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Intensive Artificial Selection Jeopardizes Animals' Well-Being: A Short Review

Review Article

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ABSTRACT

Domestication of animals has had some important effects on physiology, morphology, behavior and well-being of domesticated animals. Conscious or goal directed selections on animals for increasing their productions has accelerated the rate of the changes, leading to some well-being defections. This paper notes some aspects of animal domestication in context of genetic science. Then explains how domestication may happen, and how does artificial selection alter morphology, physiology and behavior of animals in both useful and harmful ways, with an emphasis on the harmful part. Also correlated responses of selection on domesticated animals are reviewed and some probable solutions to avoid unintended selection are discussed.

KEY WORDS animal well-being, domestication, artificial selection.

INTRODUCTION

Improvement of human health condition in developing countries regarding an increase in public awareness and growth of human population in general has increased interests in utilizing animal-related productions in the last decades. Consequently, increases in markets' demands for these products have also occurred. At the same time genetic science, especially artificial selection has had successful progresses. Therefore ability in producing animal-related productions has inevitably improved. These changes together had led the industry to produce more intensified and efficient products to satisfy high demands. Intensity in production and selection has had unwilling consequences which has resulted in genetically well-being problems. After more than two years of investigation, the Pew Charitable Trusts and the Johns Hopkins University Bloomberg School of Public Health in 2008 reported that "the present system of producing food animals in the United States is not sustainable and presents an unacceptable level of risk to public health and damage to the environment, as well as unnecessary harm to the animals we raise for food" (Pew Commission on Industrial Farm Animal Production, 2008).

Animal domestication is best viewed as a "process by which a population of animals becomes adapted to man and to the captive environment by genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation'' (Price, 1984). To consider an animal's behavior as domesticated behavior, animal should have ability to contact with man directly, not to be afraid of, to obey and to reproduce under the conditions which are created by him (Belyaev, 1979). In this regard, domestication can be considered an adaptation to human prepared environment which "is achieved through genetic changes over generations and involves an evolutionary process" and accomplishes through "environmental stimulation and experiences during an animal's lifetime, which also involves ontogenetic processes" (Price, 1984). All changes in domestication process like every other permanent change in organisms are based on genetics, which cause animals to differ from their wild counterparts. Genetic changes and developmental mechanisms over generations are the result of specific biological adaptations and are achieved by captivity environment and management under human considerations (Price, 1999).

The process is referred as domestication. This continuous process modifies morphology, physiology and behavior of animals that adapt to these environments and consequently increases the probability of contribution of animals' genes to the next generations (Siegel, 1989).

There are some underlying genetic phenomena that influence the development of the domestic phenotype in captivity. They can be listed as artificial selection, natural selection in captivity, relaxed selection, inbreeding and genetic drift (Price and King, 1968; Price, 1999). Artificial selection is the unique selective mechanism to domestication and happens intentionally or unintentionally in captivity by human (Price and King, 1968; Price, 1999). Natural selection in captivity, functions as eliminating force for those animals that are unable to reproduce under man provided environments but favors those animals which can have efficient reproductions under these conditions (Mignon-Grasteau *et al*. 2005). Relaxation of natural selection in captivity, a natural consequence of environmental changes, refers to some changes in those behaviors that have been important for animal survival in the nature, e.g. food and shelter finding and predator protection (Price and King, 1968; Newman, 1994; Price, 1999; Mignon-Grasteau *et al*. 2005).

Domestication as by-product of animal taming

For the first time, Darwin (1859) on the domestication in the *Origin of Species*, stated "not a single domestic animal can be named which has not in some country drooping ears; and the view suggested by some authors, that the drooping is due to the disuse of the muscles of the ear, from the animals not being much alarmed to the danger, seems probable. "In his books, *Origin of Species* (1859) and *Variation of Animals and Plants under Domestication*, Darwin, (1868) explained how domestication happens and by mentioning that some traits are correlated, stated that human can unconsciously modify other parts of the structure by going on selection, and thus "augmenting any peculiarity".

Domestication is by-product of raising and rearing animals in captive conditions and their vicinity to humans. Generally human provides animal's food, shelter, protection from weather extremes, and protection from predators (Newman, 1994). These phenomena alter the genetic structure in long term as a product of adaptation to the novel environment. At the same time animals accept humans' vicinity and accept to be in proximate with other animals. Animals become more dependent on human and important behaviors which are required for survival, lose their importance. Therefore, in long term there will be loss of certain behaviors in domesticated species, e.g., foraging behavior, reproductive isolating mechanisms, food and shelter seeking, and predator avoidance (Price and King, 1968; Newman, 1994; Price, 1999; Mignon-Grasteau *et al*. 2005).

