



# Genetics and genomics of animal behaviour and welfare—Challenges and possibilities

Per Jensen<sup>a,\*</sup>, Bart Buitenhuis<sup>b</sup>, Joergen Kjaer<sup>c</sup>,  
Adroaldo Zanella<sup>d</sup>, Pierre Mormède<sup>e</sup>, Tommaso Pizzari<sup>f</sup>

<sup>a</sup> IFM Biology, Linköping University, SE-581 83 Linköping, Sweden

<sup>b</sup> Danish Institute for Agricultural Research, Research Center Foulum, Department of Genetics and Biotechnology, Blüchers Allé 20, PO Box 50, 8830 Tjele, Denmark

<sup>c</sup> Federal Agricultural Research Centre, Institute for Animal Welfare and Animal Husbandry, Doernbergstrasse 25-27, 29223 Celle, Germany

<sup>d</sup> Department of Production Animal Clinical Sciences, Norwegian School of Veterinary Sciences, PO Box 1537 Dep., 0033 Oslo, Norway

<sup>e</sup> Neurogenetics and Stress, INRA, University of Bordeaux, France

<sup>f</sup> Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom

Available online 20 February 2008

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## Abstract

Traditionally, the contribution of applied ethology to animal welfare science has concentrated on understanding the reactions of animals to their housing conditions. Domestication has had small effects on fundamental aspects of animal behaviour, and therefore, the needs of present day domesticated animals are closely related to the evolutionary history of the ancestors. However, the last decades have seen an unprecedented intensification of selection for increased production, which has significant side-effects on behaviour and welfare. Understanding the nature of such side-effects have therefore emerged as a central problem to animal welfare science. Modern genetics and genomics offer tools for such research, and this review outlines some of the available methods and how these have been, and could be, used to enrich animal welfare science. An outline is given on traditional genetic selection methods applied on behaviour and welfare related variables. Significant improvements in levels of fearfulness and abnormal behaviour have been achieved by selecting populations against these traits. As a next step, it is necessary to map the loci involved in affecting these traits, and quantitative trait locus (QTL) analysis have been used for this. An overview of QTL-analyses of welfare related traits in different species is given, including how this analysis has provided new insights into the genetic architecture of the stress response. Beyond allelic differences, which can be mapped with QTL-analysis, welfare related biological responses may be mediated by acquired modifications in expression levels of genes and gene complexes. This can be analysed with cDNA

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\* Corresponding author. Tel.: +46 13 281298; fax: +46 13 281399.

E-mail address: [perje@ifm.liu.se](mailto:perje@ifm.liu.se) (P. Jensen).

microarray technology, and a review of relevant work in this respect is given. Many of the changes in genetic control mechanisms observed during selection are results of evolutionary responses, for example related to sexual selection. An overview with a genetic perspective is provided of this often neglected aspect of domestication in relation to animal welfare problems. It is concluded that modern selection of farm animals pose a serious challenge to animal welfare, but also previously unknown possibilities to improve welfare by using high precision breeding techniques.

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*Keywords:* Selection; QTL-analysis; Microarray; Stress; Sexual selection; Behaviour; Welfare

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## 1. Introduction

Ever since the release of the Brambell report (Brambell, 1965), applied ethology and animal welfare science has mainly concentrated on investigating problems occurring in the interaction between animals and their environments. This has led to a significant increase in our understanding of the needs and wants of farm animals, and in many cases has deeply affected the development of farming systems. For example, many countries, including those in the European Union (EU), are phasing out battery cages for laying hens and tethering and individual stalling of sows, largely as a consequence of scientific evidence from applied ethology. Extensive research has been carried out to study the natural behaviour of domestic animals, and in many cases, this has shown that fundamental aspects of behaviour differ only marginally from that of the wild ancestors. For example, pigs released into natural settings will perform the full range of wild boar behaviour around farrowing, including removing themselves from the group and building an elaborate nest (Jensen, 1988). Detailed studies have shown that frequencies as well as sequences of nest building behaviour are virtually indistinguishable between domestic sows and wild boars (Gustafsson et al., 1999).

However, over the last few decades, new challenges to animal welfare have appeared in animal farming. A rough estimate shows that the average production levels of farm animals have more or less doubled since the publication of the Brambell report, and a number of undesired side-effects on animal welfare have been documented (Rauw et al., 1998). Selection during this period has been intensely focused on production, but it is clear that behaviour and welfare have been affected as well. It has been suggested that some of these side-effects can be explained by resource allocation theory, which suggests that animals make adaptive adjustments in the allocation of resources to different life processes when facing changing selection pressures (Beilharz et al., 1993). There is some experimental evidence that this happens and may be important for the sake of understanding animal welfare under intense selection for increased production (Beilharz and Mittpaiboon, 1994; Rauw et al., 2000). This raises the issue of how such trade-offs are controlled genetically, and how this relates to the process of domestication in general.

Domestication is the process whereby populations of animals change genetically in order to adapt to an environment where reproduction is controlled largely by man (Price, 1997). Even though many fundamental behaviours are largely unaffected by the process, there are several important changes induced by domestication (Jensen and Andersson, 2005); ontogenetic processes are changed, social tolerance has increased, sexual and reproductive behaviours have been altered, and adaptive ability has been affected in different ways. All these changes are possible to understand in terms of resource allocation. Of course they lead to the question what

constitutes normal behaviour for modern, highly productive strains of domesticated animals. One example of this is the highly reduced activity levels of modern broilers. Is this an adaptive modification of behaviour in order to allocate energy chiefly to growth, or is it an abnormal side-effect caused by inability to move and behave in accordance with the motivation of the animal (Bizeray et al., 2000)?

