Feed efficiency and resource allocation trade-offs: theory, evidence and prospects

Frédéric Douhard, Rachel Rupp, Hélène Gilbert

HAL Id: hal-03779772
https://hal.inrae.fr/hal-03779772

Submitted on 20 Sep 2022

Feed efficiency and resource allocation trade-offs: theory, evidence and prospects

F. Douhard[1*], R. Rupp[1], and H. Gilbert[1]

[1] GenPhySE, Université de Toulouse, INRAE, ENVT, 31326 Castanet-Tolosan, France; [*]frederic.douhard@inrae.fr

Abstract
The resource allocation theory has long been of interest in livestock as a framework to explain the correlated responses to selection for high productivity. Increasing limitations on feed resources and genetic improvement of feed efficiency (FE) should further promote allocation constraints. Yet, predicting those consequences for breeding critically depends upon the possibility to get testable predictions from the current framework. Here we assessed the changes in energy allocation when selecting for FE, and the consequences of those changes on health and reproduction. For this, we used two approaches; a survey of selection experiments among various species and a case study in sheep focusing on a potential trade-off between FE and response to an infectious challenge (parasite infection). Overall, results provide weak evidence for the current allocation framework. We outline several directions to better appraise the consequences of breeding for FE in increasingly challenging environments.

Introduction
Global pressures on feed resources require livestock that consume less feed to produce under controlled conditions but also emphasize the challenge of producing when feed quantity or quality can drop unexpectedly. Although those issues well translate into separate researches on new breeding objectives for FE and for robustness, the links between those two types of traits remain unclear whereas most of their mechanisms should share a common nutritional basis. Moreover, those links may have key implications in terms of trade-offs and genotype-by-environment interactions. A framework representing how nutrition affects multiple traits responses to selection would be thus insightful. For this purpose, the evolutionary theory of resource allocation has become of interest in animal breeding since it provides a simple way to consider the responses to selection according to the feed availability and to the competing demands for nutrient among the different functions of an organism (Beilharz et al., 1993; Rauw, 2009). Yet, this framework only had a limited impact on the study of FE so far. Moreover, some responses to selection for FE have called into question the occurrence of resource allocation trade-offs (Rauw, 2012; Gilbert et al., 2017). Although the resource allocation theory has been introduced in the livestock context since the 90's, its applicability to these conditions remains seldom questioned and tested. The fast-growing body of research on FE thus provides new opportunities to assess the mechanistic bases of resource allocation trade-offs and how they might shape selection responses.

Why should selection for feed efficiency lead to energetic trade-offs?
Recently, we have reconsidered the theoretical background to predict trade-offs, focusing on energy allocation (Douhard et al., 2021). Our framework is based on the classic 'Y model' of a resource acquisition and allocation (van Noordwijk and de Jong, 1986) applied to animals typically selected under non-limiting resources. For each animal, the daily rate of metabolizable energy intake is split into one part allocated to productivity ('P'; energy retained as new biomass such as muscle, fat, milk, egg or wool plus the associated energy of biosynthesis dissipated as heat), and the other part allocated to activity and self-maintenance.

