

Metabolic costs of growth in free-living Garter Snakes and the energy budgets of ectotherms

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Summary

1. The metabolic or respiratory cost of growth (R_G) is the increase in metabolic rate of a growing animal, and it represents chemical potential energy expended in support of net biosynthesis but not deposited as new tissue.
2. Two statistical methods (multiple non-linear regression and analysis of regression residuals) were used to calculate R_G from data ($n = 68$) from a doubly labelled water study of free-ranging Garter Snakes (*Thamnophis sirtalis fitchi*) in northern California.
3. The sample-wise ('ecological') cost of growth was 2.07 kJ per gram of net growth (equivalent to 8.63 kJ g⁻¹ dry tissue); reanalysis of a subset of efficient growers yielded a more conservative 'physiological' estimate of 1.67 kJ g⁻¹.
4. Our empirical estimate of R_G , among the first reported for squamate reptiles and free-living animals of any kind, compares closely with published, laboratory-derived values for ectotherms.
5. The metabolic costs of growth accounted for an average of 30% of total field metabolic rates for these snakes, which were growing at a mean rate of 3% of body mass per day. However, our method probably underestimated the total ecological cost of growth for large animals, because potential growth costs that covary with body size were not included.
6. Distinction between conceptual and empirical energy budgets clarifies relationships among body size, metabolic rates, and the physiological and ecological costs of growth.

Key-words: Ecological energetics, field metabolic rate, protein synthesis, *Thamnophis sirtalis*

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Introduction

Animals grow, and growth requires chemical potential energy. In addition to the energy actually deposited as the chemical constituents of new tissue, growth processes also require an obligatory expenditure of energy to fuel the anabolic biochemical reactions of biosynthesis. For example, deposition of new protein requires both a supply of amino acids and sufficient ATP for the formation of peptide bonds (Haselkorn & Rothmans-Denes 1973; Aoyagi *et al.* 1988); additional energy from ATP is required for other physiological processes inherent to growth (e.g. RNA transcription, mitosis, and lipid metabolism and biosynthesis, as well as the ingestion, digestion and absorption of the molecular components of new tissue). Such use of ATP to fuel growth is manifested as increased heat production and oxygen consumption of a growing animal, a quantity which is known as the metabolic or respiratory cost of growth (Millward,

Garlick & Reeds 1976; Parry 1983; Jorgensen 1988; Wieser 1994).

This metabolic cost of growth (R_G), though variously defined, is a concept that has long been familiar to animal scientists, aquaculturists and fisheries scientists because of its direct relationship to the efficiency of production, and therefore to net economic profit. For example, the concept appears in Brody (1945, p. 2), as 'Organizational energy or the energy expended for the "work" of growth and morphogenesis', and, according to the interpretation of Wieser (1994), it is implicit in the growth coefficient K_3 of Ivlev (1945). Physiological, theoretical and historical aspects of the concept (including important contributions from microbiology) have been reviewed recently by Wieser (1994). However, R_G is rarely discussed in the ecological literature. With few exceptions (e.g. Ricklefs 1974; Vleck, Vleck & Hoyt 1980; Drent, Klaasen & Zwaan 1992; Weathers 1996), R_G is usually ignored in studies of autecological energetics, despite theory

suggesting that it may be a very important component of an organism's total energy budget, particularly for ectotherms (Parry 1983).

We have taken advantage of a unique data set (comprising field metabolic rates for a large sample of rapidly growing individuals) to calculate the metabolic cost of growth in free-ranging Garter Snakes. Ours are among the first data for R_G in terrestrial ectotherms, as well as for the 'ecological R_G ' under natural, free-ranging conditions for any animal. We report that R_G accounts for 30% of total field metabolism in these snakes, and discuss implications of this finding for the construction, partitioning and interpretation of ecological energy budgets.