Human inadvertent selection for domestication correlated traits may cause regression of certain organ or change in a certain behavior of animal. Genetic correlation is defined as a change in an unselected trait resulting from selection of another trait during a breeding program (Bourdon, 1997) or in other words is a measure of strength (consistency and reliability) of the relationship between breeding values for one trait and breeding values for another trait. One explanation for these correlated changes is pleiotropy. This phenomenon affects "the frequencies of genes that influence correlated characters" through selection for another traits (Lerner, 1954). Although it seems that few changes in master genes result in a huge change in animal behavior and morphology, but differences between domestic and wild animals seems to be the effect of pleiotropic interactions (Dobney and Larson, 2006). Domestication requires environmentally influenced genetic changes in behaviors (Newman, 1994); and since selection for behavior is accomplished unconsciously through domestication (Belyaev, 1979) it seems that pleiotropy has affected frequencies of regulatory master genes. Therefore, it can be concluded that every components of the domestication phenotype is most likely polygenic (Jensen, 2006).

Destabilizing selection is another concept that was proposed by Belyaev (1979) for the first time. Based on this concept selection for traits such as tame behavior would result in breaking up previously integrated ontogenetic systems and thus change other phenotypes that seem genetically unrelated to the selected one. In this manner, those genes that are related to timing and amount of gene expression probably are selected. Effect of this kind of selection is mainly on systems that control ontogenesis through neuroendocrine pathways. Nervous and endocrine systems are closely related to each others. Changes in behavior are affected by alteration of the hormonal state and have developmental ontogenetic consequences in animals. For example, it seems that there are "similarities between domestication associated traits and those indicative of hypothyroidism" (Crockford, 2002).

Destabilizing selection can change normal patterns of gene activation and inhibition (Belyaev, 1979) and it can lead to many undesirable characteristics in the course of domestication.

Silver Fox experiment, under the subject of selection in silver foxes for non-aggressive behavior toward human (i.e., tameness behavior), was conducted at the Institute of Cytology and Genetics in Novosibirsk, Siberia, and is an example of artificial selection (Belyaev, 1979; Trut, 1999). In his domestication experiment, Belyaev (1979) showed that hypothalamic-hypophyseal-adrenal system changed during selection for tame behavior in domesticated foxes and led to a different level of female steroid hormones. Therefore, selection for tame behavior improved fertility of tame female foxes as compared with their wild counterparts.

As mentioned above, because of progressive developments of artificial selection techniques in the last century, morphology, physiology and behavior of animals have experienced rapid and huge changes. These changes have had both useful and harmful effects on the modified organisms. Physiology, morphology and behavior are intrinsically related; inducing a selection pressure on one attribute of an organism and might have a significant impact, although unintended, on other characteristics (Belyaev and Trut, 1975). Reduced sensitivity to changes in environment of domestication in animals, i.e. response to unfamiliar living environments, novel objects, strange conspecifics and humans is the main effect of domestication process on the behavior of captive animals (Price, 1999). In captivity, reproductive success is not dependent on animal's social status; therefore rate of maturation of sexual behaviors, accelerates. Also due to improved nutrition, domestication has led to improvement in reproductive efficiency of many species (Hale, 1969; Setchell, 1992). The changes in phenotypes affected by domestication can be summarized in five categories (Jensen, 2006):

1. External morphological changes (e.g., altered fur and plumage colors, changes in body size and growth pattern, changes in relative size of different body parts).
2. Internal morphological changes, (e.g., an overall decrease in brain size, and modified relative sizes of other internal organs).
3. Physiological changes, (e.g., changes in endocrine responses and reproductive cycles).
4. Developmental changes, (e.g., earlier sexual maturity and changes in the length of sensitive periods for socialization).
5. Behavioral changes, (e.g., reduced fear, increased sociability, and reduced anti-predator responses).

