$  would be positively related. From studies of hatchling birds, Klaassen & Drent (1991) determined that metabolizable energy and growth rate were positively correlated and they concluded that rapid growth required the hypertrophy of organs of nutrient and energy supply. In contrast, Konarzewski (1995) subtracted the cost of biosynthesis from resting metabolism in growing birds and determined that  $R$  and  $P$  were negatively related, implying a trade-off between growth and other functions in energy-constrained chicks.

West *et al.*'s model implicitly assumes that provisioning is limited by the capacity of the organism to assimilate and distribute nutrients and energy to the tissues, which is limited centrally by the design of the circulatory system (but see West *et al.* 1997; Dodds *et al.* 2001). These design aspects of an organism's delivery systems also establish the  $3/4$  allometric scaling of growth rate to body mass, in their view. An alternative to this supply-based perspective was proposed by Ricklefs (1969, 1979), who suggested that growth rate in birds is inversely related to the functional maturity of tissues and is therefore constrained peripherally by the growing tissues themselves. Because tissues develop increasing functional capacity through development, this model predicts that the exponential growth rate of tissues should decrease continuously through development, as does West *et al.*'s model. Furthermore, at any particular mass relative to asymptotic mass, growth rate should be inversely related to functional capacity. Thus, precocial species should grow more slowly than altricial species, which is born out by comparative analysis (Ricklefs 1973, 1979; Starck & Ricklefs 1998b).

When the exponential growth rate of an individual organism or organ [ $1/m \cdot dm/dt$  or, equivalently,  $d \log(m)/dt$ ] decreases linearly with functional maturity, and functional maturity increases linearly with the logarithm of mass, the resulting form of the growth curve is that of a Gompertz function (Ricklefs *et al.* 1994). When functional maturity increases linearly with mass, rather than the log of mass, a logistic growth function results. In a comparative study by Choi *et al.* (1993), an index of functional capacity of skeletal muscle, based on dry matter fraction and pyruvate kinase activity, was negatively related to the exponential growth rate of muscle in a species of quail *Coturnix coturnix* (precocial) and the European Starling *Sturnus vulgaris* (altricial). The coefficients of the relationship did not differ between the species in spite of considerable displacement in the timing of increase in muscle function. Thus, the difference in the maturity index between the quail and the starling at a particular proportion of asymptotic size was reflected in the growth rate of muscle tissue. The index of functional capacity increased as a function of the logarithm of mass, consistent with a Gompertz function. Further analyses by Shea *et al.* (1995) showed that quail selected for rapid growth exhibited delayed the maturation of skeletal muscles. Comparisons of two species of shorebird, the rapidly growing Dunlin (*Calidris alpina*) and the more slowly growing Whimbrel (*Numenius phaeopus*), show a similar relationship between maturity and growth rate in the muscles of the legs (Krijgsveld *et al.* 2001).

The issue of central (supply) vs peripheral (demand) control over organism function has been developed in contexts other than growth and has been a major theme in comparative physiology and physiological ecology. The predominant view, that organism function

is limited by food processing, developed from simple correlations of organism metabolism with body mass (Drent & Daan 1980; Kirkwood 1983; Kirkwood & Webster 1984). These authors believed that gut function imposes a metabolic ceiling that limits the performance of the organism, whether metabolism, reproduction or growth (Lilja 1983; Diamond & Hammond 1992). Supply limitation by the design of the circulatory system (West *et al.* 1997) imposes a similar limit to organism function. The discovery that supply and demand are closely correlated (the principle of symmorphosis; Weibel *et al.* 1991, 1998) was sometimes interpreted to mean that supply controls organism performance (Richardson *et al.* 2000), although the message should be that organisms minimize excess capacity regardless of where performance is controlled in the chain leading from supply to demand. Experimental studies that have manipulated peripheral demand, for example, by increasing cold stress or number of offspring in mice, have shown that the digestive system is responsive to demands placed by peripheral organs, which ultimately limit organism performance (Hammond *et al.* 1994, 1996). To increase food processing is costly in terms of the allocation of tissue and maintenance requirements. However, through a wide range of supply rate these costs must be small compared to the benefits of increased performance of peripheral organs (Obst & Diamond 1992).