Materials and methods

DATA

In this paper, data (Fig. 1) that have been reported previously in detail (Peterson, Walton & Bennett 1998) are reanalysed. Briefly, the doubly labelled water

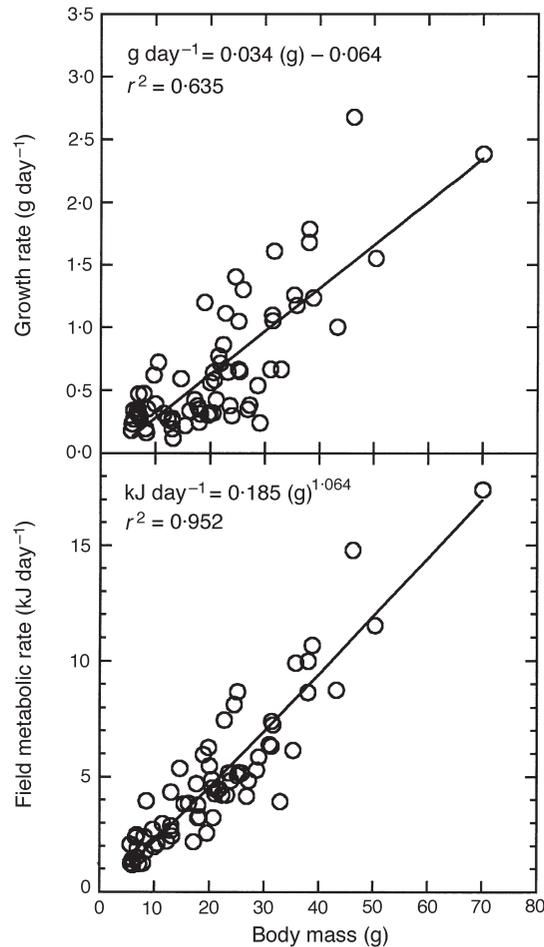


Fig. 1. Relationships of (top) growth rate in mass and (bottom) field metabolic rate (measured with doubly labelled water) to body mass in a northern California population of Garter Snakes (*Thamnophis sirtalis*) in July 1992 (Peterson *et al.* 1998). Lines are the least-squares linear regression (growth rate) and non-linear allometric regression (field metabolic rate) from which mass residuals were calculated.

method (Nagy 1983a, 1989) was used to measure field metabolic rates (FMR) and growth in body mass simultaneously in a large sample ($n = 68$) of juvenile and non-reproductive adult Garter Snakes (*Thamnophis sirtalis fitchi*) from a population near Eagle Lake in Lassen County, California. (Four values have been eliminated from the original data set: two obvious outliers with anomalously high FMRs and two for snakes that lost body mass during the FMR measurement period. Estimates of the cost of growth are altered by only 6% by exclusion of these data.) Body mass was measured in each individual at the beginning and end of the FMR measurement period, which averaged 12.5 days (range 8–18 days). Several lines of evidence suggest that the increases in body mass observed (average 3% day⁻¹) reflected bona fide lean tissue growth, as opposed to fat storage or increase in stomach contents (e.g. no food was palpable on recapture, and growth in length was significantly correlated to increase in mass; see Peterson *et al.* 1998 for details).

FMR, in units of ml CO₂ day⁻¹, was converted to energy equivalents by multiplication by 25.8 J ml⁻¹ CO₂ (Nagy 1983a). Snake tissue was assumed to contain 0.76 ml H₂O g⁻¹ (Peterson *et al.* 1998) and 22.8 kJ g⁻¹ dry matter (Reichenbach & Dalrymple 1986).

ANALYSIS

Animal scientists conventionally view a non-reproductive animal's metabolic rate as partitioned between costs of growth and costs of maintenance, with maintenance defined as a condition of energy balance or no change in body mass. Growth costs therefore can be calculated by subtraction of the energy requirement for maintenance (assumed to be constant and independent of growth rate) from the total metabolic rate (Brody 1945; Kleiber 1961; Blaxter 1989). The difficulty with this approach lies in the measurement or estimation of maintenance costs in growing animals, particularly if study animals vary in body size (Millward *et al.* 1976; Jorgensen 1988; Blaxter 1989). Because of the additional complexity of field metabolic rates (as opposed to controlled balance trials; see Kam & Degen 1997) and the wide range of body sizes in our sample (5–70 g), this method could not be applied to our field data.