Allocation to maintenance can be approximated by resting metabolic rate (RMR) and is supposed to maximize the chance of survival and future reproduction (Figure 1a). Most undesirable side effects of selection for high productivity are thus thought to stem in the extent to which RMR is reduced in the total energy budget (once its covariation with body size has been accounted for). However, a same selective increase in productivity could be mediated through different changes in energy allocation depending on the relationships between productivity, maintenance and intake (Figure 1b). A higher rate of biosynthesis could require higher maintenance costs (path n°1 where P and RMR are positively associated) or could be simply fuelled through higher intake (path n°2 where RMR and P are independent). Alternatively, constraints on intake could favour a reduced energy allocation to maintenance (path n°3 where RMR and P are negatively associated). All those cases can lead to an increase in P relatively to energy intake and thus improve FE. However, if an energy allocation trade-off occurs then selection strategies that promote a reduction in RMR should increase the risk of an impaired health or reproduction.
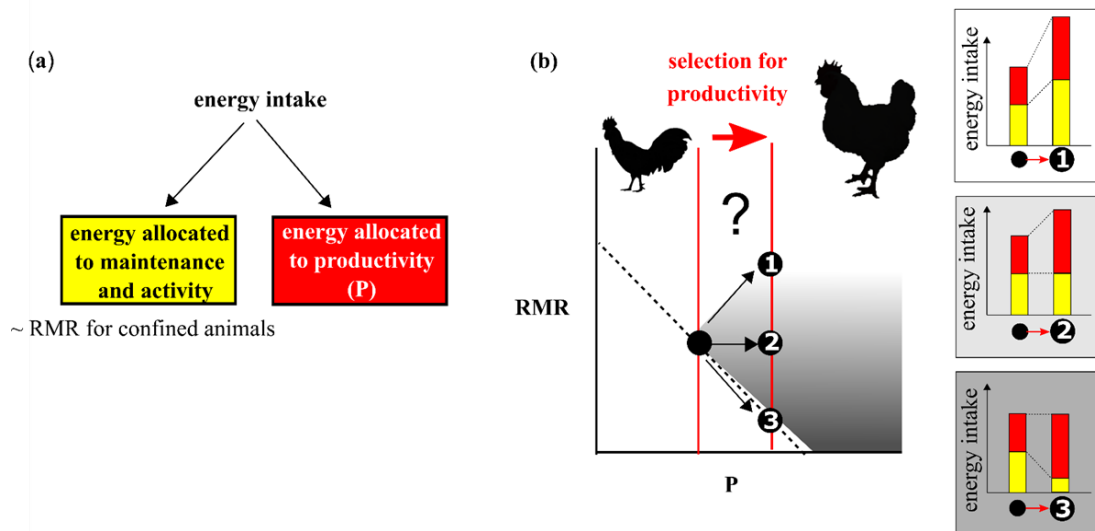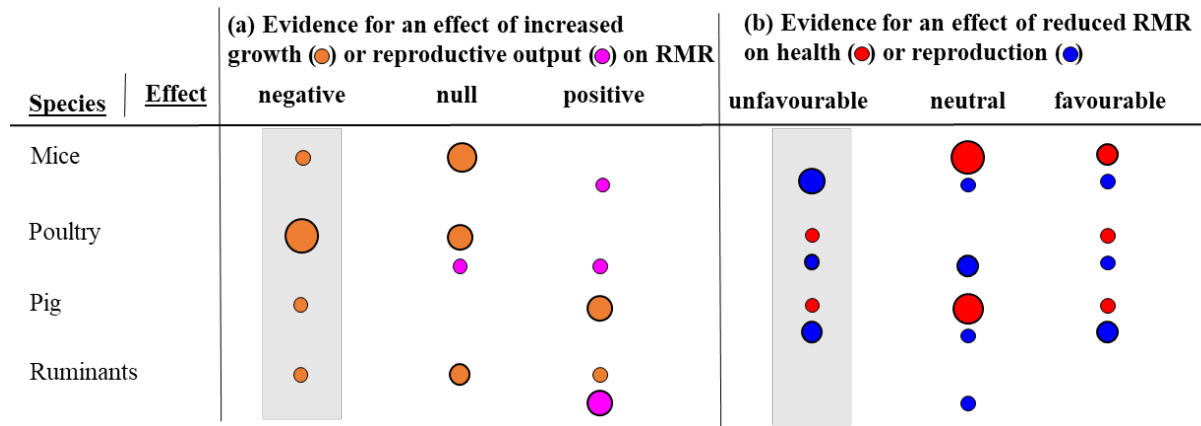

Figure 1. The 'Y model' of energy allocation applied to livestock (a) and the different paths through which increased productivity could translate in terms of changes in energy allocated to productivity or maintenance (b). Maintenance can reasonably be approximated by resting metabolic rate (RMR) for confined animals. Grey shade reflects the trade-off intensity. Adapted from Douhard *et al*. (2021).

What is the evidence for energy allocation trade-offs?
Review of comparisons between breeds or lines selected in favourable environments
First, to assess the relationships between maintenance, productivity and feed intake in the context of livestock and artificially selected laboratory mammals and birds, we surveyed studies that compared RMR between breeds or lines of contrasting yields when feed intake was not constrained (Figure 2a). Only few studies provided some support for an energy allocation trade-off (path n°3 in Figure 1b), in particular during growth in poultry. In contrast, during reproduction, increased maternal productivity seemed often associated with an increased RMR (path n°1 in Figure 1b). Then, to explore the correlated effects of a reduced RMR on different aspects of health or reproduction, we reviewed selection experiments on FE or RMR (Figure 2b). Indeed, responses to selection for FE or for RMR were consistently and positively related which suggests that selection for FE generally leads to some genetic decrease in RMR (but also in some behavioural activities), even though feed intake is not

restricted. Despite this constraint on metabolism, we found little evidence for unfavourable effects on components of health (e.g. oxidative stress, neonatal survival, humoral or cell-mediated immunity) and reproduction (e.g. sperm traits, litter size, milk output).

Species	Effect	(a) Evidence for an effect of increased growth (🟠) or reproductive output (🟣) on RMR			(b) Evidence for an effect of reduced RMR on health (🔴) or reproduction (🔵)		
		negative	null	positive	unfavourable	neutral	favourable
Mice		🟠	🟠	🟣	🔵	🔴 🔵	🔴 🔵
Poultry		🟠	🟠 🟣	🟣	🔴 🔵	🔵	🔴 🔵
Pig		🟠		🟠	🔴 🔵	🔴 🔵	🔴 🔵
Ruminants		🟠	🟠	🟠 🟣		🔵	

Figure 2. Evidence for association between resting metabolic rate (RMR) and selection for growth or reproductive output when feed intake is not restricted (a), and effects of a genetically reduced RMR on health or reproduction (b). The size of the circle indicates the number of supporting comparisons ($1 \leq n \leq 5$) between selected lines or breeds. In (b) when different components of health or reproduction were investigated within a same pair of lines there were considered as different comparisons. The scenario corresponding to an energy allocation trade-off (path n°3 in Figure 1b) is highlighted in grey.

