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Physiological aspects of compensatory growth in pigs

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ABSTRACT

Compensatory growth is a specific type of growth exhibited by animals, which were previously exposed to nutritional restriction. This restriction could be induced by feed quantity and quality consumed by animal. When feed and nutrients supply again become abundant (realimentation period) growth rate of these animals accelerates and exceeds this achieved by comparable animals fed well and continuously. Animal's homeostatic mechanism, which responds to an increase both amount of feed available during realimentation as well as its quality is biologically complicated. During this time a lot of changes occur in: voluntary feed intake, partitioning of energy and protein in daily gain, protein turnover, body metabolism and endocrine state as well. Recognizing of these events allow precisely described a place of organism where compensatory growth occurs as well as to understand role of these processes in mechanism of compensatory growth.

KEY WORDS: pigs, compensatory growth

INTRODUCTION

Growth is usually defined as an increase in the size and weight of an animal in a particular environment when the limitations imposed by this environment allow an animal to fully express its growth potential (Ryan, 1990). An animal's growth from birth to maturity is described by a sigmoid curve, whose shape, due to environmental factors, never achieves its theoretical potential (Campbell, 1988). One of the most important factors affecting the course of a growth curve is variable supply of feed, especially energy and protein. The supply of these feed components is not always sufficient to allow animals to express their genetic potential for growth and, in

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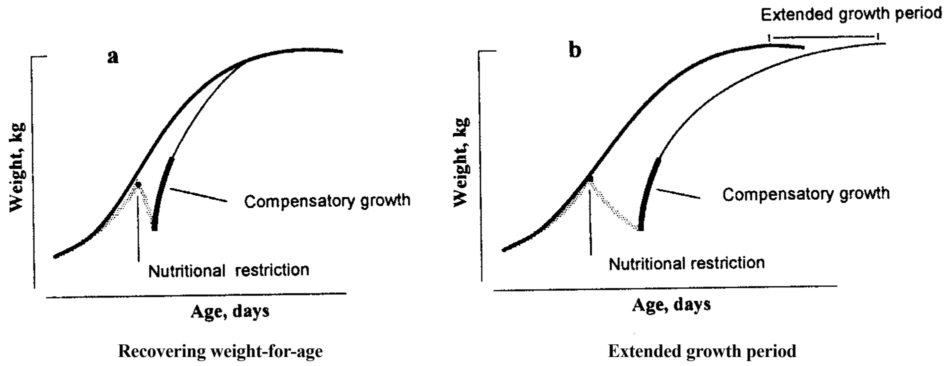

Figure 1. Compensatory growth (adapted from Hogg, 1991); a. recovering weight for age (complete compensation), b. extended growth period

this case, their growth rate falls. In such cases, the genetically encoded smooth progression along the sigmoid-shape of the growth curve is disrupted. However, when the nutrient supply again becomes abundant, the growth rate increases and achieves or even exceeds that expressed by comparable animals consistently fed well (Donker et al., 1986; Anugwa et al., 1989; Kyriazakis et al., 1991; Stamataris et al., 1991; de Greef, 1992; Bikker, 1994). This accelerated growth rate (live weight change, kg/day) is called compensatory growth. Theoretically, animals can exhibit two types of compensatory growth. The first is called recovering weight for age or complete compensation (Figure 1) and occurs when compensatory growth is so strong that the pig attains the same weight (size) and body composition at the same age as genetically identical, non-restricted animals. The second type of compensatory growth is called an extended growth period or partial compensation and occurs when animals increase their growth rate temporarily (mainly for a short time after restriction is changed to realimentation), then returns to a rate represented by non-restricted animals. For this reason, it is impossible for these animals to achieve the same weight (size) and body composition at the same age as pigs growing along the "normal" pathway.

