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Restrictive nutrition and compensatory growth of broilers: Impact on growth production results and carcass characteristics

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Abstract. Increase in growth rate through genetic selection and improved nutrition in broiler chickens has been associated with high body fat deposition. This is particularly evident under *ad libitum* feeding that is normally practiced. Excessive fat deposition in the body of broilers is a common problem for poultry producers and consumers. Studies have shown that feed restriction could decrease fat content and increase protein deposition in carcasses, thus resulting in their improved composition. In addition to determining the optimal time to start and the duration of the restrictive nutrition, the success of the given programs largely depends on the intensity of the restriction, as well as the type of applied technique. Considering that in a large number of studies, the application of restrictive programs resulted in a reduction of body fat in broilers, but at the same time the desired body weight was not achieved at the slaughter (market) age, these programs should not be *a priori* rejected as ineffective. It is necessary to determine whether the market price of the obtained product (poultry meat) with its reduced fat content justifies the lower body weight of broilers achieved at the end of the fattening period.

1. Introduction

Exceptional progress made in the field of animal nutrition during the past few decades, along with constant (sharp) genetic selection aimed at increasing body weight of broilers and improving feed efficiency, have resulted in reaching the biological limit for achieving animal production results in this segment of poultry production. In the last 50 years, body mass growth rates in broiler chickens have increased by more than 300% [1]. This dramatic increase in broiler growth intensity was manifested primarily during the first four weeks of fattening [2]. Unfortunately, these improvements in production results have led to a number of problems: reduced animal resistance, increased susceptibility to stressors, high incidence of metabolic diseases (the most common are sudden death syndrome, ascites and foot problems), and increased body fat storage [3, 4, 5]. Although a large number of nutritional techniques have been proposed to overcome these problems, the concept of limitation, i.e. slowing down the growth of broilers during the early period of fattening, by applying a restrictive diet and the subsequent manifestation of compensatory growth, has found the widest application in practice.

2. Compensatory growth

The growth of an animal implies primarily an increase in the amount of structural body tissues – muscles, bones and organs, and is characterized by the deposition of proteins and minerals in the body of the individual. Genetic potential largely determines the growth intensity, body structure and definite body weight of an animal, and feed is the substrate from which the body should be built [6]. The growth intensity of an animal is estimated on the basis of the percentage ratio of the achieved gain in a unit of time in relation to its initial body weight or size. Under optimal conditions of nutrition and environment, animals show undisturbed growth in accordance with their (genetically) predetermined growth curve. Under unfavorable conditions for growth (such as insufficient / inadequate nutrition, disease, poor housing conditions, heat stress and many other factors), the animal deviates from its original growth path. However, animals retain the endogenous growth impulse persistently and for a long time, so that when favorable conditions are provided again, they often show compensatory growth (in the literature it is also referred to as "catch-up" growth). Compensatory growth is most often defined as: "The rate of growth exceeding that normally observed in the same breed of chicken at the same age" [7] or as: "A physiological process whereby an organism accelerates its growth after a period of restricted development, usually due to reduced feed intake, in order to reach the weight of animals whose growth was never reduced" [8].

As a consequence of compensatory growth, the individual manages to make up for the previous growth retardation and reaches (even exceeds) the body weight of animals that grew under optimal conditions. The described phenomenon is especially interesting for livestock production, and since the diet during the winter period is often insufficient (lack of quality bulk feed), the original experiments were focused on sheep and cattle as experimental models [9]. Soon after, compensatory growth found its application in poultry production, first in the rearing of laying hens, and then in the fattening of broilers. Numerous programs have been developed that intentionally cause growth restriction at a certain age, after which the animals manifest accelerated growth. In addition to improving the growth intensity, the application of the given programs has other advantages, such as improved feed conversion and reduced deposition of adipose tissue in the body of animals, while many trials have confirmed a positive impact in controlling the occurrence of metabolic disorders.

