PHYSIOLOGICAL CONSEQUENCES OF SELECTION FOR INCREASED PERFORMANCE

W.M. Rauw

Department of Animal Biotechnology, University of Nevada, Reno, NV 89557, USA

SUMMARY

Undesirable side effects of increased production efficiency in farm animal species are becoming increasingly apparent. The present paper presents new evidence of side effects of high production in dairy cattle and fowl. These observations are discussed in relation to resource allocation patterns, residual feed intake and animal welfare issues.

ANIMAL DESIGN AND RESOURCE ALLOCATION

In 1981, Taylor and Weibel proposed the principle of optimal biological design or symmorphosis, based on 'the firm belief that animals are built reasonably' (Bacigalupe and Bozinovic 2002). Symmorphosis suggests an economic use of resources by all parts of a biological structure, such that the parts are qualitatively and quantitatively coadjusted to their common role: never used excess in biological capacity in any of the parts of a biological structure is costly in terms of maintenance, materials and space and would therefore not be favored by nature (Taylor and Weibel 1981). An important prediction of this principle is that if functional needs change, then structural components must change accordingly (Bacigalupe and Bozinovic 2002). It is mainly evolutionary biologists that have contested that evolution by natural selection can lead to 'optimal' rather than merely 'adequate, sufficient' design. The main reason why symmorphosis would not be widespread is that particular structures are often used in different functions, making it unlikely that optimization could be achieved for each of them (Lindstedt and Jones 1987). Indeed, evidence in favor of symmorphosis is as abundant as the evidence against (Bacigalupe and Bozonovic 2002). Excess capacities should indicate a suboptimal design (Bacigalupe and Bozonovic, 2002) and indeed, organisms often possess capacities somewhat in excess of what they normally use. Such buffer capacities provide environmental flexibility and allow individuals to withstand short-term stresses and adapt to long-term changes in the environment (Hammond *et al.* 1994). The genetic diversity that these non-extreme phenotypes represent allows species to adapt to environmental conditions at the genetic level (Rauw *et al.* 1999). Therefore, adaptation to environmental stresses will never reach a state of perfect optimality, but may be considered as a 'process of becoming', resulting in organisms 'designed' the best that they could be (Garland, 1998).

According to the alternative theorem of natural selection proposed by Beilharz and Nitter (1998; alternative to the Fundamental Theorem of Natural Selection by Fischer (1958)), it is the resources and challenges that each environment presents that is the prevailing constraint to evolutionary change. Briefly, the alternative theorem is described as follows: organisms require resources from the environment to live and reproduce. The individual genetic potential can only be realized in an environment in which essential resources are adequately supplied. Natural selection rewards those organisms who utilize available environmental resources most efficiently. Therefore, the resources available in every environment determine the phenotype that can be sustained most efficiently and therefore the genotypes that are selected on the basis of such phenotypes (Beilharz 1998). With selection for increased production in farm animals, genetic changes cannot result in sustainable levels of growth, milk production or reproduction beyond those which can be supported by farm resources. An example of such a genotype × environmental interaction is given by Deeb *et al.* (2002). In broilers, increased environmental temperatures reversed the positive correlation between 'actual growth rate' under normal temperatures and 'potential growth rate' to a significant negative correlation ($r = -0.411$) during the heat-stress period, indicating that breeding values of families under heat stress have little association with their expected breeding values under normal conditions (Deeb *et al.* 2002).