Instead, the 'specific net cost of growth' (Wieser 1994) was calculated, the energy expended per unit tissue synthesized (J g⁻¹). Regression of FMR on growth rate would be confounded by the strong correlation of both variables to body size. Therefore, we applied two techniques to remove the confounding influence of body mass and isolate the metabolic effects of growth alone:

1. Multiple nonlinear regression. This technique (suggested by David Vleck; see also Jobling 1985)

assumes that the metabolic cost of growth per gram new tissue is constant and independent of body size and growth rate, but that maintenance and activity costs are exponentially related to body mass. Variance in FMR was therefore partitioned into components related to body mass and to growth by stipulating the equation:

$$\text{FMR} = aM^b + cG, \quad \text{eqn 1}$$

where FMR is field metabolic rate in kJ day^{-1} , M is body mass in g, and G is growth rate in g day^{-1} . The iterative non-linear regression module of SYSTAT (Wilkinson 1989) was used to solve for a , b and c , with c representing the metabolic cost of growth in kJ g^{-1} .

2. Analysis of regression residuals. This technique, a modification of conventional methods for removing the confounding effects of body size on other variables (see Bennett 1987), is essentially equivalent mathematically to method 1 above, but facilitates graphic presentation and calculation of confidence intervals for the metabolic cost of growth. Mass residuals for each individual were calculated from the linear regression equation for growth rate on body mass and the non-linear allometric equation for FMR on body mass (Fig. 1). To preserve FMR in units of kJ day^{-1} , the linearized equation for log-transformed variables was not used, as is conventionally done. Upon regression of mass residuals of FMR against mass residuals of growth rate, the calculated slope (with confidence intervals) is interpretable as the metabolic cost of growth with units of kJ g^{-1} .

Results

The two methods gave very similar estimates for the cost of growth. Multiple non-linear regression yielded the following best fit to our prestipulated equation:

$$\text{FMR (kJ day}^{-1}\text{)} = 0.153M^{1.020} + 2.084G, \quad \text{eqn 2}$$

($n = 68$, $R^2 = 0.965$, corrected $R^2 = 0.879$), where M is body mass (g) and G is growth rate (g day^{-1}). The coefficient of growth rate is 2.084 kJ g^{-1} , which represents the metabolic cost of growth in terms of energy required to deposit 1 g of tissue (wet mass). Analysis of mass residuals (Fig. 2a) produced a least-squares regression slope of 2.061 ± 0.836 (95% CI) kJ g^{-1} ($n = 68$, $r^2 = 0.268$, $P < 0.01$).

Our analyses of the relationship between growth and metabolic rates in free-ranging Garter Snakes suggest a metabolic cost of growth of 2.07 kJ g^{-1} , which is equivalent to 8.63 kJ g^{-1} dry tissue. This estimate may be further refined by considering that field metabolic rate is a complex integration of the energy costs of everything an animal does, not just growth (Nagy 1987). Our analyses adjusted total variance in FMR only for body size and growth rate, and our estimates of the cost of growth therefore also incorporate an ecological component of FMR

(the additional costs of inefficient foraging and other activities, unquantified variation in body temperatures, etc.). In an attempt to identify a more conservative index of the *physiological* cost of growth per se, a subsample of our data was reanalysed for the most efficient growers (i.e. the most negative 'meta-residuals' in Fig. 2a; in other words, snakes with relatively low metabolic rates for their growth rates). As expected, that analysis yielded a much tighter regression (Fig. 2b) and a lower value for the net cost of growth: $1.668 \pm 0.318 \text{ kJ g}^{-1}$ ($n = 14$, $r^2 = 0.915$, $P < 0.01$), equivalent to 6.95 kJ g^{-1} dry tissue.

