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Differential effects of food availability on minimum and maximum rates of metabolism

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Metabolic rates reflect the energetic cost of living but exhibit remarkable variation among conspecifics, partly as a result of the constraints imposed by environmental conditions. Metabolic rates are sensitive to changes in temperature and oxygen availability, but effects of food availability, particularly on maximum metabolic rates, are not well understood. Here, we show in brown trout (*Salmo trutta*) that maximum metabolic rates are immutable but minimum metabolic rates increase as a positive function of food availability. As a result, aerobic scope (i.e. the capacity to elevate metabolism above baseline requirements) declines as food availability increases. These differential changes in metabolic rates likely have important consequences for how organisms partition available metabolic power to different functions under the constraints imposed by food availability.

1. Introduction

Whether migrating thousands of kilometres or diving towards the deep ocean bottom, animals are capable of accomplishing remarkable aerobic feats. Not all organisms, however, are endowed with such high metabolic power. Maximum rates of aerobic metabolism are typically reached during or following exhaustive exercise but can differ by up to threefold among individuals [1] and greater than an order of magnitude across species [2]. The origins and scope of this diversity are due in part to the energy demands associated with the different ecological roles of organisms (e.g. [2,3]), but environmental conditions can also constrain metabolic processes and contribute to observed variation. Aerobic metabolism uses oxygen to convert food into more usable forms of energy and, as such, is sensitive to both acute and long-term changes in both temperature and oxygen availability [4–6]. However, we know little about whether maximum metabolic rates are affected by food availability.

Changes in maximum metabolic rate (MMR) may have important consequences for an organism's ability to cope with variable food conditions. This is because MMR not only defines the upper boundary to aerobic capacity, but together with standard metabolic rate (SMR, the minimum oxygen consumption required to maintain homeostasis) also determines an organism's aerobic scope (AS). AS is the absolute difference between maximum and SMR and is a measure of the degree to which metabolism can be increased above baseline requirements to finance important functions such as digestion, locomotion, growth and reproduction. SMR is thought to reflect the cost of maintaining the metabolic machinery needed to finance MMR [7,8] and is known to be a flexible trait, typically changing as an increasing function of food availability [9,10]. As such,

Table 1. Results from linear models testing the effects of food level and measurement time on the maximum metabolic rate (MMR), standard metabolic rate (SMR), and aerobic scope (AS) measured before and after juvenile brown trout (*Salmo trutta*) had been kept on low, intermediate or *ad libitum* rations for one month.

trait	parameter	F	d.f.	p-value
MMR	food	0.29	2,113	0.746
	time	0.08	1,112	0.782
	food × time	1.50	2,112	0.227
	body mass	349.80	1,112	<0.001
SMR	food	2.83	2,113	0.063
	time	1.18	1,113	0.279
	food × time	9.08	2,113	<0.001
AS	food	1.04	2,113	0.357
	time	0.37	1,112	0.545
	food × time	4.24	2,112	0.017
	body mass	245.18	1,112	<0.001

food-induced shifts in SMR may also affect MMR in parallel. However, if MMR does not increase with food intake then AS would be expected to become more constrained at higher food availabilities, but this remains untested. Here, we use a food manipulation experiment to examine flexibility in the standard and maximum metabolic rates of juvenile brown trout (*Salmo trutta*) in response to food availability and its consequences for AS.

2. Material and methods

Juvenile wild-caught brown trout were collected and brought into the laboratory, housed in individual compartments in a flow-through stream system, and fed *ad libitum* for three months while they acclimated to the temperature controlled room (11.5 ± 0.5°C) and its 12 L : 12 D cycle. Fish ($n = 116$) were then placed on an intermediate food ration (see below). After 28 days, their standard and maximum metabolic rates were measured. At this time, the fish ranged in body mass from 5.37 to 12.67 g (mean ± 1 s.e.: 8.45 ± 0.13 g). The fish were then placed on one of three rations: one-third of the fish remained on the intermediate ration, while the other two-thirds were placed on either a low or an *ad libitum* ration until their metabolic rates were measured again 28 days later. Rations (in calories) for each fish were calculated as a function of its body mass (W, g) and the water temperature (T, °C) for the three food levels as follows: low food = $2.04 \, W^{0.73} e^{(0.10T)}$, intermediate food = $2.91 \, W^{0.737} e^{(0.154T)}$ and *ad libitum* food = $4.29 \, W^{0.767} e^{(0.21T)}$ [11]. The daily ration (mg trout pellets) for each fish was then determined by converting the required daily caloric intake into trout pellets (mg) using values for the energetic content of the trout pellets (Inicio Plus from BioMar Ltd, Grangemouth, UK). Body mass was measured half way in between respirometry trials to adjust food rations as the fish grew.