RESOURCE ALLOCATION PATTERNS

Resources come from food intake or body stores. Weiner (1992) proposed the 'barrel model' of an organism's resource allocation pattern. Input constraints (foraging, digestion, and absorption) are engaged in series, whereas outputs (maintenance, growth, production) are parallel and independently controlled. If the sum of output rates does not match the input, the balance is buffered by the storage capacity of the system. In the long run, however, energy expenditure must balance energy intake (Weiner 1992). The next question concerns the allocation of metabolizable energy to the components of an animal's energy budget, like maintenance, activity, growth, and reproduction, and possible trade-offs between these components. When stable patterns of energy allocation are affected by changing environmental conditions, energy budgets may be affected in one of three different ways or combinations thereof (Wieser 1994): (1) the energy input into the system increases or decreases but the relative pattern of energy allocation remains more or less unaffected, resulting in a *proportional effect*, (2) both energy input and relative pattern of energy allocation are affected, resulting in a *disproportional effect*, and (3) energy input into the system may or may not be affected, but metabolic energy is allocated preferentially to a selected function at the expense of other functions, resulting in a *trade-off*.

In the case of a disproportional allocation effect, when more resources become available, most of the additional energy gained may be invested into a single function, such as production. When resources become limited, maintenance is usually found to have a higher priority than growth and reproduction (Wieser 1994). However, with artificial selection, preferential allocation of resources may occur because the animal is 'genetically pre-programmed' to allocate a disproportionally large amount of resources to the trait selected for (Rauw *et al.* 1999).

Many interactions occur in the form of trade-offs. One would assume a trade-off to be required only when the organism involved approaches a limit to its metabolic capacity. However, this is not the case (Wieser 1994). One could think of metabolic sensors initiating the re-allocation of metabolic energy when the load of one process exceeds a critical threshold (Wieser 1994). One such system is homeorhetic regulation. Homeorhesis represents the orchestrated or coordinated changes in metabolism of body tissues to support a physiological state. For example, to ensure that lactation proceeds successfully, there are coordinated adaptations in the metabolism that reallocate available nutrients towards the mammary gland away from tissues that are not essential to lactation (Bauman and Currie 1980). Also, activation of the immune system during infection, tissue injury and stress changes the priority of partitioning of nutrients from growth to host defense (Colditz 2002).

We can assume that all traditional farm environments are providing a limited amount of resources (Beilharz 1998). Animals that are genetically driven to produce at high levels, may reallocate resources away from other processes, leaving the animal lacking in ability to respond to other demands, such as coping with disease and stress (Rauw *et al.* 1998). Buffer capacities and traits not defined in the breeding goal may be the first to be affected, because they are given no importance (Rauw *et al.* 1998, 1999).

RESOURCE ALLOCATION PATTERNS QUANTIFIED BY RESIDUAL FEED INTAKE

Resource allocation can be summarized with the following equation:

$$R_i = (k_A \times A_i) + (k_B \times B_i) + (k_C \times C_i) + \Sigma(k_Q \times Q_i), \quad (1)$$

where R = total amount of resources available to individual i, k = resource conversion factor, $(k_A \times A_i)$ = resources used for maintenance, $(k_B \times B_i)$ = resources used for growth, $(k_C \times C_i)$ = resources used for production, and $\Sigma(k_Q \times Q_i)$ = resources used for other processes (Beilharz *et al.* 1998). This equation is very similar to the equation that is used for the calculation of residual feed intake (RFI). Residual feed intake is estimated from a linear regression of feed intake on the main resource demanding processes:

$$FI_i = b_0 + (b_1 \times BW_i^{0.75}) + (b_2 \times BWG_i) + (b_3 \times PROD_i) + e_i, \quad (2)$$

where FI_i = feed intake of individual i, $BW_i^{0.75}$ = metabolic body weight, BWG_i = body weight gain, $PROD_i$ = level of production, b_0 = population intercept, b_1, b_2 and b_3 = partial regression coefficients representing maintenance requirements, feed requirements for growth, and feed requirements for production, respectively, and e_i = the error term, representing RFI (Rauw *et al.* 2006b). Regression coefficients represent the average ‘cost’ of body maintenance, growth and production, based on the population on which the model is formed. Individual deviations from this average accumulate in the error term, which is unique for each individual. Residual feed intake is thus defined as the part of the feed intake that is unaccounted for by feed requirements for maintenance and production. Apart from variation in partial efficiencies for maintenance, growth and production, variation in RFI can be caused by variation in metabolic food demanding processes not included in the model, such as behavioral activities, responses to pathogens and responses to stress (Luiting 1990).

