UNFAVOURABLE SIDE IMPLICATIONS OF ANIMAL BREEDING IN LIVESTOCK SPECIES: A REVIEW

IMPLICAÇÕES DESFAVORÁVEIS DO MELHORAMENTO ANIMAL NAS ESPÉCIES ZOOTÉCNICAS: UMA REVISÃO

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SUMMARY

Unfavourable side effects associated to animal breeding in livestock species have become more evident because of problems regarding the performance of populations with high genetic merit, resulting from trade-offs of indirect selection for behavioural, physiological and immunological traits. Especially in dairy cattle, swine and broilers, selection for economically interesting traits have brought about great impact on growth, reproduction and general metabolism, often demanding more attention from breeders than the responses correlated to the selection criteria used. Thus, this review aims to cover the main aspects of this unfavourable impact concerning animal breeding in livestock species which might favour a more adequate establishment of the strategies used in selection programs.

RESUMO

Os efeitos desfavoráveis associados ao melhoramento de espécies zootécnicas têm se tornado mais evidentes devido a problemas de desempenho detectados em populações com elevado mérito genético, resultantes da seleção indireta para características comportamentais, fisiológicas e imunológicas. Especialmente no gado leiteiro, suínos e frangos de corte, a seleção para características de interesse econômico trouxe grande impacto sobre o crescimento, reprodução e metabolismo geral dos animais, muitas vezes exigindo mais atenção dos melhoristas às respostas correlacionadas dos critérios de seleção utilizados. Assim, esta revisão tem como objetivo discorrer sobre os principais aspectos desse impacto desfavorável do melhoramento das espécies zootécnicas, o que pode contribuir para um estabelecimento mais adequado das estratégias utilizadas nos programas de seleção.

INTRODUCTION

Animal breeding has increased production rates in livestock species bred for economic purposes. Traits such as meat, milk and eggs production, carcass composition and food conversion are directly related to the economic efficiency of the production systems and they consequently receive special attention in breeding programs (Pereira, 1999).

High accuracy of genetic values associated with genetic variability of the populations and moderate to high heritability of the productive traits, have allowed the success of breeding programs. However, together with the desirable effects of selection for high production and economic efficiency, negative effects have become more evident. These effects are generally associated to behavioural, physiological and immunological traits (Rauw *et al*., 1998), because selection for high production efficiency may result in a correlational response in other traits, because the traits involved may be genetically correlated (Pereira, 1999).

Therefore, selection criteria used in animal breeding programs may lead to an indirect selection for other traits, which may affects animal welfare as so as animal health, often not favourable to the animal's development or performance. This review aims to present several of these unfavourable effects and their consequences for breeding programs strategies.

HOMEOSTASIS AND TRADE-OFFS

To understand the effects of genetic progress in domestic animals it is necessary to familiarise oneself with the concept of homeostasis (Figueiredo, 1998).

The latter describes the property of a system to regulate its internal environment in response to changes in the external environment to maintain a stable, more or less constant condition (Manuila *et al*., 1997). Additionally, any selective pressure may interfere with the regular biological functions abilities, and the individuals may respond internally during the breeding process settling at a new homeostatic level. It may predispose the animal to diseases and impair reproduction as well as causing insufficient metabolism operation, thus impairing animal welfare and production (Ferreira *et al*., 2005).

In view of facts, the artificial selection spaces the animal from its natural condition because selection always changes the gene pool, and the mechanisms of physiological control might be altered and adapted to the new conditions (Ferreira *et al*., 2005). Therefore, it is easily conceivable that genetic selection interferes with physiological and metabolic processes which may eventually lead to unfavourable outcomes. In this manner, some traits may be indirectly selected, resulting in a trade-off between both traits, which may be evaluated by the correlational responses, which are defined as the impact on a trait caused by the selection for another one (Pereira, 1999; Van Eerden *et al*., 2004; Greer, 2008). This impact depends on the selective pressure and the heritability for the selection criteria, and mainly depends on the genetic correlation between both traits (Pereira, 1999).