Defects in animals undergoing artificial selections

When domestication happens, some traits that are important for survival in wild will have a decreased value in total fitness (Mignon-Grasteau *et al*. 2005). This happens because human choose the breeder animals and provide shelter for captivated ones. Therefore, there will be an increase in other components such as production. This continuous selection for production related traits will increase the occurrence and magnitude of undesirable effects of physiological, immunological and reproduction traits, and consequently jeopardizes animal welfare (Rauw *et al*. 1998). Behavior as a fundamental mechanism of adaptation allows animals to adapt to the new environments (Jensen, 2006). On the other hand, genes under selection pressure for increased production simultaneously affect behavior; therefore affecting the adaptive capacity of the selected animals. To explain this phenomenon, Beilharz *et al*. (1993) proposed the resource allocation theory, in which under selection within a particular environment, the resources used by the animal are optimally distributed between the important traits of breeding and production. Consequently, any additional selection in performance of a production-related trait without a concurrent increase in resources, leads to declines in other traits, due to a re-allocation of resources. Therefore, effects of selection on behavior may have serious consequences on the welfare of animals (Jensen, 2006), since domestication is a process of selection for behavior (Belyaev, 1979). Van der Waaij (2004) proposed a model to describe underlying mechanisms and the consequences of selection on allocation of resources to production which decreases survival and reproductive rate. For example, individuals with high genetic potential for growth may divert resources to achieve that potential from immunoresponsiveness and, therefore, become more vulnerable to pathogens and diseases (Siegel, 1989). Rauw *et al*. (1998) reviewed undesirable effects of selection for high production efficiency in food producing animals such as broilers, turkeys, pigs and dairy cattle. In addition, Greger (2009) reviewed these undesirable consequences of selection in genetically engineered animals. In this paper, findings of undesirable correlated effects of selection on farm animals of the last decade which are new to the paper of Rauw *et al*. (1998) are reviewed. Although a trend for genetically improving machinery milking ability of milking goats has been observed (Casu *et al*. 2008), however, there is some evidence that selection only on the trait of milk in goats has led to an unfavorable increase in somatic cell count (SCC) and evolution toward baggy udders which makes machine milking hard and also increases the susceptibility to mastitis (Barillet, 2007). Selection for increasing fleece weight and lamb growth rate has been correlated with higher fecal worm egg count in Romney sheep (Morris *et al*. 1996). On the other hand, selection for reduction of fecal egg count was correlated with increase in fat depth of Merino sheep (Pollott and Greeff, 2004). Also it seems that there is an antagonistic relationship between selecting for scrapie resistance and growth, carcass, and meat quality traits in crossbreds of Dorset and Romanov sheep (Isler *et al*. 2006). An additional copy of growth hormone gene in transgene Merino sheep enhanced live weight gain, carcass leanness, and wool production but decreased reproductive efficiency and increased disease problems (Adams and Briegel, 2005).

There is a negative correlation between well-being related behaviors and economical traits in most livestock species (Newman, 1994). It seems that extreme selection on cattle has positive effects on carcass quality, but it negatively affects meat quality (Pethick *et al*. 2005). Increasing genetic merits of Holstein-Friesian dairy cows has been associated with decreased reproductive efficiency and low body condition score in Australian (Fulkerson *et al*. 2001; Fulkerson *et al*. 2008), English (Pryce *et al*. 2001) and Scandinavian (Buch and Norberg, 2008; Roxström *et al*. 2001) dairy herds (Veerkamp *et al*. 2003). Selection just for milk production increased calving interval and decreased reproductive performance (Pryce *et al*. 2002). High milking frequency in cows was associated with lower peak of progesterone concentration which resulted in a poor protein balance (Windig *et al*. 2008). Also high milk yield in dairy cattle was genetically correlated with ketosis, mastitis (Simianer *et al*. 1991) and udder edema (Van Dorp *et al*. 1998). There was an unfavorable genetic correlation between protein yield and functional traits (Norberg *et al*. 2009). Also cattle carcass weight was negatively correlated with bovine respiratory disease (Snowder *et al*. 2007).

It seems that domestication has led domesticated animals to less-energy demanding behaviors (Price, 1999) and selection for high production in laying hens has decreased general activity and social interaction (Schütz and Jensen, 2001). Lindqvist *et al*. (2009) showed that red jungle fowl (*Gallus gallus*) responded more actively to food deprivation than the White Leghorn layers. Also, in comparison to red jungle fowl, White Leghorn seems to be less cautious, more fearless and having impaired spatial learning ability (Schütz *et al*. 2001; Lindqvist and Jensen, 2009; Lindqvist *et al*. 2009).