The similarity between these models implies that calculation of RFI can be used to quantify the amount of ‘buffer’ resources available to an animal for, e.g., physical activity and the ability to cope with unexpected stresses. Laying hens with low RFI were less adapted to cope with high temperatures (Bordas and Minvielle 1997) and maintained elevated corticosterone levels for a longer time after injection with ACTH (Luiting *et al.* 1994). Antigen-specific antibody responses were not different between low RFI and high RFI laying hens, but high RFI hens had a higher level of nonantigen specific antibodies (Van Eerden *et al.* 2004). Male (Schütz *et al.* 2002) and female (Jensen *et al.* 2000) layers with high RFI had more active fear responses. Schütz *et al.* (2002) suggested the existence of a trade-off between energy-demanding behavior and high production. Hens with lower RFI spent more time close to social stimuli, had lower mean distance to companions, and performed less contrafreeloading (Väisänen *et al.* 2005b). Richardson and Herd (2004) hypothesize that susceptibility to stress is a key driver for many of the biological differences observed following divergent selection for residual feed intake in beef cattle.

Application of RFI estimation is not restricted to intensive production systems. Rauw *et al.* (2006a) developed a model for estimating grazing efficiency in extensive free-range conditions by rewriting model (2):

$$GE_i = GI_i - b_0 - e_i = (b_1 \times BW_i^{0.75}) + (b_2 \times BWG_i) + (b_3 \times PROD_i), \quad (3)$$

were GE_i = grazing efficiency of individual i, GI_i = grazing intake of individual i, and other parameters are as in model (2). The amount of resources ingested is confounded with the efficiency of resources allocated. Preliminary results on a grazing experiment in sheep in the cold Nevada desert showed that 94% of 915 ewes lost body weight during the grazing period, while pregnant animals in particular must gain weight (Rauw *et al.* 2006a). Therefore, for the farmer it is more important to know if the animal has been able to ingest a sufficient amount of resources than if the animal is more efficient in allocating those. Since feed intakes and the partial regression coefficients cannot be estimated in the field, estimates from literature can be used, or better, estimates from controlled experiments on a sub-group originating from the animal population of interest (Rauw *et al.* 2006a). With these estimates, feed intakes do not need to be estimated. Body weights can be estimated before and after animals are allowed to range freely on the rangelands, and metabolic body weight and body weight gain can be calculated. Gomez-Raya *et al.* (2007) analyzed grazing efficiency in free-range Merino ewes grazing 75 days on the rangelands. Values were adjusted for days in pregnancy and age. The ewes used an average 2861 ME (kcal/d) with a standard deviation of 325 ME (kcal/d). The estimated heritability of grazing efficiency was 0.34 (± 0.056), which would assure a significant response to selection when selected for. In the context of resource allocation, GE presents an estimate of the individual ability to graze at resource limiting rangelands and can be applied to different range species. Selection for improved grazing efficiency would foremost result in healthier ewes that can produce lambs and wool without compromising welfare of their own and that of their offspring.