Individuals have to make a trade-off between the distribution of resource-demanding life traits to obtain maximal fitness (Van Eerden *et al*., 2004). However, a trade-off may occur between performance and physiological or immunological traits that may bring several unfavourable consequences, and the next topics of this review approach the effects of inadverted co-selection of unfavourable traits in main livestock species and the so-called production diseases.

SIDE EFFECTS OF ANIMAL BREEDING IN DAIRY CATTLE

In most of the dairy cattle breeding programs, selection is directed at milk production. Such high-yield production comes at the cost of shortening of life expectancy, increase in animal mortality, reduced fertility, and compromised health (Loeffler *et al*., 1999; Leroy *et al*., 2008).

Digestion

In order to establish and to maintain a high-yield production, cattle have to be fed with a diet richer (than their normal grass diet) in easily digestible nutrients with a lower content of effective fibres (Rauw *et al*., 1998; Ferreira *et al*., 2005). However, this new feed composition has exposed animals to digestive disorders. Their physiology is not well adapted to this new diet, and they were not co-selected for physiological traits (Rauw *et al*., 1998;

Ferreira *et al*., 2005). Among main digestive disorders is the metabolic acidosis, which is caused by the increased intake of grain or other highly fermentable fodder. Clinical signs of the disorder are appetite loss, depression and potentially death. In addition, it may cause laminitis. This hoof disease develops due to fibre-digesting bacteria which function only in a very stable pH environment and do not adapt well to fluctuation in acidity (caused by the fermentation of low-fibre but starch-rich diet). The resulting endotoxins and exotoxins may then be absorbed into the bloodstream. The endotoxaemia results in impaired circulation, in particular in the feet, which in turn results in laminitis. Thus, lack of quality and quantity of fibres, respectively, are important parts of the etiopathogeny of laminitis (NRC, 2001).

Reproduction

An antagonistic relationship between high milk production and some fertility traits has been observed (Hansen *et al*., 1983; Hoekstra *et al*., 1994), because high-yield cows allocate their energy into the trait they were selected for, thus decreasing their body fat supply, which in turn has a negative impact on the animal's reproductive performance (Veerkamp *et al*., 1994; Gallo *et al*., 1996). Loss of body condition in the beginning of lactation is high in high-yield cows, creating a greater negative energy balance in these animals, which is associated with metabolic disorders and reduced fertility, such as more days open, days to first service, reduced conception at first service, longer intervals between parturitions and a greater number of services per conception/parturition (Gallo *et al*., 1996; Loeffler *et al*., 1999; De Vries and Veerkamp, 2000; Dechow *et al*., 2002; Norman *et al*., 2007). The reproductive traits are also strongly influenced by environmental factors in dairy cattle (Holmberg and Andersson-Eklund, 2006). In addition, there is also a correlation between the negative energy balance and the return of luteal activity (Veerkamp *et al*., 2000). The negative energy balance has genetic causes (Bewley and Schutz, 2008; Madalena, 2008) and may be included in the genetic evaluations, but it also can be mended with management and nutritional arrangements (Bewley and Schutz, 2008).

The quality of embryos and oocytes is reduced in these selected animals (Leroy *et al*., 2008). Therefore the selection for reproductive traits in dairy cattle as well as management and nutritional adjustments may be an important tool to profile these trades-offs.

Besides, for many years it has been highly commented among dairy cow breeders and milk producers that a superior dairy composition, associated with a high angularity of the cow's phenotype, is associated with greater milk production. However, greater angularities implies worse body condition and lead to compromised fertility (Madalena, 2008). Moreover, heifers sired by bulls selected for better angularity have a greater incidence rate of metabolic disorders as well as of foot and leg diseases (Rogers *et al*., 1999; Hansen *et al*., 2002).

Foot and leg

The progress made in dairy cattle in the selection of genes for productively desirable traits was not accompanied at the same speed by improvements in foot and leg stability. These traits, besides not having been of initial concern and thus largely ignored, are traits of low heritability (Onyiro and Brotherstobe, 2008), and are strongly vulnerable to environmental effects. Therefore, many generations have to pass until satisfactory breeding results will be obtained (Ferreira *et al*., 2005). Low impact absorption capability, excessive wearing of hoof and great pressure to the joints due to weight - associated to animals selected for high production - are the main factors which cause hoof problems in cattle (Ferreira *et al*., 2005). Hoof problems are also caused by physiological disorders as discussed above (see laminitis).