Experiments on growth rate are of two kinds: force-feeding and selection of growth rate. In chicks of the domestic fowl, overfeeding (force-feeding) leads to an increase in the size and processing rate of the gut, and an increase in accumulated fat, but no increase in the rate of somatic growth (Nir *et al.* 1974, 1978). Thus, as in many studies (e.g. Secor & Diamond 1995, 1998), digestive function is responsive to rate of food intake as well as peripheral demand, indicating that maintenance of unneeded capacity is costly. Such experiments do not fully test supply vs demand hypotheses, however, because if the performance level (i.e. growth rate) of peripheral organs were genetically fixed, one would not expect to observe a response in demand-based or supply-based experiments.

Meat-producing lines of domestic fowl (*Gallus*) and quail (*Coturnix*) have been selected for large body size at a particular age, which causes an increase in asymptotic mass and, to a lesser extent, rate of growth (Visser 1991). In quail selected for high body mass, the size of the brain remains unchanged, in spite of a more than two-fold increase in total mass (Ricklefs & Marks 1984), mass growth rate increases slightly (Marks 1978), the functional maturity of the leg muscles decreases (Shea *et al.* 1995) and the size of the digestive organs increases (Lilja *et al.* 1985). Similar patterns have been found in the domestic fowl (Konarzewski *et al.* 2000). These responses are consistent with a trade-off between growth rate and function in peripheral organs, in this case skeletal muscle, and with the capacity of the digestive system to respond to the

demands of growing tissues. If supply itself limited organism growth rate, one would not have expected a decrease in the functional maturity of skeletal muscle, which presumably would have negative fitness consequences for precocial birds outside domestication.

#### OPTIMIZATION OF GROWTH RATE

West *et al.* considered growth in the absence of its environmental context. Their model is based narrowly on the structure of the digestive and circulatory systems and the maintenance requirements of tissues. Environmental factors, such as predation, food supply and sibling competition, clearly exert strong selective pressures on the rate of growth and pattern of development (Ricklefs 1984, 1993; Sibly & Calow 1987; Perrin & Sibly 1993; Perrin *et al.* 1993; Kozłowski & Weiner 1997; Konarzewski *et al.* 1998). Comparative and physiological studies on birds indicate that functional maturity sets an upper physiological (tissue-level) limit to growth rate, but that within this constraint predation or sibling competition can influence both growth rate and the development of functional maturity (Konarzewski *et al.* 1998). This gives rise to variation in allometric scaling of growth rate and metabolism to body mass, which in turn influences both the rate of growth and the shape of the growth curve.

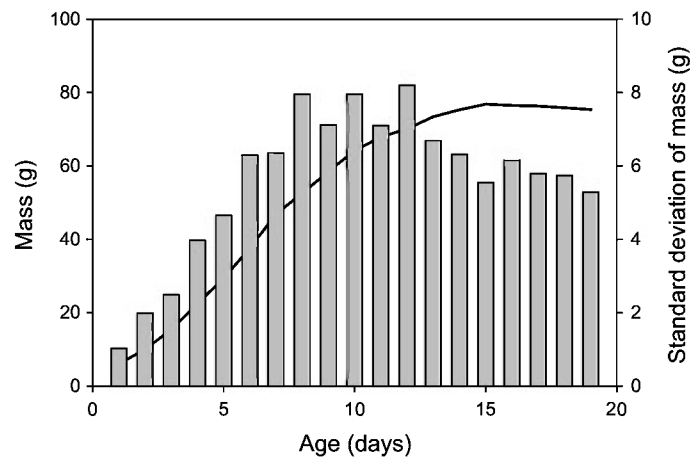
Does the  $3/4$  scaling observed *on average* within families of birds validate the West *et al.* model, or could it derive from other scaling factors, perhaps related to the pattern of acquisition of mature function by birds of different size? Consider the following simple model. Larger birds hatch at a smaller proportion of asymptotic size than do smaller birds. Suppose that the exponential growth rate declines linearly as the logarithm of mass approaches the asymptote and that the growth rate at hatching is constant, reflecting similar functional maturity. Further suppose that the ratio of hatching to asymptotic mass scales as the  $-h$  power of the asymptote. According to this model, absolute growth rate would scale as the  $1-h$  power of the asymptote and relative growth rate ( $a$  or  $b$ ; see Table 2) would scale as the  $-h$  power of the asymptote. In birds, hatching mass scales as approximately the  $2/3$  power of asymptotic mass within orders of birds ( $0.654 \pm 0.010$  SE, Ricklefs & Starck 1998a), which would make growth rate scale as the  $-1/3$  power of asymptotic mass. Based on a function-growth rate tradeoff, a  $-1/4$  scaling exponent would require hatchlings of larger species to possess less functional capacity in constraining tissues than smaller species, which apparently is the case in some orders of birds (Dietz & Ricklefs 1997; Ricklefs & Starck 1998b; Krijgsveld *et al.* 2001). Thus, the observed allometric scaling of growth rate in birds can be derived from a model having a different premise than that of West *et al.*, namely a tissue-level trade-off between growth rate and mature function that represents incompatibility between alternative cellular processes.