Artificial selection in domestic turkeys has resulted in an inability of males to copulate and domesticated turkey females must be artificially inseminated (Price, 1999). Long-time selection for egg production and body weight in turkeys has decreased disease resistance, walking ability and semen production (Nestor *et al*. 1996), also egg production and hatching fertile eggs in these birds (Nestor *et al*. 2000). In laying hens, selection for non-broody behavior has resulted in strains of chickens which don't incubate eggs or brood chicks (Price, 1999). Selection for body weight in chicken has depressed immune performance (Miller *et al*. 1992), antibody production (Cheema *et al*. 2003) and damaged the hypothalamic satiety mechanisms (Burkhart *et al*. 1983) which has led to a failure in diminishing the hunger drive and consequently to hyperphagia or overconsumption. Body weight was negatively correlated with feather pecking behavior in female line of White Leghorn layers (Kjaer and Sørensen, 1997). Also selection for higher body weight decreased bursa weight in turkeys (Li *et al*. 2001). It is reported that there is a negative correlation between bursa weight at hatching and post-hatching weight in chicken (Muir and Jaap, 1967).

Newman (1994) reported a negative relationship between body weight and reproduction in poultry, both across and within stocks mentioning that selection for egg production or growth has correlated response in unselected traits including behavior. Domestication and artificial selection for production have increased fearfulness of the White Leghorn compared to red jungle bird (Schütz *et al*. 2004).

Domestic fowls which are selected for growth are phlegmatic and have excessive appetites and reduced motor ability (Siegel, 1989). This enhances the propensity for obesity and affects their well-being. Intensive selection for higher growth rate in broilers was negatively correlated with increasing the incident of ascites syndrome (Deeb *et al*. 2002) and caused leg problems (Christensen, 1998). Gaya *et al*. (2007) showed that there is a genetic trend of decreasing heart weight in broiler line which can cause higher mortality rate. In comparison to fast growing, slow growing strains of chicken had better locomotor activity and lower mortality rate (Castellini *et al*. 2002).

Selection for high quality and high percentage of lean has increased leg weakness (Sather, 1987; Pajor *et al*. 2000; Fan *et al*. 2009) and can increase fearfulness (Shea-Moore, 1998) in pigs.

Beside farm animals, intensive selection on other animals has developed problems. Ovarian structure and reproductive efficiency in mice is affected by long-term selection for body weight (Bernardi, 2009). Selection for high litter size allocated the resources to maintenance in mice (Rauw *et al*. 2001).

Kolstad *et al*. (2006) showed that selection for increasing body weight in Atlantic cod (*Gadus morhua*) is positively correlated with spinal deformity. Selection response for body length of brown trout was correlated with food intake capacity and increased feeding requirements (Mambrini *et al*. 2004).

Implications

Increase in animal related productions due to recent growth of human population, increase in markets' demand and development of developing countries is inevitable.

On the other hand, accelerated selection for high production in last decades has become an issue in animal well-being. Thus, we should try to find a solution both to consider markets' demand and animal well-being at the same time. First, we suggest a balanced selection considering all aspects of organism (i.e. production, reproduction, health and well-being) and a prospect to improve these aspects altogether. Although, it may not be beneficial in short term but selection regarding all aspects of organism may prevent non reversal defects in animals or the species. In order to achieve this goal, this paper suggests a selection of animals based on their species or breed specific characteristics (typical characteristics of a breed) and balanced in traits.

It should be assessed if we want to increase animal productions and maintain (or decrease) defections for long term or not. Our hypothesis is that we can define typical criteria for every breed.

Obtaining an advantageous solution for increasing animal productions and which is also less harmful for animal well-being at the same time, seems to be in contrary with breeders' short term benefits.

Thus, a probable resistance for long term applications is expected. This paper suggests some executable protocols or rules for anyone and anywhere as law. Lately, establishment of ethical codes is suggested for European animal breeding system (Olsson *et al*. 2006) which could be applicable and globalized especially in developing countries. It is also suggested to select the animals based on their robustness (Star *et al*. 2008) which is still a vague concept. Second, by determining Quantitative Trait Loci (QTL) for unwilling traits we can avoid selection of these unintended traits (Jensen *et al*. 2008). QTL for body weight in layers is identified and it seems possible to map QTL for improvement of more than one trait at the same time (Siwek *et al.* 2004).