Diseases susceptibility

High-yield cows of high genetic merit display a greater incidence rate for disorders of skin, of skeleton formation, as well as infections of the mammary glandule and adjacent tissues edema and mastitis (Rauw *et al*., 1998). A QTL (quantitative trait loci) affecting both milk production and mastitis is reported (Khatkar *et al*., 2004), and class I bovine lymphocyte antigen complex alleles were associated with mastitis, milk and fat production (Weigel *et al*., 1990). Bovine class I MHC (major histocompatibility complex) alleles were also associated with fat production (Ariëns *et al*., 1996), indicating an association between immunological responses and fat contents in milk.

Brown Swiss cows carrying the Weaver gene, which causes gradually the loss of their control on hind limbs, have a greater milk yield (Hoeschele and Meinert, 1990). In cattle, selection for high milk production appears to be associated with a reduced heat tolerance (Madalena, 2008).

SIDE EFFECTS OF ANIMAL BREEDING IN SWINE

In swine production, selection is usually directed towards high growth rate, minimum backfat thickness, high rate of lean meat deposition and low feed conversion (Irgang, 1998). Selection for high growth rates is associated with physiological and anatomical dysfunctions.

Reproduction

Selection for sexual precocity in gilts must be prudent because of the economic limitations the animals might present, especially concerning a low conception rate and the number of piglets per litter, which has been observed mainly in genotypes selected for low backfat thickness and high meat yield (Irgang, 1998). The problem seems to be related to the fact that sows are still not fully grown and therefore experience physical stress during the first lactation which may lead to low ovulation and fertilization rates during the next oestrus (Irgang, 1998). Sows with a high percentage of carcass lean meat have a delayed puberty, a less intense and shorter pro-oestrus, and a vulva less red and swollen (Rauw *et al*., 1998), despite of the environmental effects which have a great impact on reproductive traits (Buske *et al*., 2006).

Selection against feed conversion may also affect significantly the reproductive performance, especially in litter size and weight, and growth rate is inversely correlated with the ability to exhibit a standing reflex, oestrus duration and age of onset of puberty (Rydhmer *et al*., 1995). Moreover, favourable alleles of estrogen receptor gene for litter size were associated with a decrease of average daily feed intake in pigs (Short *et al*., 1997).

Males with a higher growth rate are less able to mate a sow in oestrus than males with an intermediate growth rate, and the sperm quality is inferior in males with a bigger growth rate (Irgang, 1998; Robinson and Buhr, 2005), pointing that those males do not present physiological maturity for precocious reproduction.

Unfavourable side effects for reproduction may occur as a result of the direct selection for high growth rates. However, fertility in swine has increased enormously during the last decades, showing, for example, growing litter size and more litters per year, which is due to direct selection for this kind of trait applied during the last years (Pereira, 1999). This situation indicates the importance of considering both performance and fertility selection objectives in the selection process.

Litter development

Selection for large litter size is directly related to the weight reduction at birth, thus increasing variability in piglets' weight, number of weak piglets and risk of mortality (Le Dividich, 1999; Lima, 2007), therefore delaying the development of the animals. Piglet weight is positively related to backfat thickness and a strong correlation between the size of placenta and foetus weight was found (Rauw *et al*., 1998), as well as between placenta blood flow and foetus weight (Wootton *et al*., 1977), showing that piglets of larger litters are lighter because uterus blood flow decreases with the increase of the number of foetuses (Pere *et al*., 1997). Searching for individuals who display/ exhibit compensatory growth during their productive life may be an alternative to counteract the low weight at birth (Fabian *et al*., 2002).