NEW EVIDENCE OF SELECTION FOR HIGH PRODUCTION EFFICIENCY

In 1998, Rauw *et al.* reviewed over 100 references on undesirable correlated effects of selection for high production efficiency, with respect to metabolic, reproduction and health traits, in broilers, pigs and dairy cattle. In dairy cattle in particular, a considerable additional number of publications on compromised health and welfare (Collard *et al.* 2000) and declined fertility (Royal *et al.* 2000) resulting from intense selection for production have been published since 1998. Within 3904 different herds, Windig *et al.* (2005) observed that highest producing cows had higher somatic cell count levels, longer days to first service, a higher frequency of drops in milk production, a lower conception rate, and required a higher number of inseminations. In several other studies an unfavorable genetic correlation between milk production and both somatic cell count and clinical mastitis was observed (Hansen *et al.* 2002; Carlén *et al.* 2004). Zwald *et al.* (2004) observed that length of productive life was negatively associated with displaced abomasums, ketosis, mastitis, lameness, cystic ovaries and metritis. High genetic merit Holstein-Friesian cows grazing pasture in Australia had more days open, took longer to commence luteal phase activity, took longer to first observed estrus post calving, had a lower pregnancy rate, and were treated more often for abnormal ovarian activity (Fulkerson *et al.* 2001). It was suggested that this was possibly due to genes favoring partitioning of energy to milk yield rather than maintenance of body condition. Horan *et al.* (2005) observed that in a grass-based system, aggressive selection for increased milk production in the North American Holstein Friesian has resulted in greater loss of body weight and body condition score post calving. Søndergaard *et al.* (2002) concluded that minimum body weight during lactation is reached before peak yield is reached and peak feed intake is reached later than peak yield. Cows with lower body weight gains during lactation will be less prepared to meet the energy requirements of subsequent lactations. An increase in somatic cell count levels with increased mobilization of body reserves indicates that increased production levels leads to metabolic stress (Søndergaard *et al.* 2002). Genetic selection for milk yield generally results in higher genetic potential for growth (Mäntysaari *et al.* 2002; Coffey *et al.* 2006). Genetically heavier cows are found to require more services and have a longer interval from first service to conception (Hansen *et al.* 1999; Berry *et al.* 2003). In addition, Brotherstone *et al.* (2007) observed a positive genetic association between growth at weaning and mastitis ($r_g = 0.24$). Also, increased weight ($r_g = 0.65$), growth rate at weaning ($r_g = 0.38$) and maximum growth rate ($r_g = 0.71$) all contributed to increased feet disorders. Nygaard Kristensen *et al.* (2004) observed a presence of heat shock proteins (Hsp72), that are believed to be strictly stress inducible, in plasma of Danish Holstein-Friesian dairy cows without clinical disease symptoms at different ages and different stages of production. They suggest that these apparently healthy individuals are experiencing some degree of stress, possibly as a result of extreme selection for increased production.

In broilers, fast growing strains showed a lower activity level than slow growing broilers (Reiter and Kutritz 2001), perched, walked, and scratched less and performed more sitting on the floor, eating and drinking (Bokkers and Koene 2003). Väisänen and Jensen (2003) suggest that the adaptability of layers to their social and physical environment may have been influenced by means of selection for increased production capacity, as results suggested that White Leghorns may have greater problems in adapting to a new environment (Väisänen and Jensen, 2003) and have poorer social learning capacity with a weaker ability to cope with group disruptions (Väisänen *et al.* 2005a) than the ancestral breed, the red junglefowl. Broiler families with higher potential growth rate under normal conditions are more likely to suffer from ascites under cold stress (Deeb *et al.* 2002; Pakdel *et al.* 2005). Results of the study of Cheema *et al.* (2003), comparing the immune response of a 2001 commercial broiler with a 1957 randombred broiler strain, suggested that genetic selection for improved performance has resulted in a decrease in the adaptive arm of the immune response but an increase in cell-mediated and inflammatory responses. In the study of Castellini *et al.* (2002), good adaptation to extensive rearing conditions was better in slower-growing poultry genotypes, while faster growing genotypes showed unbalanced muscle response to the greater activity and the oxidative stability of the meat was reduced.