FACTORS AFFECTING COMPENSATORY RESPONSE

Body development at the beginning of the restriction period

Control of body size at the tissue level occurs through DNA content, which reflects cell number; cell size, however, reflects the protein:DNA ratio (Grant and Helferich, 1991). In the early stage of growth, hyperplasia (cell proliferation) is the main process, followed by a period in which both hyperplasia and hypertrophy (cell enlargement) occur concurrently; later growth predominantly involves hypertrophy (Winik and Noble, 1965). In pigs, tissue and organ growth by cell proliferation continues for more than 7 weeks after birth (Sarkar et al., 1977). Therefore, if restriction falls on the stage of growth in which hyperplasia predominates, cell number can be strongly reduced, and, after realimentation, normal body size and composition will not be achieved. If, however, restriction of similar severity and duration is imposed later, restricted hypertrophic growth has no permanent effect on the final body size and composition of the animal. This could partially explain the discrepancies in results among authors reporting the presence or lack of a compensatory response.

Type of underfeeding

From the nutritional point of view, the growth of pigs is usually inhibited by the quantity or quality of feeds offered them, mainly by protein (amino acids) and energy content, however, lately also by substitution of some part of commercial feed by high-fibre components due to increased interest in incorporating the compensatory growth phenomenon in out-door rearing of pigs (e.g., Skiba et al., 2004).

Depending on the type of undernutrition, the body of animals changes differently (Tables 1 and 2). The main differences concern fat and protein stores in the body as well as the size of entrails. Pigs that consume less feed have a lower entrail weight, especially of those metabolically highly active organs like the liver, kidneys, large and small intestines (Kong et al., 1982; Close et al., 1983; Skiba et al., 2001), and lower fat but higher protein stores. Whereas those that consume low protein but the same amount of energy as adequately fed animals have higher fat and lower protein stores in the body and their entrails do not differ from adequately fed pigs (de Greef, 1992; Skiba et al., 2001).

Table 1. Influence of feed (energy) deficiency on body protein and fat stores, and size of entrails

Author	Restriction		Difference in body composition, %		
	duration kg-kg	daily allowances %	protein store	fat store	size of entrails
Campbell et al. (1983)	2 - 6	-12	nd	-36	nd
Campbell et al. (1983)	6 - 20	-46	nd	-40	nd
Gadeken et al. (1983)	5 - 25	-55	+16	-43	nd
Sarkar et al. (1983)	2 - 10	-67	+44	-53	nd
Stamataris et al. (1991)	6 - 12	-45	+11	-37	-26
Bikker (1994)	20 - 45	-40	+8	-22	-18
Skiba (2000)	15 - 25	-40	+7	-30	-20

nd - not determined

Table 2. Influence of protein deficiency on body protein and fat stores, and size of entrails

Author	Restriction		Difference in body composition, %		
	duration kg-kg	daily protein intake, %	protein store	fat store	size of entrails
Wylie et al. (1969)	5 - 24	-68	-19	+122	nd
Campbell et al. (1978)	5 - 20	-35	-13	+75	nd
Campbell et al. (1983)	6 - 20	-25	-17	+64	nd
Rao et al. (1990)	33 - 55	-37	-1	+16	nd
Kyriazakis et al. (1991)	6 - 12	-40	-18	+113	-4 (ns)
De Greef et al. (1992)	28 - 65	-72	-20	+87	Nd
Fandrejewski (1994)	15 - 30	-40	-8	+27	-4 (ns)
Quiniou et al. (1995)	22 - 50	-27	-10	+54	Nd
Skiba (2000)	15 - 25	-40	-6	+43	-3 (ns)

nd - not determined, ns - insignificant

Pigs restricted by substituting some part of a commercial feed with a high fibre component (e.g., by mixing a standard diet with grass meal) have unchanged protein but lower fat stores and their entrails are heavier than in commercially fed pigs (Skiba et. al., 2004). In restrictively fed pigs, changes in organ size (weight), especially those that belong to the alimentary tract, are positively correlated with duration of restriction. The findings shown in Tables 1 and 2 clearly indicate that feed (energy) deficiency increases the protein:fat ratio in the body, while protein deficiency decreases it. This regularity is found in all of the cited works, regardless of the duration and severity of the restriction and body weight of animals. Scarce data on the body composition of pigs as influenced by previous underfeeding by increasing the fibre content in the diet do not make such a comparison possible. However, a study by Skiba et al. (2004) indicates that the protein:fat ratio of pigs so fed is also increased (similarly to those underfed with in terms of feed intake).