Skeletal formation

Animals selected for high growth rate and lean meat deposition tend to have bone weakness in limbs (Rauw *et al*., 1998), and the length of productive life of an animal is intensely influenced by reproductive disorders and also by bone weakness, since there is a genetic association found between length of productive life and leg soundness score (Serenius *et al*., 2006). The occurrence of osteochondral lesions were associated with high food conversion rate, low daily weight gain, besides low initial meat pH and high paleness, both associated with poor meat processing and sensorial attributes (Kadarmideen *et al*., 2004). Continuous selection for large amounts of muscle meat deposition and high growth rate can intensify this problem (Kadarmideen *et al*., 2004).

Carcass and meat quality

Growth rate and daily feed intake are positively and genetically associated in swine (Pereira, 1999). However, daily feed intake is directly correlated to fat deposition and carcass meat yield, selection for growth rate without intake limitation results in increase of appetite, fat deposition and in reduction of carcass meat deposition (Irgang, 1998). A QTL affecting both growth and backfat thickness is reported (Bidanel *et al*., 2001). An alternative to high feed intake is the selection for residual feed intake (RFI), which is the difference between observed feed intake and expected feed intake, whereby the latter is based on metabolic body weight and growth; its negative values indicate a higher efficiency in the conversion of the food intake into weight, reducing waste of intake and consequently the fat deposition (Johnson *et al*., 1999).

Selection for muscle deposition increase might be associated with the arising of the PSE (pale, soft, exudative) phenomenon in meat, which is caused by recessive homozygosis for the Halothane gene. Breeds with muscular hypertrophy tend to develop this condition (Seller, 1998) because the genes involved in both aspects are located in the same linkage group. Recessive homozygote pigs show better feed efficiency, and greater carcass yield and carcass lean content (Leach *et al*., 1996). A QTL affecting lean meat quantity and meat paleness is also reported (Jeon *et al*., 1999).

The PSE phenomenon is triggered by animal stress before slaughter, and this situation can be increased due to the lower ability to stand environmental stress evidenced in selected pigs (Rauw *et al*., 1998). Therefore, management procedures to avoid stress conditions before slaughter could prevent PSE phenomenon.

Diseases susceptibility

Swine with greater growth rate exhibit high incidences of gastric, cardiac, renal and pulmonary problems such as pneumonia and pleuritis. These factors may bring the necessity of a limited selection emphasis for high daily growth (Irgang, 1998; Nielsen *et al*., 2006), resulting in reduction of animal productive performance, increase in mortality and production costs and impairing animal welfare.

SIDE EFFECTS OF ANIMAL BREEDING IN POULTRY

Selection in poultry is focused on fast growth, food efficiency and high carcass yield (Scheuermann, 2004). Nearly 85 to 90% of existing growth speed and body weight increase has resulted from animal breeding for weight increase at a young age (Havenstein *et al*., 1994). However, growth rate increase in broiler has caused several metabolic disorders (Rauw *et al*., 1998).

REPRODUCTION

Rapid growth selection turns into responses correlated negatively with reproductive traits such as an increase in numbers of defective eggs and infertility. Both might be attributed to neural-endocrine unbalance, disruption of gametogenesis synchrony, disorders in ovulation, oviposition and libido (Barbato *et al*., 1984). Selection for muscle weight increase might generate problems related to natural mating, because natural mating becomes unfeasible due to male sizes, therefore provoking injuries to dorsum lumbar region in females (Barbato *et al*., 1984). Nevertheless, artificial insemination has allowed carrying on with body weight selection.

Excessive body weight also seems to be associated with fertility decrease in broiler via reduced semen quality. Concentration, volume and sperm mobility reduction and an increase of death or abnormal sperm cells are reported (Rauw *et al*., 1998).

High body weight selection is also associated with an enlarged number of eggs; however, it is related to a high incidence of defective eggs as well (extra calcification, two yolks) which is caused by a lack of syntony during ovulation (Rauw *et al*., 1998). There is also a reduction in eclosion and a high frequency of chromosome abnormalities in embryos. Regarding to laying hens, selection for body weight decrease might result in a population of reduced size which has their reproduction capacity impaired (Rauw *et al*., 1998).