Questions such as this can only be solved by a deeper understanding of the genetic processes involved in controlling behaviour and other welfare related traits. This review paper aims at outlining some of the challenges and possibilities offered by genetic selection, and by the modern revolution in genetics and genomics. We are rapidly moving towards not only understanding the genetics of welfare, but also of manipulating it dramatically with molecular technology. The ethical implications of this are beyond the scope of the present paper, but any ethical statement should be based on thorough knowledge of the biology involved.

## 2. Classical selection experiments on behavioural traits

Classical selection experiments for specific behaviours have been done using a variety of animal species. The main objectives of these experiments are typically to gain knowledge of the genetic mechanisms underlying the trait as well as investigating changes in other behavioural traits and physiological variables due to co-selection (correlated responses). The single genetic parameter of greatest interest is the heritability ( $h^2$ ) which gives information on the probability of changing a trait through genetic selection in a specific population (Falconer, 1989). Some examples of classical selection experiments as well as heritabilities of various behavioural traits estimated from these selection experiments are given in Table 1. In the following a few specific examples will be presented on foxes, mink and chickens.

### 2.1. *Tameness in foxes*

Tameness (the non-aggressive behaviour toward man) is a very important trait in relation to the domestication process. One of the most prominent examples of classical artificial selection for a behavioural trait is selection for tameness in silver foxes (*Vulpes vulpes*). Through more than 20 years of selection, lines were developed showing dog-like behaviour towards humans (Belyaev, 1979). The trait of selection, ‘tameness’ (reaction to an experimenter), was evaluated twice, at 2 and 4 months of age. Those foxes showing less avoidance and, at a later stage in the selection program, those that actively sought contact with the experimenter were selected. Foxes of the unselected control line continued to exhibit wild-type behaviour, including strong defensive responses (aggression and fear) toward humans. The selected foxes actively sought human contact and whined and wagged their tails when people approached.

A wide range of correlated responses were associated with the selection on ‘tameness’ such as morphological changes (tail position, ear shape and changes in colour pattern of the fur), changes in sex hormones and hormone cycles (breeding any time of the year contrary to mono-oestrus in the spring) and higher levels of the neurotransmitter serotonin. Belyaev (1979) termed this phenomenon ‘destabilizing selection’ due to the fact that the massive correlated changes observed could not be explained by correlated changes in gene frequencies. He proposed the selection broke up previously integrated ontogenetic systems and thus led to multiple phenotypic effects that seemed genetically unrelated to the selected character.

Table 1

Examples of selection experiments for various behaviours (modified after Faure et al. (2003) and Kjaer and Hocking (2004))

Species	Character	Generation number	Heritability	Reference
Tameness, fear, aggression				
Silverfox	Tameness	20		Belyaev (1979)
Silverfox	Aggression	20		Belyaev (1979)
Bluefox	Tameness	3	0.16–0.20	Kenttämies and Smeds (2002)
Mink	Fear	10	0.20–0.25	Hansen (1996), Berg et al. (2002)
Quail	Tonic immobility	8	0.12–0.28	Mills and Faure (1991)
Domestic fowl	Tonic immobility	1	0.18–0.32	Campo and Carnicer (1993)
Domestic fowl	Open field	3	0.00–0.40	Faure and Folmer (1975)
Cattle	Calf protection, temperament	60 years		Lasater (1972), in Grandin and Dessing (1998)
Sheep	Temperament of females	4		Murphy et al. (1998)
Abnormal behaviour				
Domestic fowl	Feather pecking	3	0.20	Kjaer et al. (2001)
Domestic fowl	Feather pecking	5	0.14–0.18	Su et al. (2005) (continued selection on lines of Kjaer et al. (2001))
Domestic fowl	Feather pecking	1	0.09–1.04	Bessei (1996)
Domestic fowl	Feather pecking and cannibalism	2	0.65	Craig and Muir (1993)
Egg laying behaviour				
Domestic fowl	Floor laying	6		McGibbon (1976)
Domestic fowl	Pre-laying pacing	2		Mills et al. (1985)
Other				
Quail	Dustbathing	7	0.18–0.38	Gerken and Petersen (1985)
Quail	Locomotor activity	5		Bessei (1979)
Domestic fowl	Male mating behaviour	11	0.14–0.36	Siegel (1965)
Domestic fowl	Colour preferences	3	0.03–0.23	Hurnik et al. (1977)

## 2.2. Fear in mink

The potential scope for reducing fearfulness (the propensity to be easily frightened by a wide range of potentially alarming stimuli) through selection is illustrated by a selection experiment using mink (Hansen, 1996). Controlled selection of mink based on their behaviour towards humans has been based on the stick test and Trapezov's hand test in which approach and avoidance are considered to reflect the fear level towards humans. After 10 generations of selection, the percent of animals within a line scored as fearful was around 5% in the "Confident" line, 40% in the control line and about 95% in the "Fearful" line (Malmkvist and Hansen, 2001).

A cross fostering experiment showed that the behaviour of the kits was more dependent on their genetic origin than of the genotype of their foster mother. The mink lines obtained by selecting on these specific tests generalized their fear reactions over several social (contact to other mink, contact to human) and non-social situations (novel object, x-maze test, novel food)

(Malmkvist and Hansen, 2002). Also their reproduction and the hypothalamic-pituitary-adrenal axis response to stress were changed. Confident mink could be mated earlier than the fearful mink (Malmkvist et al., 1997). Fearful mink had a higher cortisol combined with a lower ACTH secretion than confident mink in response to capture and blood sampling (Malmkvist et al., 2003).