EVENTS OCCURRING DURING COMPENSATORY GROWTH

Feed intake

After removal of a growth suppressor, pigs exhibit changes in voluntary feed intake depending on the type of previous restriction. Animals previously consuming smaller amounts of feed usually increase feed intake (Anugwa et al., 1989; Stamataris et al., 1991). The course of feed intake during realimentation differs depending on its phase (Figure 2). Immediately after cessation of the restriction, feed intake increases rapidly, which is connected with filling of the alimentary tract. This response is also the main reason for increasing the growth rate during this period of realimentation. During the following two weeks, due to the restricted capacity of the gastrointestinal tract as a consequence of previous restriction leading to a smaller size of the intestines, the feed intake of these pigs is even lower in comparison with pigs fed continuously according to their requirements. Beginning from about the fourth week of realimentation, feed intake increases gradually, becoming significantly larger during the last two weeks of realimentation. Such a response indicates that growing pigs previously restricted by feed intake need some time (about 3-4 weeks) to recover the capacity and size of their gastrointestinal organs to *ad libitum* feeding.

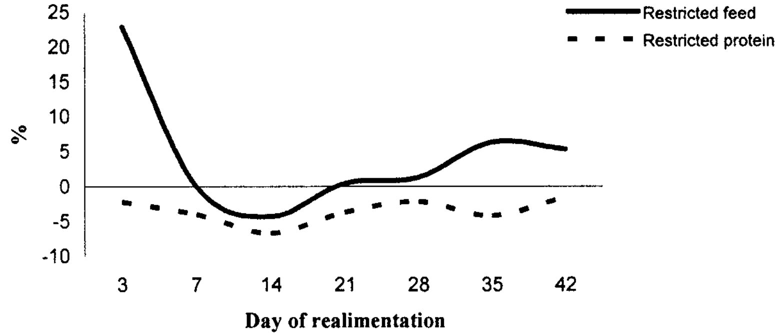

Figure 2. Difference in daily voluntary feed intake (% of control animals) of realimented pigs previously restricted by feed or protein intake (adapted from Skiba, 2000)

The feed intake of pigs previously restricted with protein is usually lower (or insignificantly exceeds the amount of feed consumed by control animals) throughout the realimentation period. Similar findings were also reported by Kyriazakis et al. (1991), de Greef (1992), Crister (1995) and Fabian et al. (2004). It seems that body fat stores, which are greater in the pigs treated in this way, can partially the lower appetite of these pigs, as it is well known that there is an inverse correlation between body fat content after starvation and feed intake during recovery (Dullo, 1997), however another mechanism could also be involved.

Unexpected feeding behaviour is observed in realimented pigs previously fed a high fibre diet (Skiba et al., 2004). The authors observed that pigs restricted by high fibre diet, but fed *ad libitum*, gradually increased feed intake if the restriction period was prolonged. In this way at the end of restriction they were able to almost compensate daily energy and crude protein intake. This unexpected response of pigs resulted in the severity of the restriction lessening as its duration increased. For this reason, increased feed intake during subsequent realimentation was short in pigs with a previously shorter duration of restriction, but in those who had previously undergone longer restriction, there was no increase in feed intake.

Growth rate

Significantly greater growth rates of pigs previously underfed by protein intake (Kyriazakis et al., 1991; de Greef, 1992; Fandrejewski, 1994; Fabian et al., 2002, 2004) as well as those previously restricted with feed/energy (Donker et al., 1986; Anugwa et al., 1989; Stamataris et al., 1991; Bikker, 1994) have been reported. In the cited literature, both *ad libitum* and restricted feeding were applied during realimentation, which proves that feeding regime and change in feeding behaviour are not the most important factors that influence the compensatory growth of animals. The faster growth rate does not last throughout realimentation, but it is significantly exhibited throughout 4-6 weeks after the change in diet (Tulis et al., 1986; Skiba et al., 2001). In most cases of compensatory growth, pigs characterize better the feed conversion ratio as compared with non-restricted animals.