Discussion

COMPARISONS

Values of the net cost of growth for a variety of domesticated animals are available or can be calculated from the literature of animal science, and a smaller number of laboratory studies of small ectotherms also have been published. Comparison often requires conversion from the various ratios and units used to express these data. For example, our 'ecological' estimate for the net cost of growth of 2.07 kJ g^{-1} fresh tissue can be expressed (1) as a net cost of 8.63 kJ g^{-1} dry tissue ($= R_G/P_G$ in the notation

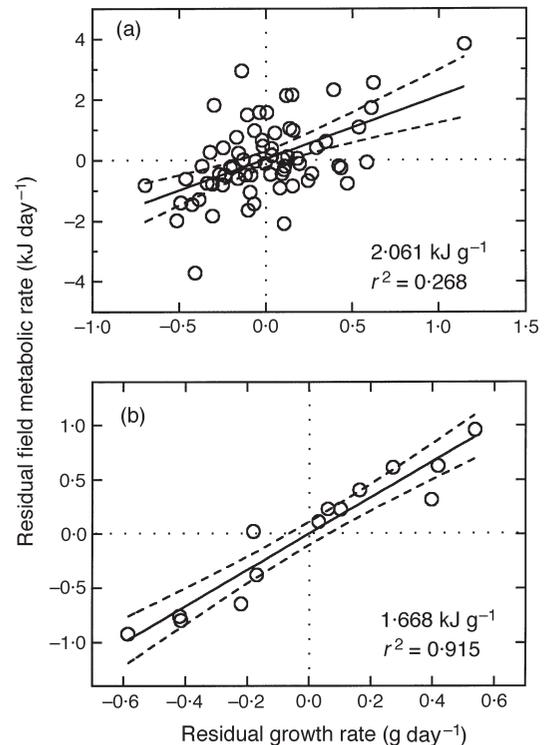


Fig. 2. Mass residuals of field metabolic rate plotted against mass residuals of growth rate for (a) all data, $n = 68$; (b) a subset of ecologically efficient growers, $n = 14$. Lines are least-squares linear regressions with 95% confidence intervals; the slope of the line (= the metabolic cost of growth) is indicated.

of Wieser 1994), (2) as 38% of the energy deposited in tissue (0.38 J J^{-1}), (3) as a total (gross) cost of growth including energy deposited as tissue (31.4 kJ g^{-1} dry or 1.38 J J^{-1}) or (4) as a partial (sometimes called 'net') growth efficiency (or efficiency of utilization for growth) of 0.73 ($P_G/[P_G + R_G]$; this ratio may be equivalent to K_3 of Ivlev 1945; see Wieser 1994; see also Kleiber 1961; Blaxter 1989).

A few illustrative comparisons are shown in Fig. 3. Among vertebrate ectotherms, laboratory data are available only for fish (reviewed by Wieser 1994) and a toad (Jorgensen 1988); our field values for Garter Snakes, particularly the most efficient, or 'physiological' subset, are very similar to these, as well as to recent data for mussels (Bayne & Hawkins 1997). Wieser (1994) advocates adoption of a cross-taxa 'consensus value' equivalent to 7.2 kJ g^{-1} dry (partial efficiency = 0.75) for all organisms exclusive of ruminants; that value is bracketed by our 'ecological' and 'physiological' estimates. Similarly, Ricklefs (1974, p. 171) assumed an 'arbitrary, representative' partial efficiency of 0.75 for birds, which has been criticized as too high (Weathers 1996) on the basis of selective comparisons to published data for pigs and rats (Pullar & Webster 1977). Variation in specific R_G among species, treatment groups and individuals probably reflects variation in the fat and protein composition of deposited tissue (because fat and protein are deposited with very different efficiencies) and variation in the amount of obligate protein catabolism that accompanies net protein deposition (Pullar & Webster 1977;

Parry 1983; Jobling 1985; Fuller *et al.* 1987; Jorgensen 1988; Blaxter 1989; van Es 1989; Wieser 1994; Bayne & Hawkins 1997), as well as differences in methodology among studies.