### 2.3. Feather pecking in chickens

Feather pecking has been recorded in a range of poultry species, game fowl and ostriches. When a bird pecks itself and the feathers, toes, etc. are damaged, this behaviour is referred to as self-pecking or self-mutilation. Pecking other birds, on the other hand, is referred to as allo-pecking. Aggressive pecking is forceful allo-pecking usually directed to the facial region (Kruijt, 1964). Feathers can be damaged, but it is generally acknowledged that aggressive pecking is not a major cause of feather loss, i.e. feather pecking is not aggression. It has been suggested by several authors that feather pecking is a redirection of behaviour related to foraging (e.g. Hoffmeyer, 1969; Wennrich, 1975; Blokhuis, 1989; Baum, 1992; Huber-Eicher, 1997). More precisely, a part of the exploratory pecking is redirected to the plumage of conspecifics, to a greater or lesser degree depending on the genetic tendency of the chicken, the environmental (including social) circumstances, and the birds' stress physiological state. These factors may influence both development and actual performance of feather pecking.

Genetic aspects of feather pecking and cannibalism were neglected for a long time, but recent experiments have shown that this abnormal behaviour has a low to moderately high heritability (Kjaer and Sørensen, 1997; Kjaer et al., 2001; Rodenburg et al., 2003). Furthermore, Leghorn chicken populations have been developed by genetic selection showing low (LFP) or high (HFP) levels of feather pecking in relation to an unselected control line. The selection criterion was based on the number of bouts of feather pecking (with no distinction between gentle or severe pecks) recorded during a 3 h observation session in which hens were kept in littered floor pens in groups of 20, consisting of 10 birds from the high pecking line and 10 from the low pecking line. Breeding values were calculated using an Animal Model procedure. After three (Kjaer et al., 2001) and four (Su et al., 2005) generations of selection, significant differences in feather pecking behaviour and plumage condition were found between the low and the high pecking line.

Correlated responses to selection on feather pecking have been found in these lines. Birds in the low pecking line had higher egg mass output and better feed efficiency than birds in the high pecking line (Su et al., 2006). This better feed efficiency was mainly due to better feather cover, but might also partly be caused by a higher general activity, as found in a study on locomotor activity in pullets during rearing. Birds of the HFP line moved more around in the pen and visited a pen littered with straw more often than pens with sand or peat (Kjaer and de Jong, 2005). Also various immunological parameters differed between the lines and the level of plasma serotonin was found to be higher in the HFP line (Buitenhuis et al., 2006).

## 3. Finding the genes—principles of QTL mapping

As seen in the previous section, selection for behaviour traits in farm animals can successfully be conducted without knowing the underlying genetic architecture (Kjaer et al., 2001; Mills et al., 1997; Muir, 1996). With the discovery and mapping of polymorphic DNA markers, dense marker maps have been developed for most farm animal species, including cattle, pigs, and chickens (Barendse et al., 1997; Groenen et al., 2000; Rohrer et al., 1996). These dense marker maps are

essential tools to dissect the underlying genetics of behavioural traits in animals by identifying chromosomal regions affecting polygenic traits, so called Quantitative Trait Loci (QTL), and the causative genes at these loci (Andersson, 2001).

Mapping QTL is conceptually simple when a linkage map is available (Weller, 2001). A common strategy is to use two lines, preferably inbred, differing in the trait of interest. A cross is made to generate an F1 population. Animals from the F1 population are used to produce a backcross or an F2 intercross mapping population. All animals from the mapping population are phenotyped, i.e., characterized for their behaviour, and genotyped, i.e., characterized for multiple DNA markers throughout the genome. The idea behind producing an F2 population is that the genotypes are mixed due to recombination, so at every locus the animals will be either homozygous for one of the grandparent alleles, or heterozygous, more or less independently of the genotype at other loci. The animals from the mapping population are divided into genotype classes based on marker genotypes, and it is tested whether there is a significant phenotypic difference between these. If there is a difference then the QTL will be associated with the marker.

The generation of an F2 population has been mainly used in laboratory animals, where inbred lines are available. In farm animals, inbred lines are not frequently available. However, crosses between lines with extreme phenotypes have been used in chickens. For larger animals, such as cattle, generating F2 populations is not practical due to high costs of maintenance and long generation intervals. For outcross populations, the structure of the breeding population can be used to map QTL segregating within the breeding population (Van Arendonk and Bovenhuis, 2003). The main difference between the QTL detected in the F2 population versus the outcross population is that QTL detected in the F2 population explain the genetic variance between two populations, while QTL detected in the outcross explain the genetic variance within the population.

Behaviour traits lend themselves to QTL-mapping in the same way as any other phenotypic trait, provided that there are extreme founder lines available, which is often the case in farm animals. In cattle and pigs not many studies dealing with QTL detection for behavioural traits have been performed, whereas in chickens the number of studies is higher. However, only a few QTLs have been detected in farm animals, for example, for the reaction to humans in ruminants (Schmutz et al., 2001a,b), for the response to a novel environment in pigs (Desautels et al., 2002), for behavioural resource allocation and feather pecking in poultry (Buitenhuis et al., 2003a,b, 2004; Jensen et al., 2005; Schütz et al., 2002), and for novel environment behaviour and tonic immobility in quails (Beaumont et al., 2005). Further investigation should eventually allow the discovery of genes involved in genetic variation of stress-related behavioural traits. In the next sections, we illustrate some of the results of these studies in more depth.

### 3.1. *QTL for temperament and locomotion*

Temperament of cattle is important for the safety of the farmer, and may have important bearing for animal welfare. The temperament of an animal can be defined as “an animal’s behavioural response to handling by humans” (Burrow et al., 1988).