Composition of daily gain

The faster growth rate of pigs showing compensatory growth is closely connected with a change in the proportion between daily gain components, especially between protein and fat, and probably water. The growth rate is most influenced by protein deposition due to increased efficiency of protein accretion resulting from concomitant water deposition. That is why 1 gram of deposited protein entails more body mass gain than the deposition of 1 gram of fat.

Greater daily protein deposition was detected in the body of pigs previously restricted with both feed (Bikker, 1994; Skiba et al., 2002) and protein intake (Kyriazakis et al., 1991; de Greef, 1992, Fandrejewski, 1994; Skiba, 2000; Fabjan et al., 2004). However, the site of this enhanced protein deposition depends on the type of previous restriction. It takes place in the carcass (de Greef, 1992; Skiba, 2000) of pigs previously restricted by protein intake, but in the case of previous feed/energy restriction, mainly in the entrails (Stamataris et al., 1991; Bikker, 1994; Skiba, 2000) whose growth proceeds to a very high rate during realimentation. Besides greater protein deposition, pigs previously restricted with feed/energy intake also deposit greater amounts of fat. Whereas lipid deposition in pigs previously restricted with protein intake is usually similar or lower as compared with continuously well-fed pigs (Bikker, 1994; Skiba et al., 2002).

A few studies carried out with ruminants (e.g., Carstens et al., 1991) also suggest that the water:protein ratio is increased during realimentation. According to this, the faster growth rate observed during early stages of realimentation could be the result not only of greater protein, but also of enhanced water deposition. However, studies addressing this question in pigs are lacking.

Upon analysing the response of previously underfed animals regarding changes in daily gain composition it could be supposed that partition of growth components between protein and fat during realimentation is steered to meet the genetically coded chemical body composition of pigs. This means that the compensatory response is directed first to this body component, or part of the body, whose growth had been reduced the most during previous restriction (Skiba et al., 2002). In the case of pigs previously underfed with protein, body protein stores are strongly reduced, so during realimentation this body component is restored first of all, even at the cost of fat deposition. In the case of pigs previously restricted with feed/energy intake, fat stores as well as size of entrails are significantly lower; after changing restriction for realimentation, the compensatory response is located in the viscera, and the remaining feed components, mainly energy, are directed to restore body fat stores.

Maintenance requirement

As mentioned earlier one of the responses of animals to restriction of their daily allowance (energy) is reduced growth of metabolically active organs (Kong et al., 1982; Close et al., 1983; Bikker, 1994; Skiba, 2000) and consequently reduced maintenance requirements, as the size of those organs directly influences these requirements (Noblet et al., 1997). Although the cost of maintenance (ME_m) is clearly defined (Wenk et al., 2001), it is very difficult to measure, especially in growing (producing) animals, as energy accretion or production are physiological processes occurring in a young organism. The situation become even more complicated as ME_m is often defined to include "normal" activity. Thus, separation of ME_m is virtually impossible and seems to be insignificant in this group of animals. For these reasons there are only a few studies supporting a hypothesis concerning a lower ME_m of animals during compensatory growth (e.g., Ryan, 1990; Skiba, 2000). In the latter study, the author suggests that ME_m of "normally" growing pigs (15-25 kg BW) amounted to 681 $kJ/kg^{0.75}$ and in those that received 40% less feed, this value equaled 603 $kJ/kg^{0.75}$ (assuming the same energy costs of protein and fat deposition in both groups). Thus, animals of a similar liveweight may start realimentation with a considerably lower maintenance requirement. This allows them to transfer more energy for faster growth (greater protein deposition). However, a rapid increase in the size of internal organs during realimentation of so-treated pigs is also observed. Consequently, at the end of realimentation, their size is the same or even larger than in control pigs (Koong et al., 1982). Due to this, it seems that lower ME_m could play a significant role, but mainly in the short time after changing restriction for realimentation.