Two hypotheses about the mechanism of compensatory growth are most often cited in the literature. The first is the "central control" hypothesis, which suggests that the body has a "pre-set point" for body size that corresponds to a particular age and that this control is located in the central nervous system. After a period of malnutrition, the body tries to reach a size that is appropriate for a given age in the shortest possible time. The second is the "peripheral control hypothesis", which suggests that body size is controlled by tissues in which the number of cells, or more precisely the DNA, determines the extent of growth after a period of malnutrition or disease [10].

A large number of studies have been conducted on the phenomenon of compensatory growth in broilers, and the results obtained are inconsistent and often contradictory. The reasons for these discrepancies should be sought primarily in the different design of applied programs (method of growth restriction, start of application, duration, restriction level, type of diet provided after restriction), differences in the duration of fattening (earlier programs included broiler fattening up to 56 or 49 days, while in modern broiler hybrids, fattening ends up to 42 days or earlier), different responses of sex of the tested individuals (males have a greater ability to show compensatory growth compared to females), differences in the tested hybrid (fast-growing broiler hybrids show less compensatory growth compared to slow-growing hybrids) and others. Having in mind all the above factors, it is clear that compensatory growth cannot be manifested after the application of any broiler growth restriction program, or more precisely, it cannot be expected the animals will reach the same final body status as those that grow under optimal growth conditions. Therefore, some authors [11] suggested that the term compensatory growth should be replaced by the term accelerated growth, regardless of whether it resulted in the desired body weight of broilers at slaughter age being achieved, while the period of *ad libitum* feeding, which is applied after a period of limited growth (caused by limited feed intake), should be named the recovery period. The phenomenon of compensatory growth in broiler chickens remains complex because the physiological, nutritional, metabolic, and endocrine aspects involved are still not well understood [12].

3. Restrictive feed intake

The most widely accepted technique for limiting broiler growth is a controlled (predefined) reduction in feed intake during the early period of fattening. This control is achieved by applying various programs of quantitative and qualitative restriction of nutrient intake.

In practice, the most common are quantitative restriction programs, which involve limitation of the amount of feed delivered to broilers over a certain period of time. The programs can be realized through:

a) Restrictions of time provided for broilers to access the feed.

Feed is given only for a certain period of time within 24 hours or the “skip-a-day” feeding system is used, i.e. one day of feed and one day without feed.

b) Changing the light regime.

The lighting period during which the animals consume feed is shortened, i.e. the period of darkness during which the animals rest is extended, all within 24 hours.

c) The use of chemicals. Restriction of feed intake by chemicals has no major practical significance and is mainly used in experimental studies. The use of 1.5% and 3% glycolic acid in the broiler diet (in the period from days 7 to 14 of fattening) reduces feed consumption by 22% and 50%, respectively [13]. Similar effects can be achieved with the use of the opioid antagonists, naloxone and naltrexone, at a dose of 2.5 to 10 mg/kg of body weight [14].

d) Changing the form of feed that animals consume.

Complete feed mixtures for broilers are mainly produced in three different forms: mash, pellets and crumbled pellets. Manufacturers of modern broiler hybrids recommend the use of crumbled pellets during the starter, crumbled or whole pellets during the grower and whole pellets during the finisher phase of fattening. The process of pelleting reduces the volume of feed mixtures, their disintegration and dustiness, provides easier manipulation, prevents decomposition, and since feed is heated with steam during preparation, it is better utilized in the animal’s body. In the literature, pellets are usually referred to as “energy more dense” in relation to mash, which practically means that by reducing the volume (by compressor pressure and passing through the matrix), a greater presence of nutrients (energy) is achieved in the same bite. Therefore, individuals spend more time consuming mash diet and expend more energy on this process. Simple replacement of pellets with a mash form of diet results in slowing down the growth of broilers during a given feeding period [15, 3, 6].

e) Reducing the amount of feed provided for individual during 24 hours, without limiting time for accessing the feed.