SKELETON FORMATION

There is an important association between leg problems and the selection for growth in broiler carcass traits (Sbardella *et al*., 2008). For modern broiler lines tissue growth rate is extremely high, which starts in a very early phase post hatching on an immature skeleton (Gonzales and Mendonça Júnior, 2005). In this context, broiler often suffer from tibial dyschondroplasia, an abnormality of growth plate cartilage featured by the presence of non-vascularised, non-mineralised tissue under the epiphyseal plate (growth plate) occurring in the proximal end of the long bones (Capela e Silva *et al*., 2005).

The manifestation of tibial dyschondroplasia is thought to be the result of a very fast growth in the early phases of development whereby the development of the bones does not keep up with the rapid weight gain of the muscle mass. Therefore, the animal is unable to support its own weight, thus causing a decrease in performance as well as the discard of the animal (Zhang *et al*., 1995). Tibial dyschondroplasia has a genetic component (Zhang *et al*., 1998; Sbardella *et al*., 2009), although it is mainly caused by environmental effects such as nutrition, housing and husbandry (Capela e Silva *et al*., 2005).

CARDIO RESPIRATORY SYSTEM AND METABOLIC RATE

Ascites syndrome is characterized by the extravasation of liquid from the liver to the abdomen cavity due to the increased pulmonary arterial pressure and the fatigue of the cardiac muscle. This extravasation of fluids occurs when there is a lack of oxygen which results in systemic hypoxia and an increase of cardiac debt. In order to cut the oxygen debt, broiler compensate with a high cardiac frequency, causing increased blood flow and pulmonary hypertension (De Greef *et al*., 2001). Although this syndrome is multifactorial and influenced by the environment a genetic predisposition for it has also been observed (De Greef *et al*., 2001).

Owing to genetic selection for muscle development and food conversion, the cardio-respiratory capacity is insufficient due to the *out-of balance* relation between heart/lung size and broiler weight. The high demand for oxygen in broilers selected for rapid growth, necessary to sustain the high metabolic rate, makes oxygen a limiting factor, predisposing broilers to heart failure (Julian, 1993).

Moreover, a genetic tendency to a reduction of the absolute and relative heart size in a male chicken line breed was found, due to indirect selection for economic traits (Gaya *et al*., 2007). The selection of animals for blood parameters, such as cardiac and haematocrit rate may help to avoid ascites (Julian, 1993).

The intense pressure for body weight selection has altered growth standards. Today broilers reach their slaughter weight at a younger age and have a higher content of body fat, as well as higher insulin and glucagon concentrations in the plasma (Rauw *et al*., 1998). Associated to that, an increase in the food passage rate in addition to high enzymatic activity in the intestine has been observed (Scheele *et al*., 1992).

CARCASS AND MEAT QUALITY

Selection for body weight increase has also altered endocrine and neural control mechanisms which affect feed consumption, therefore causing obesity in broilers. However, the main effects of these disorders remain unknown in broilers because they are slaughtered at young age (Figueiredo, 1998). In these poultry breeds voluntary consumption is beyond metabolic demands, only limited by the maximum capacity of the digestive system (Figueiredo, 1998). This is largely due to a failure of the hypothalamus to regulate appetite (Barbato *et al*., 1984). Other side-effects are the tendency for an increased abdominal fat deposition (Rance *et al*., 2002; Gaya *et al*., 2005) and an enlarged intestine (Konarzewski *et al*., 2000). As described for swine, the selection for RFI could be used in order to avoid the excessive fat deposition in broiler.

The number of fibres is relative and changes during animal growth and development; broilers selected for rapid growth have a higher number of fibres than broilers with normal growth rates, moreover, the muscular fibres diameter increases according to the age and genetic potential for breast meat production (Santiago, 2001). However, selection for high breast weight seems to decrease the number of muscular fibres but to increase the diameter and area of these fibres and thus may reduce meat quality because of water loss and increased shear force of meat, a measure for meat tenderness (Gaya, 2006; Felício, 2008).

Therefore, the selection for a large number of fibres with small diameters and fibres areas may improve meat quality by reducing water loss by exudation, defrosting, and cooking, as well as by increased tenderness (Felício, 2008), which are important traits for the industrial meat quality. A balance between histological traits, body and breast weight and meat quality is demanded, and it can be established by the selection index.