Fat stores in the body

If the smaller size of metabolically active organs can play a role in the compensatory response of pigs previously restricted with fed intake, it can also be assumed that in pigs previously restricted with protein intake, increased fat stores in their bodies, resulting from the kind of restriction, could also be utilized by animals for faster growth. Unfortunately, there is no research evidence clearly supporting this hypothesis, but our studies (Skiba, 2000), indicate that there exists a significant correlation ($r=0.33$; $P<0.05$) between fat stores at the end of restriction (beginning of realimentation) and daily protein deposition during subsequent growth stages.

Thus, it could be supposed that both lower ME_m as well as high fat stores in the body at the beginning of realimentation allow pigs to "transfer" a greater amount of energy for faster growth (greater protein deposition), thereby contributing to the compensatory response.

Protein turnover

Protein accretion is the difference between its synthesis and degradation. Four "scenarios" of overall protein turnover can explain increased protein deposition. In each "scenario" processes of protein synthesis and degradation occur differently (Table 3).

Table 3. Possible changes in protein turnover potentially increasing protein gain

Protein turnover	1	2	3	4
Protein synthesis rate	↑	↑	↑↑	↓
Protein degradation rate	↓	↔	↑	↓↓

adapted from Lars Kristensen, 2003

Millward et al. (1975) in a study on rats, measured protein synthesis and degradation rates following protein restriction and confirmed that the third "scenario" may contribute to compensatory protein gain. However, the increased synthesis rate was detectable immediately after 1 day of realimentation, whereas an increased degradation rate was detected considerably later. Jones et al. (1990) in a study with cattle, and Therkildsen et al. (2002) in a study with pigs also confirmed these findings. However, Sarkar et al. (1983) found that the faster rate of protein deposition during realimentation is a result of increased synthesis that dominates the invariable rate of protein degradation, which could also prove that scenario 2 is also possible. According to Sarkar et al. (1983), the RNA:DNA ratio, which expresses muscle-cell activity (rate of protein synthesis), was already considerably higher in the middle of realimentation in pigs that were previously restricted. After this time, cellular activity decreased to levels shown by control animals. A recent study by Danish researchers (Kristensen et al., 2002; Oksbjerg et al., 2002) also confirms that muscle-cell activity is greater in realimented animals. Oksbjerg et al. (2002) concluded that the similar final concentration of DNA in realimented vs control pigs suggests a higher rate of satellite cell proliferation in realimented pigs, as satellite cells are the only known source of postnatal DNA. They can proliferate as a response to external stimuli, e.g., injury and regeneration, and fuse with muscle fibre, adding new nuclei, thereby providing "machinery" for protein synthesis (Allen et al., 1979). Oksbjerg et al. (2002) also concluded that an increased RNA:DNA ratio in realimented pigs indicates that increased protein synthesis capacity was also partly involved in the compensatory response.

Compensatory growth vs meat quality

Degradation of protein is an inseparable part of protein turnover. However, the mechanism of proteolysis is not fully understood, and therefore difficult to control. The calpain system (m-calpain, μ-calpain and their inhibitor, calpastatin; Goll and Thompson, 1999) has a great impact on muscle proteolysis (beside other factors). It has been known for a long time that the activity of calpains positively correlates with growth rate (Brooks, 1983) and that at slaughter, its activity is strongly involved in the process of postmortem meat tenderization (Vanderwesthuyzen et al., 1981). Hence, recently much attention has been focused on the use of compensatory growth to improve the quality of pork (Kristensen et al., 2002; Oksbjerg et al., 2002; Therkildsen et al., 2002). These studies hypothesized the existence of a relationship between feeding intensity, protein turnover, muscle growth, postmortem proteolysis and the tenderization rate. These relationships are graphically shown in Figure 3. In the above cited studies, pigs were subjected to different durations of restriction/realimentation lasting from 28 to 160 days of age. Its impact on meat tenderness was found to be considerable. Therkildsen et al. (2002) stated that in order to use compensatory growth mechanisms to improve tenderness, the optimal time of slaughter may not coincide with the period of highest growth rate, but may occur at a later stage, when muscle protein degradation is maximal. In their opinion, the highest activity