Cost of growth in free-ranging animals previously has been calculated only for two species of small lizards. Karasov & Anderson (1998) used FMR data for nine juvenile *Callisaurus draconoides* to derive an estimate for the metabolic cost of growth of $1.9 \pm 1.6 \text{ J J}^{-1}$ (95% CI) ($\approx 9.27 \pm 7.72 \text{ kJ g}^{-1}$ fresh mass, or $34.3 \pm 28.6 \text{ kJ g}^{-1}$ dry). As part of a detailed study of ecological energetics, Nagy (1983b) estimated the metabolic cost of growth for *Uta stansburiana*. A multiple regression model predicted the cost of growth to decrease with increasing growth rate and increase with body size, with reported net growth costs ranging from 1.1 to 11.7 J J^{-1} . Multiple differences in methodology and analysis preclude more detailed comparison to our results.

ENERGY BUDGETS

By multiplying measured growth rates by our derived value (2.07 kJ g^{-1}) for the metabolic cost of growth, it was calculated that R_G can account for an average of 30% of the FMRs for these Garter Snakes (Fig. 4), which is higher than the estimated contribution of standard metabolic rate (at most 22%; Peterson *et al.* 1998). This surprisingly high proportion of total energy expenditure supports Parry's (1983) theoretical conclusion that R_G can be a very important component of energy budgets of ectotherms (see also Bayne & Hawkins 1997).

We believe that one reason that the importance of R_G to the energy budgets of ectotherms has been generally overlooked in the ecological literature lies in a failure to distinguish between two different kinds of energy budgets, here designated the *conceptual* form and the *empirical* form.

The *conceptual* energy budget follows from the intuitively obvious first principle that the amount of energy available to an organism over some time period is limited. This limited supply must therefore be allocated to competing, more or less mutually exclusive functions such as growth, storage, reproduction, maintenance and defence. The constraints and trade-offs predicted by this conceptual Principle of Allocation (see Sibly & Calow 1986) form the framework for much contemporary theory of life-history evolution and other topics of evolutionary ecology (e.g. Townsend & Calow 1981; Sibly & Calow 1986; Dunham, Grant & Overall 1989; Stearns 1992).

However, in part because of inherent difficulties in measuring energy allocated to conceptual categories, actual measurements of animal energy budgets most often have been built on the framework of the *empirical* form. This model has a long pedigree in ecosystem and community ecology traceable at least to Lindeman (1942); for the often-cited IBP version, see