The pectoral myopathy incidence, an ischaemic necrosis that develops in the deep pectoral muscle, has also been associated with rapid growth and muscle increase in poultry, and there is a positive correlation between age and rapid growth on one hand and the occurrence of degenerated breast muscles on the other (Santiago, 2001; Bianchi *et al*., 2006). Selection for rapid growth has produced muscles that grow more than the vital system can stand, causing injuries to the muscle and carcass discard (Bianchi *et al*., 2006).

STRESS AND DISEASE SUSCEPTIBILITY

Metabolic properties of muscles are related to the animal's capacity to cope with environmental stress. Muscles with a low proportion of glycolytic fibres (white fibres), a high blood capillary supply, high oxidative capacity and small fibres are more efficient to maintain their energy reserves, and therefore are more able to stand the environmental stress (Santiago, 2001). It has been suggested that commercial broilers are more susceptible to stress because they have a high proportion of glycolytic (rapidly contracting) fibres and only a low proportion of oxidative (slowly contracting) muscle fibres. Glycolytic fibres have high growth potential, suggesting that the increase in the proportion of glycolytic fibres is associated with the selection for a high growth rate (Santiago, 2001).

Additionally, high growth rate broilers display a reduced immune response when challenged by several microorganisms. The animals show a low resistance to sanitary challenges, they exhibit low antibody responses and high mortality rates (Rauw *et al*., 1998; Gonzales and Mendonça Júnior, 2005). In layer hens, this impaired immune response is reported for individuals with low RFI (Van Eerden *et al*., 2004).

Genetic selection for immunological traits may be used in these situations, but correct management against stress and biosecurity procedures should co-operate in order to prevent disease occurrences (Elrom, 2000; Souza, 2000).

FINAL CONSIDERATIONS

In many cases selection for high productive efficiency in livestock species are accompanied by undesirable side effects for some physiological and reproductive traits, impairing animal welfare, health and productivity, and consequently increasing production costs. Animal breeding has made animals more sensitive to these problems, changing their body composition and production capacity, causing a great impact on their homeostasis.

The undesired side effects differ in their impact in different species, breeds, lines and populations, because the selective pressure applied varies among them and thus also the impact of genetic changes due to the breeding. Most frequently undesirable effects can be found in species with reduced generation gap, as broilers, or in precocious breeds, since these effects rapidly arise in these cases and consequently can be more evident.

In several species it is possible to observe that the undesirable effects are due to their multifactorial nature. Then, the identification and the control of environmental factors concerning these undesirable traits become essential to minimise them, although several studies have proved genetic correlation between productive traits and undesirable effects. On the other hand, if at favourable management and environmental conditions the undesirable effects may not become so evident (Rauw *et al*., 1998), and the control of environmental conditions may be expensive.

Therefore, it is necessary to redefine animal breeding strategies within a wider perspective of traits as well as further studies on physiological processes under genetic selection performance. Understanding genetic selection for economic traits upon physiological mechanisms might offer an important tool to understand and prevent unfavourable side effects of animal breeding.

In this manner, the selection objectives need to be reevaluated and redefined in breeding programs. The Behavioural, physiological and immunological traits should be included as selection objectives in the selection process and/or the selection intensity for economically interested traits must be adjusted according to the dimensioning of their unfavourable correlational responses. It could be done even with withdraw of the genetic gains for economical traits decreases; nevertheless it would reduce productivity losses, discards of animals and environmental control costs.

Breeding technologies could also contribute for the optimization of the genetic gains and for the success of animal breeding programs. Reproduction techniques and DNA technologies may be helpful to correct some undesirable effects, e.g. sperm preparation techniques, sexed semen, embryo transfer and in vitro fertilization may increase the fertility indexes, and DNA analysis could be used to identify the loci involved in the trade-offs of indirect selection for behavioural, physiological and immunological traits (Kinghorn *et al.*, 2006), which could be co-selected for. However, these breeding technologies might be used carefully since they are able to accelerate the genetic progress for economic interesting traits and consequently the undesirable side effects appearance in livestock species.

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