CONSEQUENCES FOR ANIMAL WELFARE

Resource availability rose dramatically during the second half of the 20th century as a result of improved understanding of animal nutrition and disease control, and better designed housing systems (Olsson *et al.* 2006). This additional amount of resources could be invested into production, resulting, together with efficient breeding programs, in an unprecedented increase in production levels (Rauw *et al.* 1998). But undesirable effects of increased production efficiency are becoming apparent, and it is the society's understanding of these effects that has raised questions about what is ethically acceptable in animal breeding (Ollson *et al.* 2006). Selection for increased growth rate has been detrimental to poultry and pig welfare in terms of heart and leg problems (Rauw *et al.* 1998). Higher production performance animals are found to have a weakened pathogen resistance (Rauw *et al.*

1998; Garnier *et al.* 2003). The key ethical question is not whether animal breeding should be abandoned, but how we should breed (Gamborg and Sandøe 2003). The general opinion is that it is acceptable to use animals as long as it is done 'humanely' (Christiansen and Sandøe 2000) and doesn't result in physical damage, pain or distress. Breeding goals are accepted if not used to mask poor management systems or at the risk of adverse effects on other welfare aspects (Neeteson van Nieuwenhoven *et al.* 2006).

Animal wellbeing and welfare can be *improved* by breeding as well. Increased emphasis on welfare associated traits in the selection index, such as longevity and health, will result in improved welfare and increased public confidence in animal farming (Pryce *et al.* 1999; Stott *et al.* 2005). Breeding for disease resistance in a range of species is attracting increasing interest (Kerr *et al.* 2001). Breeding companies can play an important role in addressing welfare problems by defining broader breeding goals that not only include production traits but also functional traits (Ollson *et al.* 2006). In dairy cattle, veterinary-treated cases of clinical mastitis are recorded in the Nordic countries (Carlén *et al.* 2006), and this practice is being considered in other countries as well (Zwald *et al.* 2004; Stott *et al.* 2005). Several countries, such as Denmark and Finland, already include health traits in their selection indices (Pedersen *et al.* 2002). In the United States, since 1994, routinely measured indirect indicators of health and fitness traits, such as somatic cell score and length of productive life, were included in the national breeding goal (Zwald *et al.* 2004). Rance *et al.* (2002) suggest including support tissues, such as heart mass, in a selection index. Genetic variation in RFI and grazing efficiency may allow for selection for improved resource allocation patterns (Rauw et al. 2006a). Kanis *et al.* (2005) proposed a selection-index method to obtain the proper weights for societally important traits in the breeding goal, such as the welfare and health.

Questions are being asked on the future direction of agriculture in several countries, including Australia and the USA, with special emphasis on the question as to how the agricultural sector can find sustainable ways of being more productive (Garnier *et al*, 2003). Many countries independently have appointed boards to deal with the issue of animal welfare and animal ethics, including both experts and lay people (Mejdell, 2006). MacArthur Clark *et al.* (2006) recommend the establishment of a committee for the evaluation of welfare problems associated with breeding technologies that would advise on the effectiveness of existing legislation and practices relating to animal breeding procedures to assure animal welfare, and would give consideration to ethical questions associated with animal breeding even where measurable detrimental effects on animal welfare may not be immediately evident. We may expect that increased and combined efforts may result in better animal welfare in the future.

REFERENCES

Bacigalupe, L.D. and Bozinovic, F. (2002). *J. Exp. Biol.* **205**:2963.

Bauman, D.E. and Currie, W.B. (1980). *J. Dairy Sci.* **63**:1514.

Beilharz, R.G. and Nitter, G. (1998). *J. Anim. Breed. Genet.* **115**:439.

Bokkers, E.A.M. and Koene, P. (2003). *Appl. Anim. Behav. Sci.* **81**:59.

Bordas, A. and Minvielle, F. (1997). *Genet. Sel. Evol.* **29**:279.

Brotherstone, S., Coffey, M.P. and Banos, G. (2007). *J. Dairy Sci.* **90**:444.

Berry, D.P., Buckley, F., Dillon, P., Evans, R.D., Rath, M. and Veerkamp, R.F. (2003). *J. Dairy Sci.* **86**:2193.