In relation to this, two hypotheses were established: first the selection of correlated traits has led in well-being threats and second, maybe selection of more productive individuals with defective traits has resulted in these unwilling characteristics to be selected and be accumulated in population. For the latter hypothesis, selection based on group performance may result in a better animal well-being in a long period of time Rodenburg *et al*. (2008).

The major genes causing variability for similar traits in different species are not the same, therefore, for breeding purposes such as artificial selection, genome of the species should be analyzed (Harlizius, 2004). Regarding these assessments, defective traits in productive individuals could be detected and we would obtain an instruction to see if we should select a trait or avoid it. Also some other aspects regarding domestication of animals as animal behavior and welfare need to be taken into consideration in order to avoid intensive artificial selection effects on animals' well-being.

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REFERENCES

Adams N.R. and Briegel J.R. (2005). Multiple effects of an additional growth hormone gene in adult sheep. *J. Anim. Sci.* **83,** 1868-1874.

Barillet F. (2007). Genetic improvement for dairy production in sheep and goats. *Small Rumin. Res.* **70,** 60-75.

Beilharz R.G., Luxford B.G. and Wilkinson J.L. (1993). Quantitative genetics and evolution: Is our understanding of genetics sufficient to explain evolution? In: Mignon-Grasteau S., Boissy A., Bouix J., Faure J., Fisher A.D., Hinch G.N., Jensen P., Neindre P., Mormede P., Prunet P., Vandeputte M. and Beaumont C. 2005. Genetics of adaptation and domestication in livestock. *Livest. Prod. Sci.* **93,** 3-14.

Belyaev D.K. (1979). Destabilizing selection as a factor in domestication. *J. Hered*. **70,** 301-308.

Belyaev D. and Trut L.N. (1975). Some genetic and endocrine effects of selection for domestication in silver foxes. In: Dobney K. and Larson G. 2006. Genetics and animal domestication: new windows on an elusive process. *J. Zool*. **269,** 261-271.

Bernardi S.F., Brogliatti G. and Oyarzabal M.I. (2009). Ovarian structure in mice lines selected for weight. *Anatomia Histologia Embryologia.* **38,** 200-203.

Bourdon R.M. 1997. Understanding Animal Breeding. 1st Ed., Prentice Hall. Pages 259.

Buch L.H. and Norberg E. (2008). Genetic analysis of protein yield, udder health, and female fertility in first-parity Danish Holstein cows. *Acta Agr. Scandinavica Sect. A-Anim. Sci.* **58,** 5-9.

Burkhart C.A., Cherry J.A., Van Krey H.P. and Siegel P.B. (1983). Genetic selection for growth rate alters hypothalamic satiety mechanisms in chickens. In: Rauw W.M., Kanis E., Noordhuizen-Stassen E.N. and Grommers F. J. (1998). Undesirable side-effects of selection for high production efficiency in farm animals: A review. *Livest. Prod. Sci.* **56,** 15–33.

Castellini C., Dal Bosco A., Mugnai C. and Bernardini, M. (2002). Performance and behaviour of chickens with different growing rate reared according to the organic system. *Ital. J. Anim. Sci.* **1,** 45-54.

Casu S., Marie-Etancelin C., Robert-Grani´e C., Barillet F. and Carta A. (2008). Evolution during the productive life and individual variability of milk emission at machine milking in Sardinian×Lacaune back-cross ewes. *Small Rumin. Res.* **75,** 7-16.

Cheema M.A., Qureshi M.A. and Havenstein G.B. (2003). A comparison of the immune response of a 2001 commercial broiler with a 1957 randombred broiler strain when fed representative 1957 and 2001 broiler diets. *Poult. Sci.* **82,** 1519–1529.

Christensen L.G. (1998). Future market and consumer-orientated breeding goals. *Acta Agr. Scandinavica Sect. A-Anim. Sci.* **28,** 45-53.

Crockford S.J. (2002). Animal domestication and heterochronic speciation: The role of thyroid hormone. In: Dobney K. and Larson G. (2006). Genetics and animal domestication: new windows on an elusive process. *J. Zool.* **269,** 261-271.

Darwin C. (1859). The Origin of Species. Published in 1858 by Metor, New York.

Darwin C. (1868). The Variation of Animals and Plants under Domestication. Vols. 1 and 2. John Murray, London.