Reducing the amount of feed during the early period of fattening is an economically viable option for the farmer, considering that feed mixtures intended for the initial phase of fattening (starter mixtures) have a significantly higher commercial price compared to other mixtures (grower and finisher mixtures), and any reduction in consumption of these feed mixtures, if compensatory growth has been achieved, increases the economy of such production. However, the implementation of this program requires the provision of sufficient feeding space to prevent competition between individuals and their uneven growth, and an additional problem is the proper dosing of drugs and coccidiostats [16]. The most common procedure for reducing the amount of consumed feed in practice is to provide an amount of feed that meets only the maintenance energy requirements of broilers. In this case, it is necessary to apply the specific mathematical formula developed by Plavnik and Hurwitz [17] (which precisely determines the necessary parameters):

$$\text{EI (kcal ME / day)} = 1.5 \times BW^{0.667}$$

Where: EI (Energy Intake) = daily energy intake of feed, expressed in kcal ME (kilocalories of metabolic energy), $BW^{0.667}$ = metabolic body weight of the animal at the beginning of the restrictive diet (body weight of the individual expressed in grams, per exponent 0.667).

If the EI values from the previous formula are expressed in KJ values instead of Kcal, then the specified formula can be represented as follows:

EI (KJ ME / day) = 6.2 x $BW^{0.667}$

The change in the presented formula was made in accordance with the established ratio between KJ and Kcal which is: 1kcal = 4.184 kJ, so that 1.5 (kcal from the previous formula) x 4.184 = 6.2 (KJ).

After determining the EI value from the formula, the required daily amount of feed is determined from the EI value and the energy quotient value of the feed mixture the broilers are fed in a given period (usually starter or grower). By applying the equation, the broilers (during the early period of fattening) are provided with energy requirements for maintenance (35-40 Kcal ME per day per bird) and daily feed intake at the level of 35% in relation to the *ad libitum* diet can be accomplished [18].

Unlike quantitative restriction, qualitative restriction of nutrient intake implies the provision of feed with a composition (raw material and/or chemical) that deviates from the usual. This technique is realized by:

a) Formulating meal with low (below recommended values) energy levels
b) Formulating meal with low (below recommended values) protein levels
c) Diluting meal that was originally formulated in the usual way (dilution is most often achieved by introducing poorly digestible ingredients, such as rice or oat hulls, into the structure of the meal)

A practical problem with the application of qualitative restriction is the appearance of wet litter due to higher content of crude fiber in the meal (diluted diet), as well as increased feed consumption (individuals increase consumption of diluted feed to meet their energy requirements), which increases the price per energy unit of feed [3, 16].

4. The success of the feed restriction program

The extent of compensatory growth can be quantified by the compensatory index, which can be calculated as the ratio of the difference between weight variation at the end of restricted and compensatory growth periods, respectively, relative to the variation at the end of the restricted growth alone. A value of 100% indicates full recovery [8]. According to Wilson and Osbourn, [19] there appear to be six main factors (acting together) governing an animal's ability to recover weight and the final conformation and composition:

(a) The nature of undernutrition.
(b) The severity of undernutrition.
(c) The duration of undernutrition.
(d) The stage of development at the commencement of undernutrition.
(e) The relative rate of maturity of the species.
(f) The pattern of re-alimentation.

Regardless the type of applied technique, by increasing the intensity (severity) and/or duration of the restriction, the individual's ability to recover and exhibit compensatory growth reduces [19). Considering the optimal length of the restrictive feeding program, McMurtry et al. [20] suggested that for male broilers, the given period should be limited to a maximum of seven days, and for females to a maximum of five days. Jones and Farrell [21] preferred a short duration of restriction, with a period of four days being considered the best choice, because it allows individuals to fully recover and exhibit compensatory growth. It is difficult to determine the optimal age of the individuals to start applying the restrictive program, having in mind the different duration of the fattening period, the type of applied program and the desired results. The first week of broilers fattening is considered particularly sensitive given the high intensity of metabolic processes, insufficient development of the digestive tract and limited physical ability to apply the restriction to individuals [4]. In flocks with an even sex ratio, it is recommended to start a restrictive program at the age of 5-7 days. If only males are used, then this program can be successfully applied at the age of 3-11 days, while in females a decrease in body weight can be expected if program is applied at a later age (9-11 days of age). Therefore, it is recommended for females to start the restriction at the age of 5 days [17]. There are no clear explanations for these gender differences, but they have been attributed to male hormones responsible for the manifestation of accelerated growth [19, 17].