Both SMR and MMR were measured at 11.5°C. Fish were fasted for 48 h prior to measurement of their SMR to ensure that the additional metabolic costs of digestion did not inflate estimates of their baseline oxygen consumption [12–14]. SMR was measured over a 20 h period using continuous flow-through respirometry. Water flowed through the glass respirometry chambers (400 ml volume) at $1.47 \, l \, h^{-1}$ for the first metabolic measurement and then at $1.68 \, l \, h^{-1}$ for the second measurement 28 days later to accommodate fish growth. These flow rates
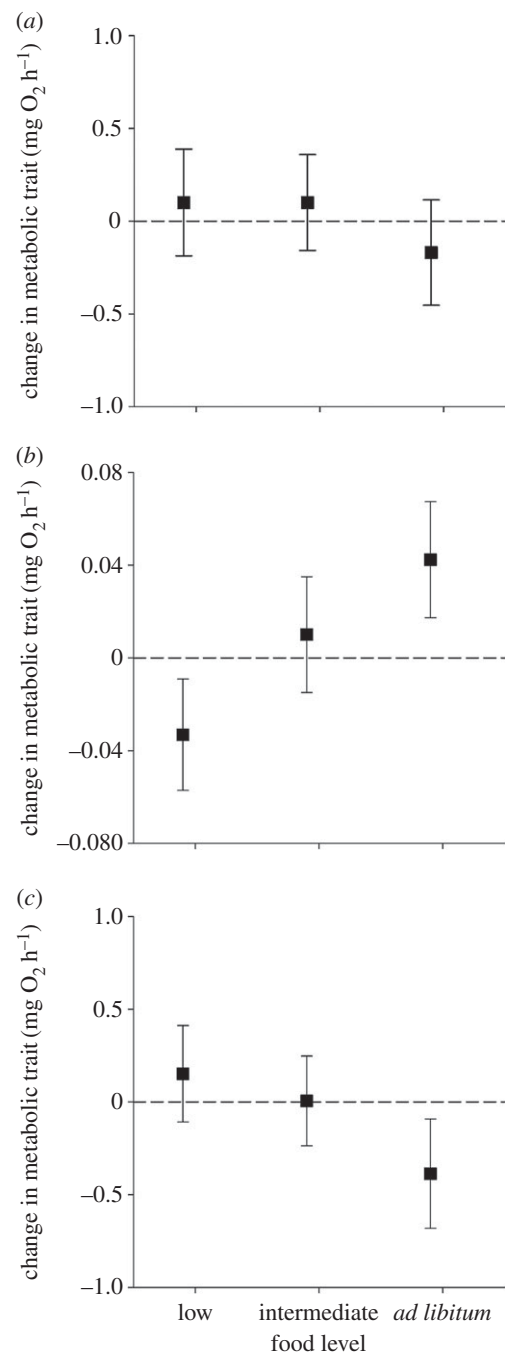

Figure 1. Change in maximum metabolic rate (MMR), standard metabolic rate (SMR), and aerobic scope (AS) of juvenile brown trout as a function of changing food availability. SMR and MMR were first measured after fish had been on an intermediate ration for 28 days and then again after they had been switched to either a lower, intermediate (i.e. the same as previously), or higher *ad libitum* ration for an additional 28 days. AS is defined as the difference between SMR and MMR for each fish. Plotted are back-transformed metabolic rate values (± 95% CI) standardized for a 10 g fish; positive/negative values indicate an increase/decrease in metabolic rate relative to initial values. Change in maximum metabolic rate (MMR), standard metabolic rate (SMR), and aerobic scope (AS) of juvenile brown trout as a function of changing food availability. SMR and MMR were first measured after fish had been on an intermediate ration for 28 days and then again after they had been switched to either a lower, intermediate (i.e. the same as previously), or higher *ad libitum* ration for an additional 28 days. AS was defined as the difference between SMR and MMR for each fish. Plotted are back-transformed metabolic rate values (± 95% CI) standardized for a 10 g fish; positive/negative values indicate an increase/decrease in metabolic rate relative to initial values.