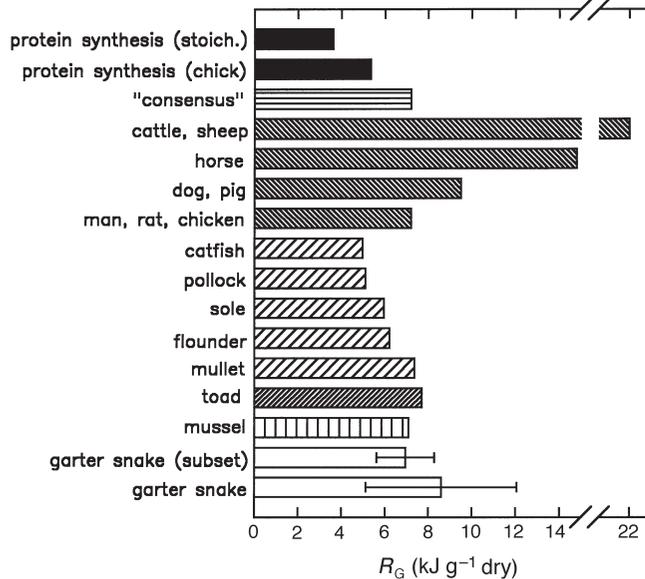


Fig. 3. Comparison of reported values for the net metabolic cost of growth in kJ g^{-1} dry tissue (assumed, where necessary, to contain 22 kJ g^{-1} dry biomass). Sources, from top to bottom: net cost of protein synthesis (theoretical cost from stoichiometry, and measured in chicks *in vivo*; Aoyagi *et al.* 1988); cross-taxa 'consensus' value advocated by Wieser (1994) and Ricklefs (1974); domestic animals, converted from partial growth efficiencies in Table 12.1 of Blaxter (1989); fishes (Wieser 1994); toad (Jorgensen 1988); mussel (Bayne & Hawkins 1997); Garter Snake (this study; efficient subset and all data). Error bars for snake data are 95% confidence limits (Fig. 2a,b).

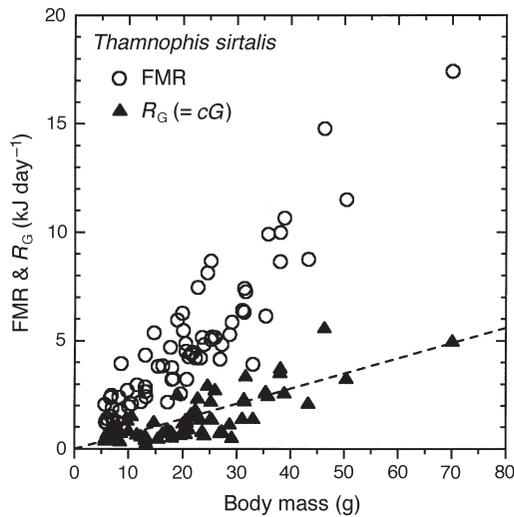


Fig. 4. Contribution of metabolic cost of growth (R_G ; triangles; calculated as growth rate [g day^{-1}] $\times 2.07 \text{ kJ g}^{-1}$) to field metabolic rate (FMR; circles) of Garter Snakes. Dashed line is 30% of predicted FMR.

Petrusewicz & Macfadyen (1970). In its simplest form, the balanced empirical energy budget equation can be written:

$$C = (F + U) + R + P, \quad \text{eqn 3}$$

where chemical potential energy consumed (C) is lost in faeces (F) or urine (U), metabolized as fuel for respiration (R), eventually appearing as heat, or stored as biomass production (P). The empirical energy budget is the basis for the often-calculated growth efficiencies usually called 'gross' (P/C) and 'net' ($P/[C - (F + U)]$) efficiencies of production (Calow 1977). The general categories P and R can be subdivided (e.g. production can comprise growth, fat storage and reproduction; respiration can include activity and resting costs) as appropriate to the questions being asked (see, e.g., Congdon, Dunham & Tinkle 1982).

Problems can occur when a measured or estimated empirical energy budget is improperly mapped onto a conceptual budget. For example, empirical standard and basal metabolic rates are often categorized as 'maintenance costs', but because they are measured under postabsorptive conditions, they must necessarily underestimate the true costs of 'maintenance' as defined as energy balance (Niewiarowski & Waldschmidt 1992). For 'maintenance' to be considered a conceptual allocation sink that is mutually exclusive of growth and reproduction (as implied by the conceptual energy budget), it must include not only the resting and postabsorptive component of R , but also production of new tissue (a component of P , here denoted P_M) required to offset intrinsic losses of biomass through turnover (Hawkins 1991; Houlihan 1991). It also must include additional metabolic costs associated with the acquisition and processing of the food necessary to provide raw materials for P_M , and

fuel to cover the total metabolic costs of body mass maintenance (R_M).