The exact way in which a behaviour is defined and quantified will affect the outcome of a QTL-analysis. For example, in beef cattle, temperament was recorded by holding the individual cow on an electronic platform scale for 1 min, while the number of movements of the animal was measured (Schmutz et al., 2001a,b). In another study on dairy cattle, temperament was defined as “nervous/aggressive or docile behaviour during milking” (Hiendleder et al., 2003). The number

of QTL for temperament as well as the locations of them differed substantially between the studies.

Recently, some breeding companies have started to measure locomotion in dairy cattle. There is a negative genetic correlation between locomotion and many claw disorders (Van der Waaij et al., 2005), so locomotion is a potentially important welfare indicator. So far, no QTL-studies on locomotion in cattle have been published, but an obvious interest for future studies would be to investigate whether QTL for locomotion coincide with QTL for lameness (Buitenhuis et al., unpublished data). Such coincidence would indicate a common genetic mechanism.

### 3.2. *QTL for fearfulness and adaptability*

Open-field reaction is generally believed to be closely related to fearfulness, and a couple of QTL-studies of this behaviour have been carried out on chickens (Buitenhuis et al., 2004; Schütz et al., 2004). Buitenhuis et al. (2004) showed that different QTL were found at different ages, indicating that genetic mechanisms behind fearful behaviour are different for young and adult animals. Beaumont et al. (2005) studied open-field behaviour in Japanese quail, an important parallel model for behaviour in chickens, which might help to verify identified QTL in birds. So far, few QTL have been verified by this method.

Other behaviours related to stress, like tonic immobility, restraint test and the novel object test, were studied by Schütz et al. (2004) and Schütz et al. (2002) have also used QTL-analysis to examine the genetic architecture of contrafree-loading, a measure of adaptability and exploration.

In a study of Désautés et al. (2002), pigs were exposed to a “novel environment” test (essentially similar to an open-field test). During this test, several behaviours indicating fearfulness were recorded, such as locomotion, defecations, vocalisations and exploration. Fearful animals do not move around much, defecate more and show less exploration behaviour than non-fearful animals. There were two QTL detected, one for locomotion and one for exploration. The QTL for locomotion behaviour was located closely to QTL for post-stress ACTH levels as well as variation in ACTH levels, indicating that the open-field test is indeed related to fear behaviour.

### 3.3. *QTL for feather pecking in chickens*

For understanding the genetic mechanism underlying behavioural traits, the chicken is a good model animal. It is cheap to maintain, and has a high reproduction capacity meaning that a high number of offspring per parent can be produced. Also, from a genetic perspective, the chicken is interesting, because it split from the human and mouse in the evolutionary lineage approximately 300 million years ago (Burt et al., 1999). Recently, a number of studies have been published dealing with different aspects of behaviour, genomics and welfare in chickens. A particularly interesting example concerns feather pecking (FP).

As was clear from Section 2 of this paper, FP has an important genetic component, and classical selection can have large effects on the frequency of the behaviour. Therefore, it is of great interest to map the loci for the genes involved in this. Buitenhuis et al. (2003a) therefore performed a QTL-study for FP behaviour in a cross of two commercial White Leghorn lines, differing in the propensity for FP, in young and adult animals. The QTL detected for FP differed between ages. Different QTL detected between young and adult animals were also observed for animals which received feather pecks (Buitenhuis et al., 2003b,c).

Plumage pigmentation of a chicken may predispose it to become a victim. Keeling et al. (2004) showed that a QTL for feather damage coincided with the dominant white locus in the chicken genome. Animals suffered more from pecking when the colour of their plumage was due to expression of the wild recessive allele at *PMEL17*. The effect of the colour gene on feather pecking damage was detected in an intercross between Red Jungle Fowl and White Leghorn. Therefore, this would not hold for White Leghorns like in Buitenhuis et al. (2003b) as these White Leghorns are dominant white on this locus. This illustrates the importance of always judging a particular QTL-study in light of the selection lines used for the analysis.

#### 3.4. General comments on QTL-studies of behaviour

The number of studies dealing with behaviour in farm animals is still limited, but increasing. Comparing the locations of the QTL detected within species, show that there is not much overlap. However, it is difficult to compare the different studies. There are mainly three reasons for this. The first is that, even though the same name is used for a trait, the definition is different. The second reason is that the age of the animals at which the study is performed may differ. Behavioural traits measured in young and adult animals can have different underlying motivations, which means that these are basically different traits. The third reason is that comparing behavioural traits over species may be very difficult, e.g., chickens have a different open-field behaviour than mice (Candland and Nagy, 1969). So far, QTL mapping of behavioural traits in farm animals is still in the phase of detecting interesting regions in the genome. Identifying causal genes will not be an easy task, because QTL for behavioural traits generally have small effects. However, with more genome sequences of farm animals becoming available, identification, verification and validation of genes for behaviour detected across species will be feasible (Fadiel et al., 2005).

### 4. Molecular genetics of stress responses

Stress is central to animal welfare, and is usually defined as the non-specific response of an organism to any demand upon it (Selye, 1973). It covers the behavioural and biological responses to a wide range of stimuli such as social interactions or rough handling, common farming practices such as castration, dehorning or teeth clipping, but also exposure to extreme climatic conditions, or restricted feeding, just to cite a few. Stress-triggering stimuli are not necessarily painful but can also initiate psychological states, altogether known as emotions, such as fear or anxiety that activate physiological responses. In most cases, stress describes a condition that is detrimental to the welfare of the animal and should be avoided. Indeed, much effort has been invested in the adjustment of breeding practices to the animal needs and to avoid unnecessary challenges. However, stress responses are related not only to the nature and the intensity of the triggering stimulus, but also to individual response tendencies or temperament (Cloninger, 1994) shaped by genetic factors, early environment and previous experiences (Dantzer and Mormède, 1983).

