



## TECHNICAL RESPONSE

### EVOLUTIONARY ECOLOGY

# Response to Comments on “Metabolic scaling is the product of life-history optimization”

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Froese and Pauly argue that our model is contradicted by the observation that fish reproduce before their growth rate decreases. Kearney and Jusup show that our model incompletely describes growth and reproduction for some species. Here we discuss the costs of reproduction, the relationship between reproduction and growth, and propose tests of models based on optimality and constraint.

Froese and Pauly’s (1) and Kearney and Jusup’s (2) comments regarding our recent paper (3) focus on: (i) the energetic costs of reproduction and the influence of reproduction on the ontogenetic trajectory of size; (ii) the effect of the onset of reproduction on growth rates; and (iii) philosophical differences between models that give primacy to optimality or constraint.

#### Growth versus reproduction: how do they trade off?

Froese and Pauly (1) begin their technical comment by stating that we (3) assume that “[...] resource allocation to survival, growth and reproduction is limited [...]” with “[...] growth ceasing when all of production is allocated to reproduction.” What we actually write is that “Life-history theory [...] assumes that total resource allocation to survival, growth, and reproduction is limited [...]”, “Here, in contrast to metabolic and life-history theories, we propose that the invocation of constraints is unnecessary to explain the ontogenetic trajectories of metabolism and growth”, and “we partitioned total production among growth and reproduction, with allocation to growth occurring early in life and growth ceasing when all of production is allocated to reproduction”.

Froese and Pauly (1) frame our theory as an argument that reproduction comes at the expense of growth, such that allocation to reproduction causes growth to decline. Hence their assertion that, if our theory were true, non-reproducing organisms should continue growing indefinitely (1). But our theory makes no such argument. They then further argue that “fish do not have to “choose” between somatic growth or reproduction, because in the real world, these do not occur simultaneously, but rather sequentially” (1). Even annual species of

fish may continue to grow throughout their single breeding season [e.g., (4)].

#### Expensive cars, expensive houses, and post-maturation growth

Throughout their comment Froese and Pauly (1) apparently assume that the existence of a trade-off in the process of allocating resources to various life history components requires the observation of a negative covariance between these components. Many life history theoreticians over the years have demonstrated why this expectation is naive and flawed [e.g., (5, 6, 7)]. Simply put, if resource availability varies, a negative relationship between different resource allocations is not inevitable and instead positive relationships are possible, or even likely. Reznick and colleagues (7) put this in human terms: car value and house value might be expected to exhibit a trade-off because personal finances are finite, and both cars and houses cost money. But such a trade-off is not observed, because people differ in resource acquisition such that people with expensive houses typically have expensive cars. Similarly, because production increases with body size, it will obscure an underlying shift in allocation from growth to reproduction. For example, consider a smaller animal that allocates 60% of its  $10 \text{ J h}^{-1}$  of total production to growth and allocates the remainder to reproduction, while a larger conspecific allocates 40% of production to growth but has, by virtue of its size, more total energy available for production ( $20 \text{ J h}^{-1}$ ). In this example there is an explicit trade-off between the processes of growth and reproduction such that the relative allocation of production to growth decreases as size increases, but the larger animal nonetheless allocates absolutely more to growth ( $8 \text{ J h}^{-1}$  compared to  $6 \text{ J h}^{-1}$ ) and reproduction ( $12 \text{ J h}^{-1}$  compared to  $4 \text{ J h}^{-1}$ ).

Hence, rather than be invalidated by the observation that growth may increase after reproduction, our model actually predicts it. For the simple case of a metabolic scaling

exponent of 0.67 and a reproductive scaling exponent of 1, for example, our model predicts that growth rate will accelerate after maturation if maturation occurs at a mass smaller than 0.296 times maximum mass. This is verified in the example provided by Froese and Pauly (1).

#### Optimization and constraint

Kearney and Jusup’s technical comment (2) elegantly differentiates our view (3) from that of physically based metabolic theories. Physically based metabolic theories assume that growth is constrained by the scaling of geometrically linked processes, such that maximum size represents an emergent steady state linked to these physical constraints (8). We, on the other hand, view the ontogenetic trajectories of metabolism, growth, and reproduction as an ultimate consequence of selection to maximize fitness, and as a proximate outcome of genetically regulated developmental programs [e.g., (9)].

Our modeling approach invoked no physical constraints, and yielded ontogenetic trajectories of growth and reproduction that are similar to those observed in nature (3). But, as Kearney and Jusup (2) highlight, substantial variation remains unexplained [e.g., figure 2 of (3)]. Kearney and Jusup’s (2) exploration of the details of growth and reproduction for the domestic chicken provides an example in which our model should perform poorly. We expect the covariances between growth, reproduction, and metabolism to arise, at least in part, as an outcome of natural selection that favors particular combinations of trait values [e.g., (10)]. In contrast to our model that maximizes lifetime reproduction, broiler chickens are the product of artificial selection to maximize growth rate, and the outcome of this selection has compromised their reproduction (11). Such an outcome is entirely consistent with our view that the trajectories of growth and reproduction are genetically based. We fully expect that strong selection for traits other than lifetime reproduction will alter the covariances predicted by our model, as appears to be the case for the domestic chicken.

Kearney and Jusup’s (2) analysis of data for common lizards *Zootoca vivipara* and sleepy lizards *Tiliqua rugosa* suggest that our model overestimates reproductive output. This is true, if one assumes that the only cost of reproduction is the energetic cost of synthesizing the clutch. However, the cost of synthesizing the clutch represents just the lowest possible bound of the total cost of reproduction and excludes the costs of gamete biosynthesis, mating, gestation, etc., all of which are likely nontrivial but have been relatively poorly resolved. We suspect that once these additional costs of reproduction are included, the gaps between our model’s predictions and reality will shrink.

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In the absence of empirical measures of the total costs of reproduction however, our model remains an imperfect description.

Thus, we agree with Kearney and Jusup (2) that empirical testing of the assumptions of models is essential, and suggest that testing our assumption of a size-independent value of  $f$  is an important first step. We note that modifying our model to accommodate a size-dependent value of  $f$  is relatively straightforward as is modifying the model to address the concern (2) that we assume that energy assimilation is always sufficient to meet en-

ergy demand, which could be achieved by reducing allocation to production when food is restricted. We did not include such parameters in the model as presented (3) because of concerns about overparameterization [e.g., (12).]

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