ensured that oxygen consumption rates were detectable but oxygen levels remained above 80% saturation. SMR was calculated by taking the mean of the lowest 10th percentile of oxygen consumption measurements after excluding the lower outliers, i.e. those measurements below 2 s.d. from this mean [1,10]. MMR was then determined using an exhaustive chase protocol followed immediately by measurement of peak excess post-exercise oxygen consumption using closed-system respirometry [1,10]. Briefly, each fish was chased to exhaustion (less than 2 min) against a circular current ($600\ \mathrm{l\,h}^{-1}$) in a bucket. Exhaustion was determined when a fish could no longer swim and was unresponsive when picked up by hand. It was then transferred immediately (less than 10 s) to a glass respirometry chamber (400 ml volume) in a closed system where water circulated at $7.35\ \mathrm{l\,h}^{-1}$ by way of a peristaltic pump. Values of SMR and MMR for each fish were then used to calculate their AS (AS = MMR − SMR).

We used the PROC MIXED procedure in SAS v. 9.3 (SAS Institute, Cary, NC, USA) to test whether metabolic rates changed with food availability. Metabolic rates and body mass were $\log_{10}$-transformed prior to analyses. Each model included metabolic rate as the dependent variable, food level and measurement time and their interaction as categorical predictors, and fish identity as a random effect to control for repeated measures. When the interaction between food regime and measurement time was statistically significant, changes in metabolism were further evaluated by testing whether the final metabolic measurement was significantly different from the initial measurement for each food regime. There was heterogeneity in the slopes of SMR versus body mass within but not across measurements, so we used the model explained above to examine changes in mass-independent SMR by using the residuals of each metabolic trait as a function of the body mass of all fish across both measurements. All data are available in the Dryad Digital Repository [15].

3. Results

MMR did not change in response to food availability (table 1 and figure 1). However, SMR changed over that same treatment period, with the direction of change differing between food levels (table 1 and figure 1). Fish decreased their SMR when switched to the lower food level ($t_{113} = -2.66$, $p = 0.009$), did not change their SMR when kept on the same intermediate ration ($t_{113} = 1.22$, $p = 0.23$), and increased their SMR when switched to the higher *ad libitum* rations ($t_{113} = 3.27$, $p = 0.001$). As a result of these shifts in SMR but not MMR, AS was also influenced by food level (table 1 and figure 1): it was unaltered in fish switched to the lower food level ($t_{113} = 1.23$, $p = 0.223$) or kept on the same intermediate ration ($t_{113} = 0.17$, $p = 0.869$), but decreased in fish switched to *ad libitum* rations ($t_{113} = -2.14$, $p = 0.034$).

4. Discussion

The key result from our study is that SMR changed in response to food intake without any corresponding shift in MMR. This differential sensitivity among the two components of metabolism is contrary to the hypothesis that SMR reflects the idling cost of the metabolic machinery needed to finance MMR [7,8] and, by extension, its prediction that changes in SMR should lead to corresponding changes in MMR. Rather, contrasting responses of SMR and MMR suggest that they are controlled by different underlying processes. Food intake is known to affect the masses of organs such as the viscera that contribute to whole organism SMR [16]. By contrast, skeletal muscle is thought to be the predominant contributor to MMR [17], but tends to decrease in mass only in response to prolonged starvation [18]. Thus, MMR may change in response to these more extreme conditions and warrants further attention.

Differential changes among SMR and MMR may, in turn, affect metabolic budgeting decisions because of their consequences for AS. AS represents the overall capacity to fuel functions above baseline energy expenditure and is known to have a positive effect on feeding capacity [19], locomotor ability [20] and growth rate [1]. However, animals cannot meet the aerobic demands of all of these functions simultaneously, so trade-offs can arise [21]. For example, swimming ability can be sacrificed to prioritize the allocation of aerobic power to digestion [22–24]. A decrease in AS with increasing food levels may therefore represent an increasing constraint on the organism [21]. However, it is important to note that the effect of food availability on AS that we observed is driven entirely by a change in SMR which itself can also have positive effects on growth rate [10] as well as digestion efficiency [25]. As such, the overall impact of metabolic flexibility on organismal performance will likely depend on the costs and benefits associated with changes in both these metabolic traits.

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