Similarly, there is a tendency to match the conceptual category of 'growth' to the empirical term P . Implicit in the empirical formulation is a different version of the Principle of Allocation: allocation of metabolizable energy can be *either* to respiration *or* to production (Clarke 1993; Wieser 1994; Konarzewski 1995). However, production and respiration are not independent, mutually exclusive allocation sinks, because production itself requires an obligatory allocation to respiration (R_G). Versions of the energy budget equation that take this obligate association into account have been proposed by Parry (1983), Jobling (1985) and Clarke (1987, 1993), among others. For a non-reproductive animal it might take the form:

$$C = (F + U) + (P_M + R_M) + (G + R_G), \quad \text{eqn 4}$$

where G is net growth (production energy), R_G is respiration (heat) due solely to net growth processes ($= cG$), R_M is all other (by definition, 'maintenance') respiration, and P_M is the energy in biomass deposited to offset intrinsic losses. This formulation unifies the empirical and conceptual forms of the energy budget; the second and third parenthetical terms represent energy allocated to the conceptual categories of maintenance and growth, respectively. Reproduction should be treated conceptually in a similar manner; it has both production and respiration components (Congdon *et al.* 1982; Nagy 1983b).

PHYSIOLOGICAL AND ECOLOGICAL COSTS OF GROWTH

In an ecological context, mapping from empirically measured total respiration (FMR) and net growth to conceptual allocation is complex. The conceptual category of 'growth' should include the chemical potential energy deposited in biomass (G) and the metabolic cost of synthesizing the new tissue (R_G as defined above). In addition, it should include the metabolic costs of foraging for food above maintenance requirements, and any metabolic costs of digesting and processing that food before its macromolecules are deposited as growth. The latter costs of digestion and absorption are components of specific dynamic action (SDA), or the heat increment of feeding. SDA has traditionally been (e.g. Brody 1945), and often still is (e.g. Weathers 1996), regarded as wasted, unusable energy. However, an abundance of recent evidence suggests instead that most of the heat production or oxygen consumption measured as SDA is attributable to the costs of anabolism (especially protein synthesis) (Jobling 1983, 1985; Blaxter 1989; Brown & Cameron 1991; Wieser 1994; Secor & Diamond 1997; and references therein). Thus, empirically, the physiological components of R_G are subsumed within SDA, and SDA represents, in large part, the physiological cost of a pulse of growth following a meal. One of the

advantages of our approach is that, in ectotherms, measurements of FMR can integrate the metabolic effects of several meals (and, hence, growth pulses) over time, in a way that short-term laboratory measurements can not.

A model of the relationship of physiological and ecological growth costs to field energy budgets, and the relationship between our equations 1 and 4, is shown in Fig. 5. The partitioning of realistic daily energy budgets is compared for two hypothetical snakes of different body sizes but identical absolute growth rate (0.8 g day^{-1} fresh tissue, which is $8\% \text{ day}^{-1}$ for a 10-g snake and $2\% \text{ day}^{-1}$ for a 40-g snake). For both snakes therefore net growth (G in equations 1 and 4) is the energy content of 0.8 g fresh tissue, or 4.38 kJ day^{-1} . Both snakes also incur identical metabolic costs of growth (cG) of 1.66 kJ day^{-1} ($= 0.8 \text{ g day}^{-1} \times 2.07 \text{ kJ g}^{-1}$). Now, our model (equation 1) partitions total field metabolic costs (FMR) into components related to body mass and growth rate. Therefore, the growth rate coefficient (c) must include, in addition to the physiological costs of protein synthesis and other growth processes, the *mini-*