The influence of genetic factors on stress responses is well documented (Mormède et al., 2002). Although most evidence for genetic variation in behavioural stress responses comes from laboratory animal studies (Ramos and Mormede, 1998), some information is also available in farm animals (Boissy et al., 2005b; Lankin, 1997; McGlone et al., 1998; Mignon-Grasteau et al., 2005). Most papers describe differences between genotypes (breeds) and a few studies have evaluated genetic parameters from family studies. For instance, Boissy and collaborators found a

high estimate of heritability for vocalisation in reaction to isolation in sheep ( $h^2 = 0.48$ ) (Boissy et al., 2005a). Furthermore, as seen in the previous sections, divergent genetic selection can generate lines with very different behavioural reactivity, such as Japanese quails selected on the basis of their tonic immobility in response to handling and social behaviour (Mills and Faure, 1991), or poultry lines selected in different social settings (Muir and Craig, 1998; Muir and Hester, 1997). As already noted in the previous section, the concept of temperament is closely related to stress response (Forkman et al., 1995) and further studies of the biology of temperament would aid the understanding of genetic mechanisms of individual variation in stress responses.

In most cases, variation in behavioural phenotypes is due to the influence of multiple gene polymorphisms interacting with environmental factors, and specific approaches must be used to explore such complex influences (Mormede, 2005). The QTL approach is therefore a helpful method for the detection of genomic regions influencing phenotypic variation in stress reactions. In the field of stress research, this strategy has been successfully used to identify the molecular mechanism of the porcine stress syndrome that results from mutations in the ryanodine receptor gene responsible for calcium movements across the sarcoplasmic membrane in muscles (Fuji et al., 1991).

The main biological stress responses are related to the hypothalamic-pituitary-adrenocortical (HPA) axis releasing corticosteroid hormones (cortisol, corticosterone, aldosterone) in to blood (Selye, 1973) and the autonomic nervous system, a major actor of homeostasis (Cannon, 1935). Although most research has been done in humans and laboratory animals (Mormède et al., 2002), some information is available in farm animals on the genetic variability of biological stress responses. In pigs for instance, considerable differences between breeds have been described in cortisol levels both in basal conditions and after stress, the highest levels being found in wild boars, followed by fatty breeds like the Meishan and the lowest levels in highly selected lean white breeds like Large White and Landrace (Bergeron et al., 1996; Desautes et al., 1997, 1999; Hay and Mormède, 1998; Mormède et al., 2004; Plastow et al., 2005; Weiler et al., 1998). The contribution of genetic factors to neuroendocrine stress responses has been firmly demonstrated by selection studies. Divergent lines for HPA axis functioning have been obtained by genetic selection in poultry (response to ACTH (Edens and Siegel, 1975) or social stress (Gross and Siegel, 1985)), Japanese quail (response to immobilization (Satterlee and Johnson, 1988)), turkey (cold stress (Brown and Nestor, 1973)), and trout (confinement stress (Pottinger and Carrick, 1999)).

Several molecular mechanisms have been identified to explain this genetic variation of HPA axis activity. The adrenal cortex sensitivity to ACTH is an individual phenotype (Hennessy et al., 1988) shown in pigs to be heritable ( $h^2 = 0.26$  as calculated from data obtained in half-sibs from 3571 from 24 boars; Hennessy, personal communication). Indeed, divergent lines could be selected on this trait in poultry (Edens and Siegel, 1975). In trout, the divergent cortisol response to confinement stress mostly results from the selection of animals with divergent adrenal gland response to ACTH (Pottinger and Carrick, 2001), together with a large difference in the expression level of genes involved in corticosteroid hormone synthesis (Geslin and Auperin, 2004). A QTL-study in a Meishan  $\times$  Large White F2 intercross uncovered the influence on cortisol levels of a locus on chromosome 7 and the comparison of genetic maps in different species showed that the gene encoding corticosteroid-binding globulin (CBG), the specific carrier of cortisol in plasma, had been mapped at this locus, so that CBG was an interesting positional and functional candidate gene (Desautes et al., 2002). Further studies confirmed the contribution of CBG in genetic variation of cortisol levels, carcass composition and meat quality

(Geverink et al., 2006; Ousova et al., 2004). Other mechanisms, as related to hormone bioavailability or corticosteroid receptors efficiency, known to support genetic variation in humans and experimental animals, should also be explored in farm animals (Mormède et al., 2002).

## **5. Stress, welfare and gene expression**

Since the expansion of molecular biology, there has been an emphasis on finding mutations in genes or regulatory regions, which may explain variation in phenotypic traits such as behaviour. As seen in the previous sections of this paper, mapping of genomic areas, identification of candidate genes and characterisation of causative mutations have been important elements of this research process. However, the modern insights into genome science has made it increasingly obvious that much phenotypic variation is not associated with mutations leading to protein alterations. Rather, significant differences between species, populations and individuals can be attributed to alterations in expression levels of clusters of genes (Hofmann, 2003). Such modifications in expression levels can be due to, for example, mutations in regulatory genes high up in the hierarchical control of gene clusters, or to changes in chromatin structure or methylation patterns of DNA associated with the genes themselves (Richards, 2006).

Gene expression patterns can vary due to genetic reasons, and cause heritable population differences, which are thought to be important driving forces in evolution (Hofmann, 2003). It is quite likely that the rapid responses in multiple traits seen during domestication are a result of a change in gene expression (Belyaev, 1979). Furthermore, expression levels are dynamic aspects of the genome, and may change as a result of experience (Richards, 2006) or exposure to stressful situations. For example, the maternal behaviour of rats, the amount of licking and grooming, has been shown to affect the expression levels of a hippocampal glucocorticoid receptor in the offspring (Weaver et al., 2004).