The restrictive program does not end with the transition to a recovery period, i.e. *ad libitum* nutrition, but requires consideration of the special (additional) requirements of broilers during this period. In most studies, after the cessation of the restriction, during the *ad libitum* feeding period, the broilers received feed common to a given fattening period. However, Fjeld et al. [22] indicated that protein content in broiler diet could be a limiting factor during the recovery period. More precisely, Plavnik and Hurwitz [23] indicated increased broiler requirements for essential amino acids during the 7-day period after cessation of restriction and the need to supplement their diets so that compensatory growth can be fully manifested. After switching to *ad libitum* nutrition, broilers greedily ingest feed (the first 24-36 hours after the restriction period), which can lead to suffocation and death. Therefore, the return of individuals to the *ad libitum* diet should be carried out gradually and carefully [16].

5. Influence of restrictive nutrition on feed conversion (feed efficiency)
Accelerated growth of broilers, after a period of restrictive feeding, is achieved thanks to energy and other nutrients from feed, which are mostly directed and used for productive purposes (for growth), and less to meet the requirements for maintenance (non-productive purposes). Lower maintenance (life support) requirements result in smaller body size, lower body weight, and slower metabolism of animals that have been subjected to restrictive program [24].

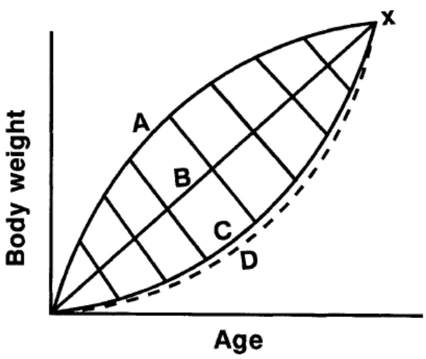

Figure 1. Different broiler growth curves (slow and fast growing lines) [25]. Lines A, B and C represent three potential growth curves of broilers reaching approximately 2 kg body weight (x) at 42 days of age.

Figure 1 gives a schematic representation of the different broiler growth curves for birds weighing 2 kg at 42 days of age, described by Leeson and Summers [25]. When broilers grow at a steady rate (intensity), their growth corresponds to line B and represents perhaps a biological ideal in terms of minimizing stress, i.e. continuous, stable growth, with no major periods of slow or rapid growth. In practice, however, few animals grow with such statistical precision. Birds with growth shown through lines A and C, also reach a weight of 2 kg at 42 days, but the routes they follow are quite different. Bird A has faster initial growth and then slower growth as it approaches slaughter weight x. Bird C initially has slower growth, which then accelerates towards slaughter weight x. Slow-growing lines of broilers (bird C) grows more slowly initially, but faster later, while the fast-growing lines (bird A) behave in the opposite fashion [26]. Bird C will achieve better (lower) feed conversion compared to bird A, because they will have lower requirements for life support, since at any age, before reaching point X, they have a lower body weight and need less nutrients to maintain life. It should be noted that smaller individuals still have (relatively) higher life support requirements than large ones, if the values are observed in relation to body weight; however, in absolute quantities (expressed in absolute values of grams of feed or KJ), they are certainly smaller too [10]. In other words, lower life support needs throughout the fattening period result in directing more ingested feed for growth, i.e. for productive purposes, and thus, improved feed efficiency, i.e. better feed conversion.