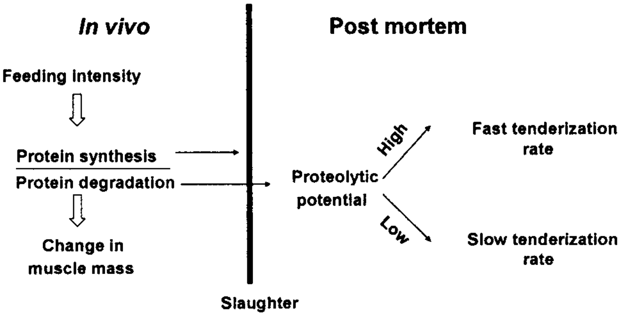

Figure 3. Relationship between feeding intensity, protein turnover, muscle growth, post-mortem proteozysis and the tenderization rate (adapted from Kristensen, 2003)

of μ-calpain for compensating pigs slaughtered at about 100 kg BW, occurs beyond 42 days of realimentation. However, the shear force of the meat of these pigs was not significantly less as compared with pigs fed *ad libitum* throughout.

Endocrine changes

A little information is available on associated hormonal changes occurring during compensatory growth. The hormones that influence compensatory growth the most are: growth hormone (GH), insulin-like growth factor (IGF-I), insulin, and thyroxine, as these hormones play a crucial role in growth regulation. Paradoxically, in animals subjected to starvation or losing weight, plasma GH levels are elevated (Ellenberger et al., 1989) followed by a rapid decrease and return to normal levels within 7-14 days of realimentation (Mosier et al., 1985). IGF-I and GH levels are closely related during normal growth, as GH stimulates production of the latter and this has a negative feedback on GH. It seems that during restriction, this relationship is uncoupled and usually IGF-I levels are unchanged despite elevated GH levels (Ellenberger et al., 1989). Changes in plasma insulin concentrations observed during both restriction and realimentation generally mirror GH changes (Blum et al., 1985). Thyroxine levels have been observed to drop significantly during restriction followed by a rapid increase during the first 3-4 days after changing restriction for realimentation. The largest peak of this hormone coincides with the time at which GH levels begin to fall.

Observations of plasma levels of the major hormones, occurring shortly after rapid changes in nutrition, suggest that the endocrine system is involved in short-term as well as long-term control of the body's physiological state (Hogg, 1991). However, clear understanding of the role of particular hormones that are involved in compensatory growth is difficult, as hormonal regulation of growth involves complex interactions among various hormones.

CONCLUSIONS

Compensatory growth should be viewed as a transitory period following nutritional stress, during which an animal's homeostatic mechanism responds to an increase in both the amount of available feed as well as its quality. During this time many changes occur in: voluntary feed intake, deposition of fat and protein in daily gain, protein turnover, body metabolism and endocrine status. Recent advances in knowledge still do not allow a clear conclusion to be drawn about which mechanism predominates in the abnormally high growth rate exhibited by compensating animals.

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STRESZCZENIE

Fizjologiczne aspekty wzrostu kompensacyjnego

Wzrost kompensacyjny jest szczególnym rodzajem wzrostu zwierząt uprzednio niedożywianych. Niedożywianie może być wywołane zarówno ilością jak i jakością pobieranej paszy. Kiedy podaż paszy i składników pokarmowych powraca do „normy” (okres realimentacji) tempo wzrostu tych zwierząt jest większe i przewyższa tempo wzrostu porównywalnych zwierząt żywionych prawidłowo przez cały okres wzrostu. Mechanizm homeostazy odpowiadający na zwiększenie ilości i jakości paszy pobieranej w okresie realimentacji jest biologicznie bardzo złożony. W tym czasie występuje wiele zmian w pobieraniu paszy, podziale energii i białka w przyroście dziennym, „obrocie” białka, przemianie energii i gospodarce hormonalnej zwierząt. Rozpoznanie tych zjawisk pozwoli na dokładne określenie miejsca w organizmie, w którym wzrost kompensacyjny występuje, jak również pozwoli na zrozumienie mechanizmów regulujących wzrost kompensacyjny.