Castelini, C., Mugnai, C. and Dal Bosco, A. (2002). *Ital. J. Food Sci.* **4**:401.

Carlén, E., Emanuelson, U. and Strandberg, E. (2006). *J. Dairy Sci.* **89**:4049.

Carlén, E., Strandberg, E. and Roth, A. (2004). *J. Dairy Sci.* **87**:3062.

Cheema, M.A., Qureshi, M.A. and Havenstein, G.B. (2003). *Poultry Sci.* **82**:1519.

Christiansen, S. and Sandøe., P. (2000). Anim. Reprod. Sci. 60-61:15.

Coffey, M.P., Hickley, J. and Brotherstone, S. (2006). *J. Dairy Sci.* **89**:322.

Colditz, I.G. (2002). *Livest. Prod. Sci.* **75**:257.

Collard, B.L., Boettcher, P.J., Dekkers, J.C.M., Peticlerc, D. and Schaeffer, L.R. (2000). *J. Dairy Sci.* **83**:2683.

Deeb, N., Shlosberg, A. and Cahaner (2002). *Poultry Sci.* **81**:1454.

Fisher, R.A. (1958). The genetical theory of natural selection, 2nd rev edn. Dover, New York. 291 pp.

Fulkerson, W.J., Wilkins, J., Dobos, R.C., Hough, G.M., Goddard, M.E. and Davison, T. (2001). *Anim. Sci.* **73**:397.

Gamborg, C. and Sandøe, P. (2003). In "Key Issues in Ethics", p. 133, editors R. Levinson and M. Reiss, Routledge Falmer, London.

Garland, T. (1998) In "Principles of Animal Design. The Optimization and Symmorphosis Debate", p. 40, editors E.R. Weibel, C.R. Taylor and L. Bolis, Cambridge University Press, USA.

Garnier, J.P., Klont, R. and Plastow, G. (2003). *Meat Sci.*:79.

Gomez-Raya, L., Rauw, W.M., Jesko, W., Sandstrom, M. and Glimp, H.A. (2007). *Submitted.*

Hammond, K.A., Konarzweski, M., Torres, R.M. and Diamond, J.M. (1994). *Physiol. Zool.* **67**:1479.

Hansen, L.B., Cole, J.B., Marx, G.D. and Seykora, A.J. (1999). *J. Dairy Sci.* **82**:795.

Hansen, M., Lund, M.S., Sørensen, M.K. and Christensen, L.G. (2002). *J. Dairy Sci.* **85**:445.

Horan, B., Dillon, P., Faverdin, P., Delaby, L., Buckley, F. and Rath, M. (2005). *J. Dairy Sci.* **88**:1231.

Jensen, P., Schütz, K., Forkman, B. and Andersson, L. (2000). Proc 34th Int Cong ISAE, Brazil.

Kanis, E., De Greef, K.H., Hiemstra, A. and Van Arendonk, J.A.M. (2005). *J. Anim. Sci.* **83**:948.

Kerr, D.E., Plaut, K., Bramley, A.J., Williamson, C.M., Lax, A.J., Moore, K., Wells, K.D. and Wall, R.J. (2001). *Nat Biotechnol.* **19**:66.

Lindstedt, S.L. and Jones, J.H. (1987). In "New Directions in Ecological Physiology", p. 289, editors M.E. Feder, A.F. Bennet, W.W. Burggren and R.B. Huey, Cambridge University Press, USA.

Luiting, P. (1990). *World's Poultry Sci. J.* **46**:133.

Luiting, P., Decuypere, E., De Groot, P.N., Buyse, J. and Room, G. (1994). 45t EAAP, UK.

MacArthur Clark, J.A., Potter, M. and Harding, E. (2006). *Livest. Prod. Sci.* **75**:313.

Mäntysaari, P., Ojala, M. and Mäntysaari, E.A. (2002). *Livest. Prod. Sci.* **75**:313.