Complex biological processes, represented by central and peripheral pathways affected by stress hormones, are not easy to study using conventional approaches (e.g. bioassays). Novel techniques that allow the measurement of expression of thousands of genes at the same time in different tissues provide unique possibilities to screen for likely pathways affected by glucocorticoid hormones released as a result of the activation of the HPA axis. Functional genomics protocols have been used recently to address questions relevant to animal welfare (Poletto et al., 2006a,b). A major problem in approaching this area has been the immense difficulties associated with analysing expression levels of large sets of genes at the same time and the lack of follow up studies to characterise that the changes in gene expression were in fact associated with differential expression of the protein in question.

Microarray technique allows the comparisons among treatments of thousands of genes (Nobis et al., 2003). Nobis et al. (2003) developed a porcine cDNA library which consists of cDNA clones isolated from the porcine brain. The unique expressed sequence tags (ESTs) were sequenced and their identity resolved by comparison with an existing database. The ESTs were spotted in triplicate in a plate. To measure the differential expression of genes, the total mRNA is extracted from the target organs and reverse transcribed, labelled with a fluorescent dye and then hybridized to a cDNA microarray. The interaction of the samples (two comparisons at the time) labelled cDNA with the sequenced ESTs present in the grid representing thousands of spots containing sequenced genes from the species will give a colour response indicative of the relative expression of all these genes. For example, it can tell if the gene is expressed in treatment A or in treatment B or in both by the amount of target cDNA which hybridizes. Using various statistical

approaches, such as cluster analysis, this method can be used to identify not only single genes of interest, but also clusters of co-regulated genes. Poletto et al. used this method for identifying 103 differentially expressed genes in early weaned and socially isolated piglets, of which several involved regulation of neuronal function, anxiety, synthesis of neuropeptides, development and brain protection in the frontal cortex (Poletto et al., 2006a). Microarray technique is primarily qualitative. It can show if the gene is expressed or not. It is highly recommended that a validation of the microarray results should be carried out. Real-time PCR is a technique that can provide precise quantification of the expression of specific genes, hence validating microarray results. Poletto et al. (2006b) selected six genes encoding proteins with known brain-related activities from the microarray experiments comparing the responses of early-weaned pigs to social isolation. The results indicated that 15 min of social isolation down-regulated the expression of five of the six studied genes representing neuronal function, structure and protection.

Real-time PCR can also provide useful information when a hypothesis driven experiment is carried out. This technique measures abundance of genes by assessing gene expression at different amplification cycles. Starting from two different experimental treatments (or two different populations), a target organ is identified, for example a specific brain region. From this organ, mRNA is extracted and reverse transcribed to cDNA. The relative levels of mRNA from the genes of interest can then be compared to a control gene by means of quantitative PCR, to yield the relative expression levels in the groups under comparison. Poletto et al. (2006a) tested the effects of early-weaning in some stress responsive genes in the hippocampus and frontal cortex of pigs. Poletto et al. (2006a) measured, using real-time PCR, the expression of mineralocorticoid and glucocorticoid receptors, the two most important receptors for stress hormones, and the expression of 11 beta hydroxysteroid dehydrogenase 1 and 2, the most important enzymes that metabolize stress hormones. Early-weaned pigs had consistently suppressed mRNA abundance for the genes tested in the hippocampus. Interestingly the abundance of the genes tested in the frontal cortex was affected by 15 min of social isolation, but not by weaning age. Holistic approaches such as microarray studies followed by real-time PCR offer ways to screen for likely pathways affected by glucocorticoid hormones released as a result of the activation of the HPA axis.

Although still in its infancy, studies of gene expression patterns and epigenetic modifications caused by stress are likely to be important future instruments in understanding the genomics of animal welfare. As more genomes are sequenced, the information contained in a cDNA microarray becomes increasingly large, and this can be utilised to gain new insights into, for example, how animals are affected by stress.

## **6. Genetics of reproductive traits and the welfare of domestic animals**

Reproductive success is a fundamental component of evolutionary fitness, and variation in reproductive performance is under intense Darwinian selection (natural and sexual). In many sexually reproducing dioecious species, diverging fitness interests of males and females foster sexual conflict and the evolution of contrasting male and female reproductive strategies (Parker, 1979, 2006). In these species reproductive success is to an important extent mediated by antagonistic interactions between prospective reproductive partners. Domestication and artificial selection may exacerbate sexual conflict and load the inter-sexual arms-race in favour of one sex with potentially critical repercussions for animal welfare. Nevertheless, reproductive traits and their genetic architecture are seldom explicitly considered in animal welfare. This section of the present review aims to briefly introduce evolutionary conflict between sexes, and to outline how

domestication and artificial selection for production traits may bias sexual conflict creating widespread potential for welfare problems.

### 6.1. *Sexual conflict and anisogamy*

In evolutionary biology, sexual conflict refers to any situation where males and females maximise fitness in different ways and sex-specific phenotypic optima cannot be achieved simultaneously, so that members of one sex can only increase their fitness while (or by) reducing the fitness of members of the opposite sex (Parker, 1979, 2006). Sexual conflict arises whenever the following conditions are met: (a) partners are not genetically identical; (b) reproduction is costly (i.e. investment in a reproductive event reduces investment in other reproductive events and/or somatic or maintenance investment); and (c) alternative reproductive events are available to at least one of the two prospective partners. In sexually reproducing dioecious species conditions (a) and (b) are the norm. In addition, condition (c) is rarely negated.