Scientists [27, 19] found that after restrictive nutrition, broilers achieve higher relative feed consumption (relative to body weight) compared to individuals who received feed *ad libitum*. In this way, broilers also consume a larger amount of energy through feed, which is necessary for achieving compensatory growth. Increased feed intake can be explained by the adaptation of the broiler digestive tract to restrictive dietary conditions, i.e. relative (in relation to body weight) increase in the weight of the digestive organs, especially the stomach, glandular and muscular stomach, pancreas and liver during and after the restriction period. In addition to the previously described factors, numerous studies have found that individuals subjected to a restrictive diet exhibit a certain degree of metabolic adaptation to given conditions, which is reflected in lower metabolic heat production, as a consequence of slowing metabolism. Lower metabolic heat production in the individual's body (since it leads to reduced energy consumption for unproductive purposes) has a positive effect on feed conversion. The mentioned metabolic adaptation continues even after the period of restriction, i.e. after the transition to the *ad libitum* diet, but it does not last long. Calorimetric measurements found no differences between broilers (in metabolic heat production) five days after the end of the restriction period [27]. Although the mechanisms responsible for these processes have not been fully elucidated, the decreased metabolic heat production during the restriction period is associated with an established decrease in serum triiodothyronine (T3) concentration [28] and lower sympathetic nervous system activity in birds (29). It should be noted, however, that low circulating T3 during energy restriction could be the consequence rather than the cause of low basal metabolism [8].

6. Influence of feed restriction on body fat storage

Increase in growth rate through genetic selection and improved nutrition in broiler chickens has been associated with high body fat deposition. This is particularly evident under *ad libitum* feeding that is normally practiced [30, 9]. The results of numerous studies have indicated an association between high fat content (and intake) in the human diet with the incidence of cardiovascular disease and cancer. Therefore, in recent years, consumer preference for chicken meat in the human diet has increased, and chicken meat products with additionally reduced fat levels would have an advantage when consumers are choosing meat products. The high deposition of fat in the body of broilers, in addition to being undesirable to consumers, also constitutes an economic loss for producers. Namely, by increasing the share of fat in the structure of growth, its energy value increases, and thus, the amount of consumed feed that is necessary for its realization increases as well [10, 6]. Field observations on the influence of obesity in individuals at an early age on the development of obesity in adulthood have initiated numerous studies on metabolic programming in poultry, i.e. the possibility of managing the processes responsible for the development of broiler obesity (hyperplasia and hypertrophy of adipocytes). Metabolic programming can be defined as a physiological process whereby early adaptation to a nutritional stress permanently changes the physiology and metabolism of the organism and continues to be expressed even in the absence of the stress that initiates it [31]. Studies have shown that feed restriction could decrease fat content and increase protein deposition in carcasses, thus resulting in improved carcass composition [32, 33].

Slowing down the growth of broilers is achieved by applying a restrictive diet, mainly during the second week of age, with the aim of changing (reducing) the hyperplastic growth of adipocytes, which at this age is of the greatest importance (participation) in adipose tissue growth. In this way, adipocyte proliferation is reduced and/or delayed, thus reducing the incidence of obesity in the broilers of market age [17]. In other words, the reduction of abdominal fat in response to restrictive feed intake in the early period of broiler fattening is the result of a reduced number of fat cells in their older age [34, 35, 36]. Also, during this restriction period, individuals mobilize body fat faster to provide the necessary energy supply [31]. It has been shown that early feed restriction results in lower hepatic acetyl-CoA carboxylase activity, a rate-limiting enzyme for fatty acid synthesis. This can limit hepatic triglyceride synthesis, causing lower serum triglyceride concentration, and therefore, it partly contributes to reduce fat accumulation [37]. It is necessary, however, to take into account the fact that after a period of restrictive nutrition, when individuals re-feed *ad libitum*, adipocytes retain the possibility of hyperplasia and this process continues, so the described technique can have negative effects on carcass quality if not applied at the right time. With a restrictive diet, the process of adipocyte hyperplasia is certainly delayed, and given the short period of broiler fattening, it is necessary to determine the optimal time (but not too early) to start a restrictive diet, in order to achieve the planned improvements. Also interesting are the observations of scientists who found that during the period of restrictive diet, the activity of enzymes responsible for lipogenesis in the liver decreases (in broilers 50% of fat synthesis takes place in the liver) [38], but after switching to *ad libitum* nutrition, their activity grows significantly. Only two weeks after the cessation of the restrictive diet, the level these enzymes decline again and reach even lower values compared to those observed in individuals in which no restrictive diet program was applied [10, 36]. The results presented indicate the importance of proper application, and above all, the importance of determining the optimal time to start a restrictive diet (not too late), which in recent studies, is usually conducted at the end of the first week (5-9 days) or at the beginning of the second week of fattening (7-11 days). In the described way, excessive fat deposition is reduced, and individuals are given enough time to show compensatory growth and reach the same body weight as those who were on the *ad libitum* diet from the beginning of fattening. In previous research, restrictive feeding was practiced during older age (mainly during the second and third weeks), as well as longer duration of the program, but at that time broiler fattening lasted much longer (up to 56 days), which had its physiological and nutritional justification.