Mejdell, C.M. (2006). *Livest. Prod. Sci.* **103**:292.

Neeteson- van Nieuwenhoven, A.M., Merks, J., Bagnato, A. and Liinamo, A.E. (2006). *Livest. Sci.* **103**:282.

Nygaard Kristensen, T., Løvendahl, P., Berg, P. and Loeschcke, V. (2004). *Cell Stress Chap.* **9**:143.

Olsson, I.A.S., Gamborg, C. and Sandøe, P. (2006). *J. Agr. Env. Eth.* **19**:37.

Pakdel, A., Van Arendonk, J.A.M., Vereijken, A.L.J. and Bovenhuis, H. (2005). *Brit. Poultry Sci.* **46**:43.

Pedersen, J., Nielsen, U.S. and Aamand, G.P. (2002). Economic values in the Danish Total Merit Index. Proc. Interbull Meeting, Interlaaken, Switzerland.

Pryce, J., Simm, G., Amer, P., Coffey, M. and Stott, A. (1999). GIFT Meeting, Wageningen.

Rance, K.A., McEntee, G.M. and McDevitt, R.M. (2002). *Brit. Poultry Sci.* **43**:518.

Rauw, W.M., Glimp, H.A., Jesko, W., Sandstrom, M., Okomo, M., Perryman, B. and Gomez-Raya, L. (2006a). 8th World Congr. Gen. Appl. Livst. Prod., Brasil.

Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N. and Grommers, F.J. (1998). *Livest. Prod. Sci.* **56**:15.

Rauw, W.M., Luiting, P., Beilharz, R.G., Verstegen, M.W.A. and Vangen, O. (1999). *Livest. Prod. Sci.* **60**:329.

Rauw, W.M., Soler, J., Tibau, J., Reixach, J. and Gomez-Raya, L. (2006b). *J. Anim. Sci*. **84**:956.

Reiter, K. and Kurtritz, B. (2001). *Arch. Geflügelk.* **65**:137.

Richardson, E.C. and Herd, R.M. (2004). *Austr. J. Exp. Agric*. **44**:431.

Royal, M.D., Darwash, A.O., Flint, A.P.F., Webb, R., Woolliams, J.A. and Lamming, G.E. (2000). *Anim. Sci*. **70**:487.

Schütz, K., Kerje, S., Carlborg, Ö, Jacobsson, L., Andersson, L. and Jensen, P. (2002). *Behav. Genet.* **32**:423.

Søndergaard, E., Sørensen, M.K., Mao, I.L. and Jensen, J. (2002). *Livest. Prod. Sci*. **77**:23.

Stott, A.W., Coffey, M.P. and Brotherstone, S. (2005). *Anim. Sci.* **80**:41.

Taylor, C.R. and Weibel, E.R. (1981). *Respir. Phys.* **44**:1.

Väisänen, J., Håkansson, J. and Jensen, P. (2005a). *Brit. Poultry Sci*. **46**:156.

Väisänen, J. and Jensen, P. (2003). *Appl. Anim. Behav. Sci*. **84**:139.

Väisänen, J., Lindqvist, C. and Jensen, P. (2005b). *Livest. Prod. Sci*. **94**:149.

Van Eerden, E., Van den Brand, H., Reilingh, G.D., Parmentier, H.K., De Jong, M.C.M. and Kemp, B., (2004). *Poultry Sci.* **83**:1904.

Weiner, J. (1992). *Trends Ecol. Evol.* **7**:384.

Wieser, W. (1994). *Biol. Rev.* **68**:1.

Windig, J.J., Calus, M.P.L. and Veerkamp, R.F. (2005). *J. Dairy Sci*. **88**:335.

Zwald, N.R., Weigel, K.A., Chang, Y.M., Welper, R.D. and Clay, J.S. (2004). *J. Dairy Sci*. **87**: 4295.