Most sexually reproducing species are characterised by sex-specific investment in gametogenesis (anisogamy), eggs being typically more costly to produce than sperm (Bateman, 1948; Trivers, 1972). Anisogamy translates into males having a higher potential reproductive rate than females (Bateman, 1948; Trivers, 1972). Therefore, at any given time an anisogamous natural population will have proportionally more males than females that are available for reproduction and its operational sex ratio is thus likely to be male-biased (Clutton-Brock and Parker, 1992). Under these conditions, male reproductive success is highly variable and dependent on the number of females a male inseminates and the number of eggs his sperm fertilise (Pizzari, 2002). Males are therefore under intense sexual selection to compete over the limited number of reproductive opportunities available. Importantly, sexual selection will promote high (relative to female) male re-mating rates and favour males that limit their investment in a reproductive event to pursue additional reproductive opportunities. Natural selection, on the other hand, is expected to stabilise female re-mating rates around a relatively low optimum (Parker, 1979, 2006; Arnqvist and Nilsson, 2000). Sexual conflict is therefore a pervasive evolutionary scenario and is particularly relevant for many domestic vertebrates which display high levels of sexual promiscuity.

At a genetic level, sexual conflict is determined by the fact that any allele that increases the fitness of one sex is unlikely to increase the fitness of the other sex to the same extent, and thus will be under sexually antagonistic selection. There are two distinct genetic mechanisms through which this may happen: intra-locus conflict and inter-locus conflict.

### 6.2. *Intra-locus conflict and genetic imprinting*

Intra-locus conflict occurs when an allele has a positive effect on fitness when it is expressed in one sex and a negative effect when it is expressed in the other (Parker, 2006). This is resolved when the expression of such sexually antagonistic alleles becomes restricted to the sex where such expression is advantageous (i.e. sex-limited expression; Rice, 1984; Parker, 2006). However, sex-limitation may be relatively slow to evolve (Rice and Chippindale, 2001) and recent evidence suggests that sexually antagonistic alleles may be relatively common (Gibson et al., 2002), particularly on sex chromosomes, where non-recombining regions enable recessive antagonistic alleles to be carried by members of the sex where they are harmful without imposing such costs (Rice, 1984).

A particular form of intra-locus conflict occurs through genomic imprinting, where the expression of an allele varies depending on whether the allele is inherited from the father or the

mother. Because an individual is asymmetrically related to maternal and paternal kin, the fitness of these relatives will have different fitness consequences for genes that an individual inherits maternally and paternally (Haig, 1997). Therefore, natural selection will act differently on gene expression depending on whether a gene is paternally or maternally derived (Haig, 1997). For example, in ZW sex determination taxa such as birds, alleles that increase the fitness of sons but harm daughters when they are maternally transmitted, are expected to accumulate on the Z chromosome, whereas alleles that benefit daughters but harm sons are expected to accumulate on the W (Miller et al., 2006).

### 6.3. *Inter-locus conflict*

Sexual conflict can be mediated by the sex-limited expression of different loci carried by members of the opposite sex interacting over reproduction. Because sexes have different optima, male alleles that maximize male reproductive success may do so while imposing fitness costs on females and vice versa. This conflict is expected to trigger evolutionary arms races between loci (Parker, 1979, 2006), and to underlie the coevolution of sexually antagonistic traits (Parker, 2006). Sexually antagonistic coevolution may be triggered by sexual conflict arising during any episode of sexual selection, over different reproductive decisions (Lessells, 1999; Pitnick et al., 2001; Pizzari and Snook, 2003). For example, conflict may arise over the number of gametes apportioned to a partner: a male may increase his reproductive success by inseminating fewer sperm into more females, while reducing the fecundity of individual females (e.g. Warner et al., 1995; Pizzari and Snook, 2003, 2004). Conflict will also arise over re-mating rates, leading to the evolution of male physical and physiological traits that prevent females from re-mating such as mate-guarding and copulatory plugs and seminal fluid peptides inhibiting female re-mating (Chapman et al., 2003; Pizzari and Snook, 2003). Similarly, traits enabling males to impose copulations on females, such as mating clasps, traumatic inseminations and sexual harassment may evolve (Chapman et al., 2003; Pizzari and Snook, 2003). These male traits result in females re-mating suboptimally and in collateral female fitness costs.

### 6.4. *Artificially loaded sexual conflict*

Artificial selection targets reproductive traits directly or imposes evolutionary changes on reproductive traits through correlational selection. This may load both intra- and inter-locus sexual conflict.

First, artificial selection for production traits is often sex-specific. For example, different measures of female reproductive investment (egg/milk production) are artificially selected beyond the naturally selected female optimum. Correlated evolutionary responses to such artificial selection are likely to compromise the welfare of females. However, in addition to creating welfare problems for females, artificial selection on female reproductive investment will load intra-locus conflict towards females, promoting alleles that enable exaggerated female reproductive investment when expressed in females but that are potentially deleterious when expressed in males. Consistent with this idea, male domestic fowl, *Gallus gallus domesticus*, of a line artificially selected for egg production have lower sperm quality than males of the ancestral wild type, the Red Jungle Fowl, *Gallus gallus* ssp. (Pizzari et al., 2004). While many factors can contribute to explain this difference, a plausible scenario is that sperm quality is sexually selected in Red Jungle Fowl where females are promiscuous and ejaculates of different males may compete for fertilisation (Pizzari et al., 2002). However, intensive artificial selection for female fecundity may have

promoted the accumulation of alleles that enable exaggerated reproductive investment when expressed in females but that may impair fertilising efficiency when expressed in males.

