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Different milk feeding intensities during the first 4 weeks of rearing dairy calves: Part 3: Plasma metabolomics analysis reveals long-term metabolic imprinting in Holstein heifers

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ABSTRACT

Adequate nutrition of calves is a fundamental requirement for efficient production in later life. Suboptimal nutrition before weaning could have detrimental long-term effects on metabolic health and could thereby decrease production efficiency. In this study, the metabolomic profiles of German Holstein calves reared on whole milk ad libitum ($n = 10$), milk replacer ad libitum ($n = 9$), and milk replacer in restricted amounts ($n = 9$) were compared. Furthermore, this profiling approach was extended to the first lactation in the same animals for characterizing the long-term effect of quantitative and qualitative dietary manipulations affecting calves during development in a period that is sensitive to metabolic imprinting. Blood plasma samples were collected on d 3, 22, and 52 of life as well as during wk 4 before and wk 3 and 8 after the first calving. Samples were subjected to a targeted metabolomics analysis using the AbsoluteIDQ p180 kit of Biocrates Life Science AG (Innsbruck, Austria). Profiling of metabolomics data was performed by principal component analysis and heatmap visualization of the metabolome, as well as by comparing fold changes and *t*-test statistics of metabolites. A quantitative identification of 180 plasma metabolites was possible, belonging to the metabolite classes of acyl-carnitines, AA, biogenic amines, phosphatidylcholines, lysophosphatidylcholines, sphingomyelins, and hexoses. Comparing metabolite concentrations between ad libitum-reared and restrictively reared animals revealed significant differences both during calthood as well as during first lactation. Most dominantly, acylcarnitines of both short- and long-

chain length were more abundant in ad libitum reared animals in the long-term, suggesting alterations in mitochondrial function, most likely indicating adaptive mechanisms of energy expenditure. Furthermore, plasma sphingomyelin concentrations were affected by ad libitum versus restricted milk replacer feeding, which can imply long-term modulatory mechanisms affecting insulin sensitivity. The functional characterization of the identified metabolic patterns, particularly the alterations of single lipid species, is required for further improving our understanding of the links between early nutrition shaping metabolic development and a healthy productive life of Holstein dairy cows.

Key words: calf nutrition, metabolic imprinting, metabolomics

INTRODUCTION

Adequate nutrition of dairy calves is considered a fundamental factor for an optimal lifetime productivity and for profitability in dairy systems (Heinrichs, 1993). Average daily gain during early age was shown to influence milk production in the first lactation (Zanton and Heinrichs, 2005). In support of this concept, several studies documented that a higher plane of nutrition during the preweaning period (i.e., ad libitum vs. restricted liquid feeding) was associated with enhanced productive performance in adult life (Shamay et al., 2005; Khan et al., 2011; Soberon et al., 2012). However, in addition to quantitative adequacy of macronutrients in liquid feed (milk or milk replacer) used for calf rearing, liquid feed quality and, particularly, presence of non-nutritive feed components such as bioactive molecules supporting neonatal development (i.e., growth factors, peptides) should be considered (Bartol et al., 2013). These molecules are present in whole milk, and calves fed whole milk ad libitum were found to produce more milk during their first lactation than calves fed milk replacer ad libitum (Moallem et al., 2010). In addition to increased milk yield,

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enhanced organ growth, mammary gland development, and gut-associated immune system development were associated with a higher plane of preweaning nutrition (Geiger et al., 2016; Wilson et al., 2017; Hammon et al., 2018). Presumably, epigenetic mechanisms play a role in maintaining long-term effects of preweaning nutrition, accounting for stable alterations in the phenotype as a form of metabolic imprinting (Bartol et al., 2013). Furthermore, early life is a critical period for shaping allometric growth and development of the mammary gland (Bach, 2012; Esselburn et al., 2015).

Previous studies reported a substantial amount of data on the links between nutrition, growth rate, and later productive performance, but less is known about the underlying metabolic pathways. In particular, we have a knowledge gap on the longitudinal changes of metabolic phenotypes at a molecular level that would extend our understanding on the differential long-term effects of preweaning nutrition. In the current study, we investigated this issue at different levels, and the present paper is the third part focusing on changes of the plasma metabolome of calves and later of the same animals as heifers. Calves were differentially reared on either whole milk *ad libitum* or milk replacer *ad libitum* or milk replacer at restricted amounts, and were followed up as heifers until their first lactation. Growth performance, production performance, and economic aspects of a higher plane of nutrition in relation to an enhanced production performance were already published as part one (Korst et al., 2017). In the second part of the study, conventionally used markers of metabolism and endocrine system in calves and heifers were analyzed (Kesser et al., 2017). However, these markers, including serum free fatty acids, BHB, glucose, insulin, adiponectin, leptin, and a surrogate index for estimating insulin sensitivity (revised quantitative insulin sensitivity check index; RQUICKI), failed to differentiate between heifers that experienced different preweaning nutrition as calves. To extend this investigation, the objective of the present paper was to perform a systemic screening of the plasma metabolome to search for acute as well as for long-lasting metabolic changes linked to the described nutrition before weaning. To do so, a targeted metabolomics approach assessing markers of basic cellular physiological and pathophysiological pathways was used to assess metabolic profiles of the animals across nutritional treatments and along the time axis. The purpose of characterizing such metabolic profiles was to visualize the dynamic development of the metabolic network influenced by nutrition-derived metabolic imprinting effects. The fundamental hypothesis of this approach was that nutrient availability and the source of nutrients (whole milk vs. milk replacer) during early life can modulate cellular physiological

pathways of growth, development, maturation of immune and endocrine systems, as well as energy sensing and expenditure. These could collectively be defined as metabolic imprinting, as a sum of processes modulating efficiency (i.e., amount of output by utilizing the available resources) of growth, maintenance, and production. The desired optimum efficiency can be described as the maintenance of cellular processes in a healthy status and assuring an equilibrium between maintenance of body resources and production output at the same time. It might be technically challenging to identify a causative relationship between metabolic imprinting and later production outcome, but analyzing the metabolic phenotype can improve our understanding of this relationship because distinct metabolic profiles can reflect associations between nutritional treatments and production profiles.

The overall aim of the study presented in this manuscript series was to establish the potential link of metabolic imprinting deriving from rearing calves on whole milk versus milk replacer and rearing calves *ad libitum* versus restrictively to an altered production efficiency profile at the time when these calves develop into heifers and enter production. We evaluated the effect of liquid feed source and availability on growth performance and later production performance as well as the associated economic investment-return aspects in the first part of this series (Korst et al., 2017). In the second part, we investigated how the endocrine system was affected in these calves and heifers (Kesser et al., 2017). Finally, the aim of the currently presented third part was to characterize phenotypic patterns linked to the previously reported production profiles as a metabolic profiling approach and to generate novel hypotheses regarding molecular mechanisms of early nutrition-derived metabolic imprinting in Holstein dairy heifers.

MATERIALS AND METHODS

Animals, Nutritional Treatments, and Sampling

All animal experiments were performed in strict accordance with the German Law for the Protection of Animals and were approved by the relevant authority (Landesuntersuchungsamt Rheinland-Pfalz, Koblenz, Germany; G 11–20–026). The trials were conducted on calves and later during the first lactation of the same animals as heifers at the Educational and Research Centre for Animal Husbandry, Hofgut Neumühle, Münchweiler an der Alsenz, Germany. The effects of different feeding intensities on performance and production, as well as on metabolic and endocrine status from birth over the first lactation, were previously published (Kesser et al., 2017; Korst et al., 2017). The current study

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