Deeb N., Shlosberg A. and Cahaner A. (2002). Genotype-by-environment interaction with broiler genotypes differing in growth rate. 4. association between responses to heat stress and to cold-induced ascites. *Poult. Sci.* **81,** 1454-1462.

Dobney K. and Larson G. (2006). Genetics and animal domestication: New windows on an elusive process. *J. Zool.* **269,** 261-271.

Fan B., Onteru S.K., Nikkilä M.T., Stalder K.J. and Rothschild M.F. (2009). Identification of genetic markers associated with fatness and leg weakness traits in the pig. *Anim. Genet.* **40,** 967-970.

Fulkerson W.J., Davison T.M., Garcia S.C., Hough G., Goddard M.E., Dobos R. and Blockey M. (2008). Holstein-Friesian dairy cows under a predominantly grazing system: Interaction between genotype and environment. *J. Dairy Sci.* **91,** 826-839.

Fulkerson W.J., Wilkins J., Dobos R.C., Hough G.M., Goddard M.E. and Davison T. (2001). Reproductive performance in Holstein-Friesian cows in relation to genetic merit and level of feeding when grazing pasture. *Anim. Sci.* **73,** 397-406.

Gaya L.G., Costa A.M.M.A., Ferraz J.B.S., Rezende F.M., Mattos E.C., Eler J.P., Filho T.M., Mourão G.B. and Figueiredo L.G.G. (2007). Genetic trends of absolute and relative heart weight in a male broiler line. *Genet. Mol. Res.* **6(4),** 1091-1096.

Greger M. (2010). Trait selection and welfare of genetically engineered animals in agriculture. *J. Anim. Sci.* **88,** 811-814.

Hale E.B. (1969). Domestication and the evolution of behavior. In: Price E.O. Behavioral development in animals undergoing domestication. *Appl. Anim. Behav. Sci.* **65,** 245-247.

Harlizius B., van Wijk R. and Merks J.W.M. (2004). Genomics for food safety and sustainable animal production. *J. Biotech.* **113,** 33-42.

Isler B.J., Freking B.A., Thallman R.M., Heaton M.P. and Leymaster K.A. (2006). Evaluation of associations between prion haplotypes and growth, carcass, and meat quality traits in a Dorset × Romanov sheep population. *J. Anim. Sci.* **84,** 783-788.

Jensen P. (2006). Domestication – From behaviour to genes and back again. *Appl. Anim. Behav. Sci.* **97,** 3-15.

Jensen P., Buitenhuis B., Kjaer J., Zanella A., Mormède P. and Pizzari T. (2008). Genetics and genomics of animal behaviour and welfare - challenges and possibilities. *Appl. Anim. Behav. Sci.***113**, 383-403.

Kjaer J.B. and Sørensen P. (1997). Feather pecking behaviour in white leghorns: A genetic study. *Br. Poult. Sci.* **38,** 333-341.

Kolstad K., Thorland I., Refstie T. and Gjerde B. (2006). Body weight, sexual maturity, and spinal deformity in strains and families of Atlantic cod (*Gadus morhua*) at two years of age at different locations along the Norwegian coast. *ICES Mar. Sci.* **63,** 246-252.

Lerner I.M. 1954. Genetic homeostasis. In: Price E.O. (1999). Behavioral development in animals undergoing domestication. *Appl. Anim. Behav. Sci.* **65,** 245-247.

Li Z., Nestor K.E., Saif Y.M., Anderson J.W. and Patterson R. A. (2001). Effect of selection for increased body weight in turkey on lymphoid organ weights, phagocytosis, and antibody responses to fowl cholera and Newcastle disease-inactivated vaccines. *Poult. Sci.* **80,** 689-694.

Lindqvist C., Lind J. and Jensen P. (2009). Effects of domestication on food deprivation-induced behaviour in red junglefowl, Gallus, and White Leghorn layers. *Anim. Behav.* **77,** 893-899.

Lindqvist C. and Jensen P. (2009). Domestication and stress effects on contrafreeloading and spatial learning performance in red jungle fowl (*Gallus gallus*) and White Leghorn layers. *Behav. Process.* **81,** 80-84.

Mambrini M., Médale F., Sanchez M.P., Recalde B., Chevassus B., Labbé L., Quillet E. and Boujard T. (2004). Selection for growth in brown trout increases feed intake capacity without affecting maintenance and growth requirements. *J. Anim. Sci.* **82,** 2865-2875.