Case study in sheep selected for response to an infectious challenge or for feed efficiency
To better detect a potential energy allocation trade-off, it may be necessary to go beyond the simple Y model (Figure 1a) notably to focus on a component of maintenance that can be specifically recruited under challenging conditions, e.g. a specific immune response to infection. For this, we studied the potential trade-off between FE and resistance to gastrointestinal parasitism based on an infectious challenge (single-dose infection with *Hæmonchus Contortus*) in growing lambs from Romane meat-sheep (experimental approval D18-174-01). In a first trial, lambs were from lines divergently selected on parasite resistance (resistant (R) vs. susceptible (S); Sallé *et al*., 2021), whereas in another trial they were from lines divergently selected for FE (low Residual Feed Intake (RFI-) vs. high (RFI+); Tortereau *et al*., 2020) from the same flock. Within each trial, direct responses to selection were consistent: fecal worm egg count of was much lower in the R line than in the S line, and FE was better in the RFI- line than in the RFI+ line. Contrary to our expectation, no evidence for a trade-off was found. Between the RFI lines, the difference in FE was maintained during infection, and no difference in parasite resistance was detected. In the R and S lines we even found some evidence for a synergy between FE and parasite resistance. Voluntary feed intake was lower for the R line than for the S line during infection, which also led to a lower RFI. Later on, we re-infected the R and S lines during the first peripartum and tested the effect of a feed restriction (protein). This restriction led to a similar decrease in body weight and condition between lines, with no interaction with parasite resistance.

Limitations and future directions
Based on our findings, the consequences of breeding for FE look much more difficult to predict than one could anticipate from the energy allocation framework alone. First, although the genetic antagonisms observed between productivity and health or fertility are often

considered as a result of resource allocation trade-offs, we did not find strong support that those trade-offs can be underpinned by changes in energy allocation. Second, even when energy allocation to maintenance is reduced during selection for FE, the expected unfavourable effects on health or reproduction were far from clear. Lastly, our case study neither indicates that selection for a particular health component (parasite resistance) deteriorates FE during a challenge, nor vice-versa. Overall, we thus confirm a lack of direct or mechanistic support for the energy allocation framework when applied to livestock.

However, there were at least three main limitations when assessing this framework. First, the energy allocation to maintenance remains difficult both to estimate and to interpret. In particular, dissecting the biological basis of FE or RMR does not simply translate into the resource acquisition-allocation framework as various maintenance processes also contribute to feed acquisition or to production. Second, the aspects of energy budgets that fundamentally constrain selection are still very elusive. Third, while the consequences of a reduced allocation to maintenance on fitness-related traits should be considered on the long-term, most studies of FE have focused on reproduction or health traits in young adult animals, which may have led to inadequate measurements to correctly assess the resource allocation framework.

Beyond those limitations, it becomes increasingly clear that resources allocation constraints do not provide a sufficient explanation for the occurrence of trade-offs and that other mechanisms underpinning unfavourable genetic correlations should be considered (e.g. nutrient-sensing signalling). Those considerations should contribute to a more integrative framework to orientate breeding objectives according to the agroecological context.

References
Beilharz R. G., Luxford B. G., and Wilkinson J. L. (1993) J. Anim. Breed. Genet. 110(1-6):161–170. https://doi.org/10.1111/j.1439-0388.1993.tb00728.x
Douhard F., Douhard M., Gilbert H., Monget P., et al. (2021) Evol. Appl. 14:2726–2749. https://doi.org/10.1111/eva.13320
Gilbert H., Billon Y., Brossard L., Faure J., Gatellier P., et al. (2017) Animal 11(9):1427–1439. https://doi.org/10.1017/S175173111600286X
Rauw W. M. (2009) Resource allocation theory applied to farm animal production. CABI International, Wallingford, UK.
Rauw W. M. (2012). Feed efficiency and animal robustness. In: R. A. Hill (ed) Feed Efficiency in the Beef Industry. John Wiley & Sons, Ames, Iowa, USA, pp. 105–122.
Sallé G., Deiss V., Marquis C., Cortet J., Serreau D., et al. (2021) Evol. Appl., 14(11): 2591-2602. https://doi.org/10.1111/eva.13294
Tortereau F., Marie-Etancelin C., Weisbecker J.-L., Marcon D., Bouvier F., et al. (2020) Animal 14(4), 681–687. https://doi.org/10.1017/S1751731119002544
van Noordwijk, A. J., and de Jong, G. (1986). Am. Nat. 128(1):137-142. https://doi.org/10.1086/284547