Second, by influencing reproductive efficiency, artificial selection may indirectly catalyse inter-locus conflict. For example, intense artificial selection on growth rate and body size in male broiler breeders is associated with male fertility problems (Emmerson, 2000) of a magnitude that may limit the growth of the broiler industry in the near future. Pollock (1999) indicated that a 1% decrease in hatchability, which is equivalent to 1.3% lost in fertility, would cost over \$1.5 million per year to Perdue Farms, which represents about 8% of the chicken meat industry in the U.S. In this case, rather than a reduction in sperm quality, impaired fertility appears to result from behavioural problems associated with exaggerated body mass (McGary et al., 2003; Bilcik and Estévez, 2004; Bilcik et al., 2005). This reduction in reproductive efficiency means that male broiler breeders may have to attempt copulation at a higher rate in order to achieve an optimal re-mating rate. This in turn will generate more intense male sexual harassment of females, and thus exacerbate welfare problems associated with female sexual coercion in this species (Pizzari, 2001). Conversely, selection for increased male fertilising efficiency may promote seminal fluid products that increase fertilising efficiency while harming inseminated females. These effects have been particularly well documented in *Drosophila melanogaster* where some Accessory gland products promote the fertilising efficiency of an insemination but have toxic side-effects on females (Chapman, 2001; Wigby and Chapman, 2005). The functional significance of seminal fluid products in domestic vertebrates remains unclear (e.g. Fujihara, 1992). However, it is plausible that seminal fluid in these species may play a similarly sexually antagonistic role.

Artificial selection has the potential to exacerbate both intra- and inter-locus sexual conflict and load it in favour of one or the other sex, leading to important sex-specific welfare problems. In order to elucidate such problems two steps are advocated: (a) demonstrate the sexually antagonistic nature of traits that show an evolutionary response to artificial selection; and (b) identify the genetic architecture of sexual antagonism. Only with detailed information of sexually antagonistic traits and of their genetic architecture can we manage sexual conflict-related welfare problems and reduce their potential in artificial selection programs.

## 7. Genetics, behaviour and welfare—future perspectives

As already mentioned, the focus of applied ethology has been on the interaction between the behaviour and the environment of the animals (e.g. Jensen, 1993). The intense selection of farm animals for increased production forces us to place more emphasis on the role of the genotype in relation to animal welfare. As seen from the present review, there are many burning issues in relation to this, where we have only begun to understand the underlying biology. Correlated responses to selection can affect behaviour and health of animals in a way which has profound effects on their welfare. For example, that the welfare of broilers may be more dependent on the side-effects of selection, than on the housing conditions and stocking densities under which they are kept (Reiter and Bessei, 1998; Bizeray et al., 2000).

Many of the problems outlined have profound effects on aspects other than animal welfare as well. For example, stress and stress hormones also have a strong influence on many production traits such as growth rate, resistance to disease, carcass composition and product quality. Reproductive problems caused by inadvertent evolutionary side-effects of the genotype selected will have important consequences for breeding efficiency and economics. Hence, there are many other reasons than concern for animal welfare to emphasize the importance of research on genetics and genomics.

It is clear that improved housing and management of the animals are important to improve welfare, but it is also important to increase the ability of animals to adapt to modern management practices. Indeed, domestication has been a long process of genetic selection for a ‘domesticated’ phenotype and is still operating throughout the evolution of breeding practices. The knowledge of the molecular bases for stress-related traits will help improve the adaptation of animals to their constantly changing environment (Mignon-Grasteau et al., 2005). A central challenge for the future will therefore be to find farming practices where the genotype and the environment harmonize.

Even if traditional breeding has reached impressive results with respect to animal production, it is also clear that it carries some detrimental effects on animal welfare (Rauw et al., 1998). It may turn out to be a slow and insecure way to reverse the process, and breed animals with equal weight on production and welfare in breeding indices. Modern molecular techniques offer unprecedented possibilities in this respect. For example, starting from a QTL for a specific trait, it is not even necessary to know which gene is involved in order to use so called marker-assisted selection for a specific trait. By selecting on closely flanking genetic markers, the genotype of an animal can be designed with high precision on a specific locus (Weller, 2001). In chickens, a locus with a strong effect on growth has been located on chromosome 1, and this locus has a wide array of pleiotropic effects on welfare related traits (Jensen and Andersson, 2005). As soon as these effects are sufficiently well characterized, it is possible to use marker-assisted selection to create populations of birds with a specific genotype on this locus, and thereby balance growth against animal welfare.

## 8. Conclusions

Classical genetic selection experiments have shown that a range of behavioural traits can be changed dramatically in a range of animal species. This selection on behaviour often induces changes in the morphology, physiology and immunology simultaneously. Knowledge of the genetic relationship between these parameters will help to apply selection for behavioural traits in production herds. Combining the classical selection techniques with new tools like QTL-analysis and marker-assisted selection, will improve selection efficiency.

The traditional focus of applied ethology on environmental problems related to the natural behaviour of domesticated animals needs to be complemented with an increased research effort on understanding the genetics and genomics of welfare relevant traits, such as behaviour. Modern genomics offers tools for mapping genes related to behaviour and stress, and to examine the regulation of expression of gene complexes in different circumstances. Paired with evolutionary theory, this may provide unprecedented biological insights into why intense selection for production traits, which are of course always related to reproduction, may lead to welfare problems. This knowledge is of course interesting in its own right, but may also provide new practical tools for developing breeding programs with high precision, where animal welfare can be given a much higher weight than today. Inclusion of selection against abnormal and damaging behaviour in animal breeding programmes has a large potential for increasing the welfare of animals used by man.

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