#### TARGETED GROWTH

West *et al.* claim that their model provides 'a fundamental explanation for the origin of determinate growth in which an asymptotic body size ( $M$ ) is reached.' This is caused by the 'imbalance' in the scaling exponents for supply and demand, which 'ultimately limits growth'. In this case, adult body size is determined by the initial values and scaling exponents of energy supply and demand. Thus, the growth curve would follow a trajectory determined by the initial conditions of the system. Alternatively, the idea of targeted growth suggests that adult body size is selected and the growth process homes in on the selected asymptote, compensating for deviations based on initial conditions and environmentally imposed variation in the growth trajectory. One prediction of the trajectory model is that variation in the parameters  $a$  and  $b$  would lead to increasing variance in mass throughout development, up to and including adult size. The target hypothesis implies compensatory growth (Schew & Ricklefs 1998) and a reduction of the variance as adult size is reached. Data for the European Starling presented in Fig. 2 are typical of birds and show a pattern of increasing variation in mass among individuals early in development, reflecting variation in growth rate, followed by decreasing variation as growth approaches a targeted asymptote. Thus, growth rate during at least the late developmental period is controlled by mechanisms beyond the discrepancy between simple intake and maintenance functions.

#### Conclusions

The different scaling exponents relating metabolism to body mass and the existence of plausible alternative models for the allometric scaling of growth rate to adult body mass suggest that it is premature to proclaim a general model for postnatal growth. Clearly, both the supplying of nutrients through the digestive and circulatory systems and demand for nutrients by peripheral tissues operate as constraints throughout development. Decreasing variance in mass towards the end of the growth period indicates the presence of internal feedbacks on the growth process and a more complex mechanism for determining growth rate than the model proposed by West *et al.* (2001). Different scaling exponents relating growth to adult mass in different taxonomic groups and within different levels of the taxonomic hierarchy contrast with the general  $3/4$  power relationship observed over a large range of organisms. This suggests that both general and taxon-specific processes must be incorporated into any general theory of postnatal growth and development. Finally, growth rate is optimized with respect to selective factors in the environment and within constraints imposed by the design of the organism and its tissues. Thus, a fuller understanding of the control of growth and its variation among taxa will depend upon estimates



**Fig. 2.** Solid line: average body mass of first-brood nestling starlings in a nest-box colony at the Stroud Water Research Laboratory, south-eastern Pennsylvania & in 1976 ( $n = 63\text{--}112$ ). Vertical bars: standard deviation among individuals of the mass at each age. Day 1 refers to measurements within 24 h of hatching. From unpublished data of R. E. Ricklefs (see Ricklefs & Peters 1979, 1981).

of physiological constraints and measurement of the costs and benefits of variation in growth parameters within these constraints.

The search for understanding must navigate a narrow path between the desire to have general laws and the empirical reality of complex nature. I have emphasized the complexities of postnatal growth in birds and focused on an alternative to West *et al.*'s model having different premises. I have no illusion that a growth rate–function trade-off controls patterns of growth variation beyond birds, and I do not doubt that other options may be important in other groups of organisms. However, I do doubt that the simple model presented by West *et al.* (2001) captures the essential features of variation in growth rate among species, and I suspect that central control by resource provisioning plays a relatively minor role in constraining growth rate in birds. Nonetheless, regardless of the mechanisms that influence growth rate, we cannot escape the pervasive relationship between size and rate that governs life processes. Whether this relationship operates over all of life through a single process, as West *et al.* believe, or whether it imposes a general, unifying constraint on a wide variety of limiting processes and relationships remains to be seen.

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