Mignon-Grasteau S., Boissy A., Bouix J., Faure J., Fisher A.D., Hinch G.N., Jensen P., Neindre P., Mormede P., Prunet P., Vandeputte M. and Beaumont C. (2005). Genetics of adaptation and domestication in livestock. *Livest. Prod. Sci*. **93,** 3-14.

Miller L.L., Spiegel P.B. and Dunnington E.A. (1992). Inheritance of antibody response to sheep erythrocytes in lines of chickens divergently selected for 56-day body weight and their crosses. *Poult. Sci.* **71,** 47-52.

Morris C.A., Clarke J.N., Watson T.G., Wrigglesworth A.L. and Dobbie J.L. (1996). Faecal egg count and food intake comparisons of Romney single-trait selection and control lines. *New Zeal. J. Agr. Res*. **39,** 371-378.

Muir F.V. and Jaap R.G. (1967). A negative genetic correlation between bursa weight at hatching and post hatching body growth of chickens. *Poult. Sci*. **46,** 1483-1488.

Nestor E., Anderson J.W. and Patterson R.A. (2000). Genetics of growth and reproduction in the turkey. 14. Changes in genetic parameters over thirty generations of selection for increased body weight. *Poult. Sci.* **79,** 445-452.

Nestor K.E., Noble D.O., Zhu J. and Moritsu Y. (1996). Direct and correlated responses to long-term selection for increased body weight and egg production in turkeys. *Poult. Sci.* **75,** 1180-1191.

Newman S. (1994). Quantitative and molecular genetic effects on animal well-being: Adaptive mechanisms. *J. Anim Sci.* **72,** 1641-1653.

Norberg E., Madsen P. and Pedersen J. (2009). A multi-trait genetic analysis of protein yield, udder health, and fertility in first lactation Danish Holstein, Danish Red, and Danish Jersey using an animal model. *Acta Agr. Scandinavica Sect. A-Anim. Sci.* **59,** 197-203.

Olsson I.A.S., Gamborg C. and Sandøe P. (2006). Taking ethics into account in farm animal breeding: What can the breeding companies achieve? *J. Agr. Environ. Ethic*. **19,** 37–46.

Pajor E.A., Busse S., Torrey S., Shea-Moore M. and Stewart T. (2000). The Effect of Selection for Lean Growth on Swine Behavior and Welfare. Purdue University 2000 Swine Day Report. Available at www.ansc.purdue.edu/swine/ Accessed on September 12, 2010.

Pethick D.W., Fergusson D.M., Gardner G.E., Hocquette J.F., Thompson J.M. and Warner R. (2005). Muscle metabolism in relation to genotypic and environmental influences on consumer defined quality of red meat. In: Hocquette J.F. and Gigli S. (2005). Indicators of Milk and Beef Quality. EAAP Publication No. 112, (95-150). Academic Publishers: Wagenigen, Netherlands.

Pew Commission on Industrial Farm Animal Production. (2008). Putting meat on the table: Industrial farm animal production in America. PCT, Washington, DC. http://www.ncifap.org/_images/PCIFAPFin.pdf Accessed Sept .2010.

Pollott G.E. and Greeff J.C. (2004). Genotype × environment interactions and genetic parameters for fecal egg count and production traits of Merino sheep. *J. Anim. Sci.* **82,** 2840-2851.

Price E.O. (1984). Behavioral aspects of animal domestication. *Q. Rev. Biol.* **59(1),** 1-32.

Price E.O. (1999). Behavioral development in animals undergoing domestication. *Appl. Anim. Behav. Sci*. **65,** 245-247.

Price E.O. and King J.A. (1968). Domestication and Adaptation. Pages 34–45 in Hafez E.S.E. (ed.). Adaptation of Domestic Animals. Lea and Febiger, Philadelphia.

Pryce J.E., Coffey M.P. and Simm G. (2001). The relationship between body condition score and reproductive performance. *J. Dairy Sci*. **84,** 1508-1515.

Pryce J.E., Coffey M.P., Brotherstone S.H. and Woolliams J.A. (2002). Genetic relationships between calving interval and body condition score conditional on milk yield. *J. Dairy Sci.* **85,** 1590-1595.

Rauw W.M., Kanis E., Noordhuizen-Stassen E.N. and Grommers F.J. (1998). Undesirable side-effects of selection for high production efficiency in farm animals: A review. *Livest. Prod. Sci*. **56,** 15-33.