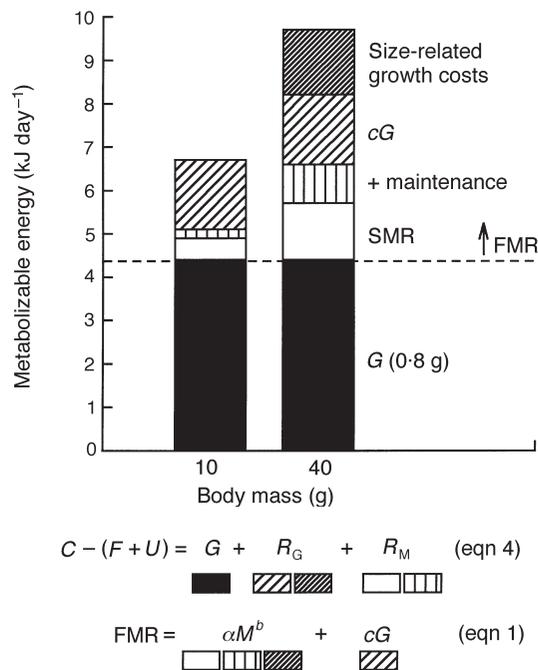


Fig. 5. Model of the partitioning of the field energy budgets of two non-reproductive snakes of different body masses, both growing at a rate of 0.8 g day^{-1} . Maintenance production (P_M) is ignored for clarity of presentation. Solid: energy deposited in net growth. Above the dashed line: field metabolic rate (FMR), partitioned as follows. Open: standard metabolic rate (SMR); vertical lines: additional metabolic costs of maintenance; medium crosshatching: metabolic cost of growth (cG), here including physiological costs and minimum ecological costs; fine crosshatching: additional ecological metabolic costs of growth associated with larger body size. Equations and symbols illustrate the components of equations 1 and 4, keyed to the model shown here. Based on actual measurements of SMR, FMR, G and R_G . See text for further explanation.

um energetic effort required to forage for, capture, swallow and digest the necessary amount of food (3.13 g of frogs, calculated from data in Peterson *et al.* 1998) to supply the amino acids and other raw materials needed to grow 0.8 g . In our comparison (Fig. 5), that minimum ecological effort is included in R_G for the 10-g snake. The larger snake must eat the same 3.13 g of frogs to supply 0.8 g of raw growth materials, and must obtain those frogs from the same spatial distribution as the smaller snake. However, because of its larger body size, it will cost the 40-g snake more energy to forage over the same amount of time and space (all else, e.g. foraging effectiveness and digestive efficiency, being equal). This additional foraging effort (symbolized by fine crosshatching in Fig. 5) should be considered an ecological metabolic cost of growth, but it covaries with body size and will therefore be partitioned into the body size-related component of our model (equation 1). Hence, our calculated metabolic cost of growth (coefficient c in equation 1) includes some, but not all, of the ecological metabolic costs of growth.

Along with the higher costs of maintenance paid by larger animals (which also could also be considered an ecological cost of growth or, more accurately, a metabolic cost resulting secondarily from growth) and the higher absolute growth rates (g day^{-1}) of larger animals, such additional foraging costs offer possible explanations for (1) the positive correlation of cost of growth and body size that emerges from Nagy's (1983b) analysis, and (2) the scaling of FMR in nearly direct proportion to body mass in our population of Garter Snakes, whereas standard metabolic rate scaled with a body mass exponent < 1.0 (Peterson *et al.* 1998). That growth is more expensive for larger animals also may help to explain the decline in growth rates with increasing size typically observed even in indeterminate growers (Andrews 1982; Parry 1983).

Conclusion

Further application of the methods outlined here for estimating the costs of growth from field data, as well as testing of the ideas explicated above, will require that FMR be measured on large samples of ectothermic animals with variable and potentially high growth rates. Snakes are ideal for this purpose for several reasons. Snakes are indeterminate growers; in our population females were sexually mature at about 30 g , but much larger individuals were occasionally found (including one of 448 g). Snakes of all sizes grew rapidly during our study; our calculations were not restricted to juveniles. The short growing season at our study site and rich food resources available contributed to the high growth rates observed and therefore to our success at determining the metabolic cost of growth. All snakes are carnivorous, so the diet is simple yet nutritionally complete. The Garter Snakes studied were consuming a diet consisting entirely of

Treefrogs (*Hyla [Pseudacris] regilla*), so potential differences in the metabolic cost of growth for different diets (Fuller *et al.* 1987) were not a factor.

Our analysis has demonstrated that if the conditions outlined are met, the metabolic cost of growth can be estimated with confidence from data on free-ranging animals. Although the energetic costs of growth are complex when considered in an ecological context, it is clear that they cannot be ignored when considering the ecological energy budgets of ectotherms.

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