In addition to determining the optimal time to start and the duration of the restrictive diet, the success of the given programs largely depends on the intensity of the restriction, as well as the type of applied technique. By increasing the intensity and duration of the restriction, the ability of the animal to recover decreases, and thus its ability to undergo compensatory growth lessens too. If the restrictive feed intake is too mild (insufficiently intensive) or its application is short-lasting, the animals will show compensatory growth, but the level of body fat will be increased. Otherwise (if the restrictive intake is too intense and lasts a long time), the animals will not be able to show compensatory growth, and the impact of the applied program on the level of body fat will not be consistent. Therefore, in order to succeed in implementing a restrictive program, it is necessary to find an optimal balance between the intensity and duration of limited feed intake. The influence of the intensity of the restriction on the success of the applied program can be summarized through three possible cases [21]:

1. If an animal loses a certain percentage of its body weight during a restriction, recovery will be slow and body fat levels will be reduced.
2. If the animal gains weight during the specified period, the recovery will be complete, but the body fat level may increase.

3. If the animal maintains a constant body weight during the restrictive period, the recovery will generally be complete and the fat level reduced.

In order to maintain a constant/unchanged body weight during the restriction phase (as in the above case 3), it is necessary to provide only life maintenance requirements through diet. Although it has been shown in previous examples that applying the formula EI (KJ ME / day) = 6.2 x $BW^{0.667}$ provides broilers with only maintenance requirements, Jones and Farrell [21] found that broilers subjected to a given diet nevertheless gain a certain percentage of body weight (which corresponds to the previously mentioned case 2). Only when they applied a more intensive restriction program (3.1 kJ x $BW^{0.667}$ per day) were maintenance requirements alone achieved, and the body weight of broilers was unchanged (without increase and without weight loss) [21]. By applying the given restriction program for 4 days (from the 7^{th} to the 11^{th} day of fattening), broilers achieved compensatory growth, and the level of body fat was reduced. By shortening the implementation of the given program to 3 days, the mentioned improvements were absent. These results illustrate very well the connection between the intensity and length of the restriction period and the possibility of achieving the desired results in practice.

In addition to the above, restriction of feed intake in broilers can be achieved by other techniques, such as the use of a diet with reduced protein content. However, after switching to an *ad libitum* diet, broilers show accelerated growth (which is not always compensatory), but this type of program, in most cases, results in an increase in body fat [35, 39]. Therefore, the application of such programs has been largely abandoned in practice. Research has also shown the frequency of feeding can also affect fat metabolism. Rare, but abundant meals encourage the development of obesity because excess of feed intake (energy and other nutrients) is deposited in the form of body fat. Yu et al. [7] found the application of a restrictive broiler diet, which included only the provision of maintenance requirements for animals in the period from 8 to 14 days of fattening, had the greatest effect on reducing body fat when applied daily, while the effects were significantly less pronounced when the same program was applied using the skip-a-day technique.

Considering that in a large number of studies, the application of restrictive programs resulted in a reduction of body fat in broilers, but at the same time the desired body weight was not achieved at the slaughter (market) age, these programs should not be *a priori* rejected as ineffective. Namely, it is necessary to consider their economic profitability, i.e. to determine whether the market price of the poultry meat with its reduced fat content justifies the lower body weight of broilers achieved at the end of the fattening period.

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