Rauw W.M., Knap P.W., Verstegen M.W.A. and Luiting P. (2001). Food resource allocation patterns in lactating females in a long-term selection experiment for litter size in mice. *Genet. Sel. Evol*. **34,** 83-104.

Rodenburg T.B., Komen H., Ellen E.D., Uitdehaag K.A. and van Arendonk J.A.M. (2008). Selection method and early-life history affect behavioral development, feather pecking and cannibalism in laying hens: A review. *Appl. Anim. Behav. Sci.* **110,** 217-228.

Roxström A., Strandberg E., Berglund B., Emanuelson U. and Philipsson J. (2001). Genetic and environmental correlations among female fertility traits and milk production in different parities of Swedish red and white dairy cattle. *Acta Agr. Scandinavica Sect. A-Anim. Sci.* **51,** 7-14.

Sather A.P. (1987). A note on the changes in leg weakness in pigs after being transferred from confinement housing to pasture lots. *Anim. Prod.* **44,** 450-453.

Schütz K.E., Forkman B. and Jensen P. (2001). Domestication effects on foraging strategy, social behaviour and different fear responses: A comparison between the red junglefowl (*Gallus gallus*) and a modern layer strain. *Appl. Anim. Behav. Sci*. **74,** 1-14.

Schütz K.E. and Jensen P. (2001). Effects of resource allocation on behavioural strategies: A comparison of red junglefowl (*Gallus gallus*) and two domesticated breeds of poultry. *Ethol*. **107,** 753-765.

Schütz K.E., Kerje S., Jacobsson L., Forkman B., Carlborg Ö., Andersson L. and Jensen P. (2004). Major growth QTLs in fowl are related to fearful behavior: Possible genetic links between fear responses and production traits in a Red Junglefowl × White Leghorn intercross. *Behav. Genet*. **34 (1),** 121-130.

Setchell B.P. (1992). Domestication and reproduction. *Anim. Reprod. Sci*. **28,** 195-202.

Shea-Moore M.M. (1998). The effect of genotype on behavior in segregated early-weaned pigs tested in an open field. *J. Anim Sci.* **76** (Suppl.1), 100.

Siegel P.B. (1989). The genetic-behavior interface and well-being of poultry. *Br. Poult. Sci*. **30,** 3-13.

Simianer H., Solbu H. and Schaeffer L.R. (1991). Estimated genetic correlations between disease and yield traits in dairy cattle. *J. Dairy Sci*. **74,** 4358-4365.

Siwek M., Cornelissen S.J.B., Buitenhuis A.J., Nieuwland M.G.B., Bovenhuis H., Crooijmans R.P.M.A., Groenen M.A.M., Parmentier H.K. and van der Poel J.J. (2004). Quantitative trait loci for body weight in layers differ from quantitative trait loci specific for antibody responses to sheep red blood cells. *Poult. Sci*. **83,** 853-859.

Snowder G.D., Van Vleck L.D., Cundiff L.V., Bennett G.L., Koohmaraie M. and Dikeman M. E. (2007). Bovine respiratory disease in feedlot cattle: Phenotypic, environmental, and genetic correlations with growth, carcass, and longissimus muscle palatability traits. *J. Anim. Sci.* **85,** 1885-1892.

Star L., Ellen E.D., Uitdehaag K. and Brom F.W.A. (2008). A plea to implement robustness into a breeding goal: Poultry as an example. *J. Agr. Environ. Ethic.* **21,** 109-125.

Van der Waaij E.H. (2004). A resource allocation model describing consequences of artificial selection under metabolic stress. *J. Anim. Sci.* **82,** 973-981.

Van Dorp T.E., Dekkers J.C.M., Martin S.W. and Noordhuizen J.P.T.M. (1998). Genetic parameters of health disorders and relationships with 305-day milk yield and conformation traits of registered Holstein cows. *J. Dairy Sci.* **81,** 2264-2270.

Veerkamp R.F., Beerda B. and van der Lende T. (2003). Effects of genetic selection for milk yield on energy balance, levels of hormones, and metabolites in lactating cattle, and possible links to reduced fertility. *Livest Prod Sci.* **83,** 257-275.

Windig J.J., Beerda B. and Veerkamp R.F. (2008). Relationship between milk progesterone profiles and genetic merit for milk production, milking frequency, and feeding regimen in dairy cattle. *J. Dairy Sci.* **91,** 2874-2884.